

Clifford Warwick · Phillip C. Arena
Gordon M. Burghardt *Editors*

Health and Welfare of Captive Reptiles

Second Edition



Springer

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Introduction

1

Clifford Warwick, Phillip C. Arena, and Gordon M. Burghardt

Abstract

Like the first edition of *Health and Welfare of Captive Reptiles*, this book ('HWCR2') invited all authors to bring the best science and novel thinking to their contributions, whilst thematically centralising reptile welfare. Arguably, the herpetological world still lags behind much of the stance of the original book, yet this second edition will continue to forge ahead and set the landscape for reptile welfare long into the future. *Health and Welfare of Captive Reptiles, 2nd edition* offers concepts, principles, and applied information that relates to the well-being of reptiles. Therefore, HWCR2 is essentially a manual on health and welfare in a similar vein to volumes addressing the sciences of anatomy, behaviour, or psychology; thus, the book is about the biology of reptile welfare and meeting biological needs. In nature, animals conduct their lives and manage their own well-being. Whatever challenges may be faced in the natural world, animals have evolved to occupy this place. However, once an individual arrives in captivity, by whatever means, its life and well-being become our responsibility. In theory, the knowledge base within HWCR2 ought to inform, inspire, and guide reptile caretakers to apply the latest findings and ideas for enhancing the welfare of the animals whose lives are substantially within their hands.

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Keywords

Captivity · Nature · Welfare

1.1 Authors

The first edition of *Health and Welfare of Captive Reptiles (HWCR)* included authors who were not only biologists, veterinarians, and scientists within the reptile field, but also pioneers in the history of herpetology: a theme that we can again boast for this second edition—*HWCR2*. A tremendously heartening feature of both editions has been the generosity and enthusiasm of so many to bring the best science and novel thinking to their work. All authors were asked to thematically centralise reptile welfare within their contributions, with an obligation to align themselves as constant allies ‘for reptile welfare’—above and beyond any other interest. Accordingly, all chapters follow the principle that wherever doubt or debate may have arisen concerning any welfare issue, reptiles were to receive the benefit of such doubt.

Across both editions, authors were invited to exercise their thinking on relevant issues that may advance reptile welfare. The thoughts and ideas founded in *HWCR* spawned global research and invaluable data, yet almost all of the concepts, principles, and research suggestions from the first edition remain current or still advanced. Whilst some original messages were intentionally speculative, various suggestions have inspired the navigational process of modern academic and applied reptile- (and other animal-) related sciences—including Springer’s own momentous and current *Animal Welfare* series. Unsurprisingly, contributors for the new edition have again been asked to push the frontiers of our understanding towards reptile welfare; and where evidence does not yet underpin these frontiers, it will likely follow. Arguably, the herpetological world still lags behind much of the stance of the original book, yet this second edition will continue to forge ahead and set the landscape for reptile welfare long into the future.

Sadly, not all of our original compatriot authors are with us today—David Chiszar, Louis J. Guillette Jr., Hobart M. Smith, and Robert E. Gatten Jr. have passed away. Also, for others, life has gotten in the way of their availability to participate this time, in this book. However, to all of those, lost or amongst us, who were unable to take part in this new venture, their contributions remain a guiding influence throughout this entire edition as well as for the future of reptile biology and welfare by continuing to bring warmth to the ‘cold-blooded’.

1.2 Peer Review and Quality Control

The quality control and developmental process for *HWCR2* is probably second to none. Contributions for this volume have undergone extensive and robust scientific peer review by the three primary editors, three external examiners, and Springer’s own series editor and expert technical editing team. The fact that one of the world’s

leading and most established scientific publishers, Springer, has overseen *HWCR2*'s production has been greatly welcomed, and will not be lost on the discerning reader.

1.3 Audience

Although this volume is primarily aimed at academic professionals, authors have adopted a user-friendly writing style where feasible to accommodate a broad readership. *Health and Welfare of Captive Reptiles, 2nd edition* offers concepts, principles, and applied information that relates to the well-being of reptiles. As such, it is fundamentally a biology book that can also inform captive reptile husbandry. Therefore, *HWCR2* is essentially a manual on health and welfare in a similar vein to volumes addressing the sciences of anatomy, behaviour, or psychology; thus, the book is about the biology of reptile welfare and meeting biological needs.

Advances in biology and improvements in animal husbandry can offer a better quality of life to individual animals under artificial conditions, but these advances should not be taken to serve as justifications for keeping reptiles in captivity. *Health and Welfare of Captive Reptiles, 2nd edition*, like its predecessor, is designed to improve the lifestyle and well-being of captive reptiles, but takes no position on whether reptiles should be kept in captivity; this is not its purpose. *Health and Welfare of Captive Reptiles (2nd ed.)* sets itself apart from the plethora of variable quality 'how to keep reptiles' type handbooks, many of which emerge from the stable of vested interest writers, who target profit and aspire to aid or proliferate convenience-led rather than evidence-based husbandry.

The complexity and often overlapping foci of the contributions inevitably influence the structuring and ordering of such diverse yet related chapters. For *HWCR2* we have adopted a structure that loosely follows the organisation of *animal* (e.g. nature, physiology, anatomy, stress, normal behaviour, cognition); *environment* (e.g. captivity, abnormal psychological and behavioural states, ontogenetic processes, deprivation and enrichment, noise and light disturbance); *management* (e.g. informed design and practice, spatial and thermal factors, nutrition, naturalistic versus unnaturalistic environments, thresholds for species suitability in captivity, record keeping); and *miscellaneous* (e.g. occupancy and post-occupancy evaluation, euthanasia, human–animal interactions, ethics).

All these, and other subjects, permeate or relate to every section of every chapter to provide an integrated and holistic text. However, whilst the book should be read as an entire resource, readers will find that individual chapters often cross-reference others, mainly to indicate where a particular continuum of information or theme exists and is most relevant.

1.4 Introducing Chapters

In the quarter of a century since *HWCR* was first published, herpetological and allied sciences have made exponential-like progress across many fields relevant to reptile well-being. As postulated in the original edition, with increased investigation and understanding of reptile biology comes greater appreciation of their true needs and the challenges required to meet them—biological revelations continue to outpace our ability to fulfil holistic husbandry. The inherent requirements of animals remain relatively constant, whereas husbandry approaches do not. Although scientific and technical improvements in care edge forward, the science of reptile welfare has long been beyond most ordinary folk who keep these animals captive, and this distance arguably is increasing. Thus, for all but a small number of reptiles in extraordinary and unique captive settings and within the custodianship of exceptional scientists, life in captivity is almost certainly one of deprivation by degrees.

Health and Welfare of Captive Reptiles championed the general priority of reptilian welfare as well as behavioural complexity, dietary subtlety, pain, stress, perception, psychology, cognition, sentience, neuroscience, sociality, and individualism, amongst other (then) ‘esoteric’ areas, at a time when little attention or regard was considered justified. Today, all these subjects are viewed in a new light and their illuminating effects will continue to breach the shadows that have for so long restrained welfare progress and maintained ignorance. Also, as hinted at in the first edition, and firmly emphasised in this revision, whether casually or systematically observing and assessing reptile behavioural, mental, or physical characteristics, it is important to remember that assumptions and tests alike need to focus on investigations that are biologically relevant to the species. In other words, to be meaningful and contextual, how we test animals must suit their evolved biologies. Were humans to be judged by many reptilian mental and physical abilities, we would actually be inferior. On these and related subjects *HWCR2* readers are, in particular, directed to the following chapters: ‘*Physiology and Functional Anatomy*’, ‘*Sensory Systems*’, ‘*Brains, Behaviour, and Cognition: Multiple Misconceptions*’, ‘*Biology of Stress*’, ‘*Normal Behaviour*’, and ‘*Social Behaviour as a Challenge for Welfare*’.

The front cover of the original edition depicted a natural lush swamp habitat in which discretely rested a basking turtle. To some, the relevance of that image to captive husbandry was as obscure as the turtle itself, yet the inference was intentional and the messages of this book again emphasise that what happens in nature should not stay in nature—the natural world must inform the artificial one. What was then an arguably provocative and less supported paradigm has today been almost normalised, although far from universally appreciated. Amongst the myriad of problems implicit to artificial conditions, one may simply be the absence of nature. Providing naturalistic environments to occupants that are imperceptible from the natural world is a major challenge, and rarely, if ever, achieved. On these and related subjects *HWCR2* readers are in particular directed to the following chapters: ‘*Psychological and Behavioural Principles and Problems*’, ‘*Controlled Deprivation and Enrichment*’, ‘*Effects of Ontogeny, Rearing Conditions, and Individual Differences on Behaviour: Welfare, Conservation, and Invasive Species Implications*’, ‘*Effects*

of *Captivity-Imposed Noise and Light Disturbance on Welfare*', and *'Naturalistic Versus Unnaturalistic Environments'*.

Much of both past and current reptile husbandry practices emerged from trial and error, or untried and untested, handed-down information about reptile biology and care. Which techniques worked and those that did not, often evaded objective scientific scrutiny, with commonly catastrophic welfare consequences. This haphazard approach is now known as 'folklore husbandry'. Although the more proactive herpetologist (and their institution) guards and educates against such laxity, the normalisation of many long-standing bad practices remains pervasive in the general hobby and private pet sectors, and also commercial production as with turtles and crocodylians. Concomitant with unreliable husbandry are issues of informed decision-making regarding species suitability for captivity, and whether there are appropriate resources and caretaker expertise to provide comprehensive care. Such questions are unavoidable queries for anyone practising responsible custodianship of another species. On these and related subjects *HWCR2* readers are in particular directed to the following chapters: *'Ethologically Informed Design and DEEP Ethology in Theory and Practice'*, *'Spatial and Thermal Factors'*, *'Nutritional Considerations'*, *'Evidential Thresholds for Species Suitability in Captivity'*, *'Record Keeping as an Aid to Captive Care'*, and *'Arbitrary Husbandry Practices and Misconceptions'*.

Inevitably, in a project of this size, topics arise that may appear singular or slightly disjointed from each other; they may also be inspired creative suggestions that warrant examination in their own right and further complement other sections. Such suggestions, at the very least, emphasise that—in terms of the welfare of captive reptiles—there is still so much to learn. On these and related subjects *HWCR2* readers are in particular directed to the following chapter: *'Miscellaneous Factors'*.

1.5 Conclusion

Building on the success and influence of *HWCR* as a definitive scientific reference volume addressing reptile welfare, the concepts and principles for *HWCR2* are unchanged from its origins, marking the enduring quality of its authors' many messages. Whether one adopts the descriptive term of welfare, well-being, or wellness in their goals for animals, achievement of such a positive state may signal the coming together of most or all of the 'right' things.

In nature, animals conduct their lives and manage their own well-being. Whatever challenges may be faced in the natural world, animals have evolved to occupy this place. However, once an individual arrives in captivity, by whatever means, its life and well-being become our responsibility. In theory, the knowledge base within *HWCR2* ought to inform, inspire, and guide reptile caretakers to apply the latest findings and ideas for enhancing the welfare of the animals whose lives are substantially within their hands.

Who amongst the present alumni of authors will be available to oversee further editions of this book cannot be presumed. However, any future revision that does not hold reptile welfare above the needs or deeds of those who may keep captive these astonishing creatures will not speak in legacy of the *Health and Welfare of Captive Reptiles*.



Harvey B. Lillywhite

**In memoriam: This chapter is dedicated to the career and memory of Robert E. Gatten, who co-authored the equivalent chapter in the first edition of this book. Bob was a special friend and colleague, and an outstanding and dedicated individual. He passed away on 23 February 2018 in Greensboro, North Carolina.*

Abstract

Physiology and morphology are interactive determinants of behaviours that are especially sensitive to environmental influences and are important to the health and welfare of captive reptiles. Although many reptiles appear to be easily managed in captive circumstances, others have special requirements to remain in health and vigour. This chapter focuses on understanding the functional attributes of reptiles as they relate to behaviour and the health of captive individuals. Comparative studies of reptilian physiology and ecology illustrate how guidelines for optimal care will vary not only among higher order taxa but also between closely related species. Ambient temperature, light, and humidity strongly influence the health of reptiles. Important aspects of physiology include ectothermy, generally low energy requirements, diet, periodic inactivity, reproductive mode and cycling, health of skin, adequate hydration, cardiovascular and respiratory health, and infectious disease. Conditions of poor husbandry may include obesity, inappropriate temperature, humidity, and lighting conditions, lack of access to seclusion, and suppression of the immune system that can interact synergistically with other forms of stress related to captivity. Further research is needed to understand stressful states and how they can be ameliorated

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in captive animals. In view of the diversity and complex evolutionary histories of reptiles, variation among species must be appreciated in order for these animals to live, thrive, and reproduce in captive settings.

Keywords

Ectothermy · Energy · Skin · Osmoregulation · Digestion · Respiration · Blood Circulation · Stress

2.1 Introduction

Consideration of physiology and morphology is important to the health and welfare of captive reptiles, particularly in view of their diversity and complex evolutionary histories. Evolutionary history endows reptiles with characteristics that can be very different from those of domesticated or laboratory mammals. Although many reptiles seem to be successfully managed in captive circumstances, others will have special requirements and can diminish in health or vigour even whilst appropriate care appears to be provided. Such problems of health and well-being are often related to some aspect of physiology that is either inadvertently neglected, or more usually, not well understood.

Structure-function relationships are essential to understanding the normal behaviours that are characteristic of a species. Physiology is an important underpinning of behaviour, and the behaviours of reptiles are especially sensitive to environmental influences on physiology. Current technologies enable investigators to map patterns of nerve activity onto behaviour and reveal which neurons constitute circuits for specific behaviours (O’Leary and Marder 2014). These same neurons can be genetically tagged. Hence, the interrelationships of structure, function, and behaviour can be understood at very sophisticated levels, and such insights enable understanding of both differences and similarities between reptiles and, say, mammals. However, in the context of this chapter, what is more important than the sophistication of current ethological studies is the understanding of functional attributes of reptiles as they relate to the normal behaviours and health of captive individuals.

2.2 Body Temperature, Energetics, and Ectothermy

Non-avian reptiles are characteristically regarded as ectothermic because they are highly dependent on external sources of heat to determine body temperature, in contrast to endothermic birds and mammals that regulate body temperature largely by means of internal metabolic heat production. There is ongoing debate regarding whether extinct reptiles, and especially dinosaurs, were endothermic (Dunham et al. 1989; Padian et al. 2001; Seymour 2013; Grady et al. 2014). Some of the stronger evidence for endothermy of dinosaurs comes from data for rapid growth rates of

bone (Erickson et al. 2001; Padian et al. 2001; Lee and Werning 2008). However, when the effects of size and temperature are considered, the metabolic rates of dinosaurs were shown to be intermediate to those of endotherms and ectotherms, suggesting that the controversial dichotomy of endothermic versus ectothermic is overly simplistic (Grady et al. 2014). Putting the controversy aside, smaller reptiles are generally ectothermic and are not capable of sustaining a body temperature above ambient by means of endogenous heat production. However, there are a few notable exceptions, including swimming sea turtles, incubating pythons, digesting rattlesnakes, yolk metabolism of hatchling snakes, and seasonal reproductive endothermy of tegu lizards (Tu et al. 2002; Lillywhite 2014; Pough et al. 2016; Tattersall et al. 2016). These examples are of much scientific interest, and they demonstrate the capacity for limited, facultative endothermy and physiological control of muscular heat production (in several species of pythons during incubation). However, in general, the majority of captive reptiles depend on external sources of heat to determine body temperature, and transient variations of metabolic heat production (independent of external environment) are usually of little significance in captive settings.

The term ‘cold-blooded’ is not appropriate for most reptiles, inasmuch as body temperatures can be considerably higher than surrounding ambient air or other features of the environment. Many species behaviourally regulate their body temperature during deliberate basking behaviour, characteristically elevating the core temperature significantly and near the upper part of the range of tolerable temperatures. The desert iguana (*Dipsosaurus dorsalis*), for example, prefers body temperatures around 38–41 °C, which exceeds the core temperature of many so-called ‘warm-bodied’ mammals (see Pough and Gans 1982 for terminology).

The body temperature of ectothermic reptiles is dependent on the net balance of heat exchanges between the animal and its environment, and this condition can be defined by an equation for energy balance that, in simplest form, states that gains of heat energy equal the losses of heat energy. A more complex form of this statement, expressed as an equation, includes a term for each of the major routes of heat gains and losses for an animal (Fig. 2.1). Such biophysical modelling of reptiles is beyond the scope of this chapter, but the reader should appreciate that considerations of the complexity of heat exchanges have improved our understanding of how reptiles regulate their body temperature, and, coupled with information about the environment, has been used to interpret or predict where various reptiles can live and what behavioural options are required for survival in extreme or changing environments. A sampling of examples can be found in Porter et al. (1973), Tracy (1982), O’Connor and Spotila (1992), Kearney and Porter (2009), and Fei et al. (2012). The design of enclosures for captive reptiles makes use of the same principles with respect to placement of heat lamps or other devices that modify the temperatures that are available to a captive animal (see Arena and Warwick 2023).

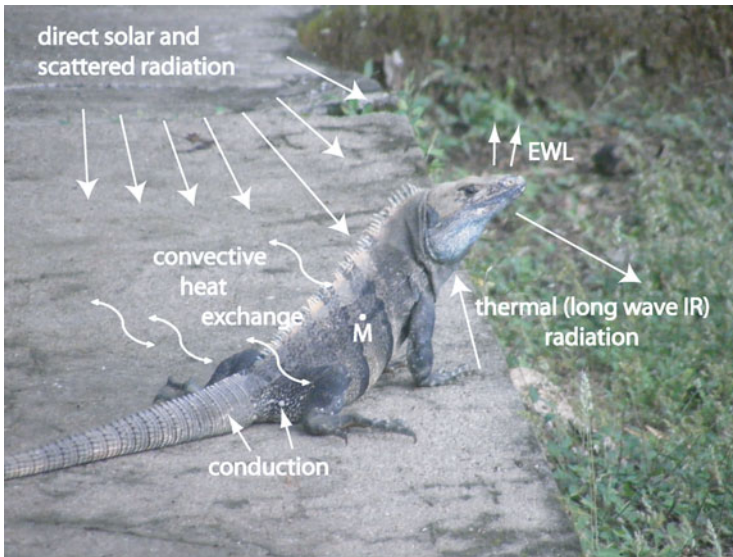


Fig. 2.1 Pathways of heat exchange featuring an iguana on a roadside in Guanacaste, Costa Rica. The hypothetical body temperature of this lizard is determined principally by direct solar radiation that is absorbed by the dorsal skin surfaces and conduction of heat from the heated surface of the road that is assumed to be warmer than the body of the animal. Convective heat transfer to or from the lizard will depend on the relative temperatures of the body and the surrounding air. Metabolic heat production (\dot{M}) and thermal radiation contribute relatively modest amounts of heat to determine the body temperature. Thermal radiation is in bidirectional flux with respect to the lizard which is assumed to be cooler than the road surface but warmer than the grass at the edge of the road. Evaporation of water (EWL) from the respiratory passages removes heat from the nasapulmonary surfaces. Photograph by the author

2.2.1 Temperature and Energy Expenditure

The significance of ectothermy in context of coupled biological advantages has been discussed by Pough (1980). Two important consequences of ectothermy are very relevant to the husbandry of reptiles. First, the rate of energy expenditure derived from food or fat stores is comparatively low because metabolic heat is not required to maintain body temperature. Therefore, to maintain a steady state with respect to energy balance, relatively few calories from food are required as input to match the low rate of energy use. The requirement for food is further lowered by behaviours that might include relatively long periods of inactivity and nocturnal seclusion. Thus, night-time cooling and long periods of inactivity contribute to a low rate of energy expenditure of many reptiles, roughly 2–5% of that of a bird or rodent of equivalent size (Nagy 1983). Energy requirements are minimal for fasting and inactive reptiles at low body temperature, and they increase to substantially higher levels in animals that are active at elevated body temperature. As an example, a red-eared turtle (*Trachemys scripta*) has a rate of aerobic metabolism during vigorous movement at 40 °C that is 270 times as great as during rest at 10 °C (Gatten 1974). The coupling

of food requirements to both temperature and activity varies with species and the circumstances of captivity. One should be vigilant of animals that might experience weight loss due to excessive energy expenditure related to ‘escape’ or exploratory activity whilst in new or inadequate enclosures, conspecific aggression or related stress, and disease or parasitism (see Warwick 2023). The reproductive status of females should also be taken into account and monitored carefully.

Much research has been conducted in relation to quantifying the metabolic energy expenditure of both ectothermic reptiles and endothermic avian reptiles and mammals (McNab 2002). Perhaps the broadest generalisation to emerge is that body size and temperature account for most of the known variation in the rates of energy expenditure of organisms. Rates of energy expenditure are typically measured in the laboratory whilst animals are at rest, and these rates generally underestimate the rates of metabolic energy expenditure when animals are free-ranging in the field. Thus, numerous data are now available for field metabolic rates measured in free-ranging animals using dual-isotope techniques. This is done by administering a dose of doubly labelled water (deuterium and oxygen-18), then measuring the rates of elimination of the heavy isotopes in the animal over time. Conventionally, this involves regular sampling of heavy isotope concentrations in body water by sampling blood, urine, or saliva (see Speakman 1997). Studies of field metabolic rates have shown that in some cases, the energy requirements of animals in nature (e.g. moving, digesting) are roughly threefold greater than those measured under standard conditions in the laboratory, and that rates of energy expenditure can be roughly 25- to 40-fold greater in mammals and birds than in a lizard (Bennett and Nagy 1977). These differences reflect the greater activity of the endothermic mammals and birds and the lower nocturnal body temperatures of the lizard. More generally, variation in field metabolic rates of 229 species of terrestrial vertebrates studied by Nagy (2005) is largely attributable to body size, and much of the remaining variation is attributable to differences in physiology related to temperature with rates of energy expenditure in endothermic mammals and birds being about 12 and 20 times greater, respectively, than that of ectothermic reptiles of similar size (Fig. 2.2).

Growth and reproduction of course also influence the energetic state of reptiles. Both of these factors may also be confounded by changes in body temperature in various states and various species (McNab 2002). Reproductive costs are different between oviparous and viviparous species. As an example, in the bimodal lizard (*Zootoca vivipara*), oxygen consumption of females increases progressively during the course of reproduction, peaking just prior to giving birth when it was 46% (oviparous form) and 82% (viviparous form) higher than it was at the pre-reproductive stage (Foucart et al. 2014). The total increase in post-ovulation oxygen consumption was threefold higher in the viviparous than oviparous females, whereas the pre-reproductive oxygen consumption of both reproductive modes was similar. Substantial energy costs are likely incurred by prolonged embryonic retention in viviparous species. However, reproduction in gravid females may incur an energetic cost that is greater than what is required to meet the energetic demands of developing embryos (Beuchat and Vleck 1990). When the rate of metabolism in

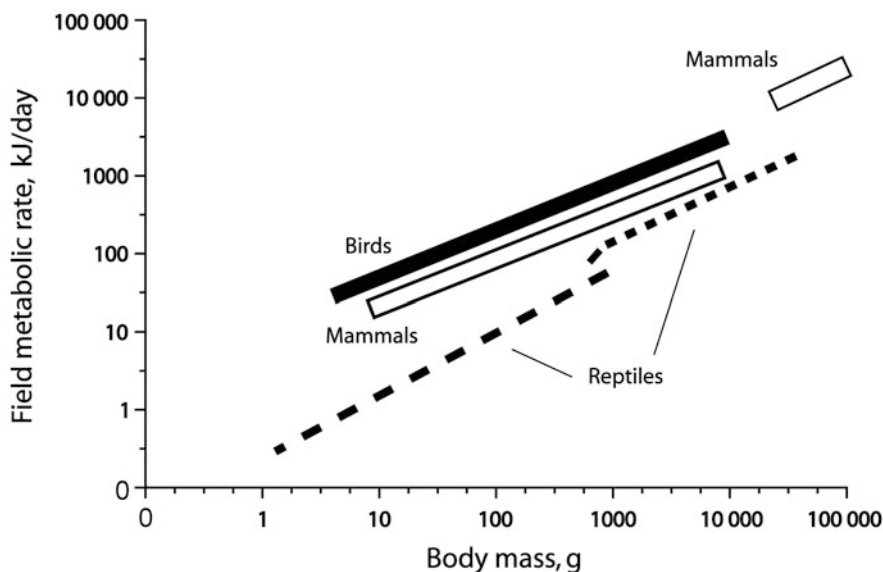


Fig. 2.2 Field metabolic rates shown as a function of body mass in 229 species of non-avian reptiles, birds, and mammals. The bars represent the central densities of collective data points for the various taxa, estimated by eye. The relationships are adopted from data in Nagy (2005)

female lizards (*Sceloporus undulatus*) was adjusted for that of embryos, the energy expenditure of females when gravid was elevated by 122% compared with that when non-gravid (Angilletta and Sears 2000). Energy expenditure of reptiles also can be correlated with growth rates, which generally are 10- to 30-times higher in mammals and birds (McNab 2002). Growth rates may vary seasonally and are increased with the selection of higher body temperatures, which can be dictated by the amount of food energy available. Maximal growth rates of ectotherms may be associated with preferred body temperatures that are maintained in the laboratory or the field (Lillywhite et al. 1973).

With respect to husbandry, persons unfamiliar with reptiles may not fully appreciate the comparatively low rates of feeding (either frequency or quantity) required to sustain individuals in a healthy state. Daily or frequent feeding is often not necessary, and voluntary periods of fasting are not harmful, especially for intermittent feeders such as snakes. In fact, many reptiles such as snakes and crocodylians that are kept for public display are abnormally obese compared with conspecific individuals that are living in nature. Our current understanding of the health risks of obesity in reptiles is minimal, but optimal care most likely involves balancing energy availability and energy expenditure. Allowing animals to fatten excessively represents poor husbandry. The low requirement of energy by reptiles is often misunderstood or not appreciated. The amount of food that is fed or offered to captive reptiles should be based on direct observations of the condition of animals and at least a basic understanding of seasonal behaviour and dietary requirement of

each species rather than a uniform protocol that is intended for application to all species. For further review of the energetics and feeding of ectotherms, see McNab (2002), McCue (2012), and Andrade et al. (2016). There is also veterinary literature on topics potentially related to obesity; examples include hepatic lipidosis (Divers and Cooper 2000; Gumpenberg et al. 2011), cardiovascular disease (Schmidt and Reavill 2010; Stephens and Rosenwax 2018), and intestinal obstruction (Corbit et al. 2014).

2.2.2 Regulation of Body Temperature

The second important consequence of ectothermy is the variation of body temperature that is possible (or obligatory) in relation to the physical surroundings of an animal. However, reptiles are not strictly poikilothermic, and most are capable of impressively precise thermoregulation by behaviour (DeWitt 1967; Huey 1982; Hertz 1992; Goller et al. 2014). Nonetheless, a prolonged constancy of temperature for periods of weeks or months is not a physiological requirement in most cases and, in fact, can be deleterious to the health of many species. Variability of body temperature has importance with respect to species variation (phylogeny), seasonal acclimatisation, feeding and nutrition, activity, reproduction and physiological state, including immunity and disease (Goessling et al. 2017).

‘Regulation’ of body temperature implies that the activity of an animal maintains a particular level or narrow range of temperature relative to the variation of temperature in the surrounding environment. Such a feature of homeostasis requires an active neuronal system in which sensory input from central and peripheral thermoreceptors is compared with single or dual ‘set points’ (Heath 1970; Firth and Turner 1982). Deviations of body temperature from such set points are ‘corrected’ (controlled) principally by behaviour in most species of reptiles. In context of the controlling system, ‘body temperature’ might be represented by the brain, core, or peripheral tissue temperatures, or some combination of these. However, such considerations are beyond our focus here. For many purposes, ‘body temperature’ can be considered as the temperature of the central ‘core’ of body tissue, including the central nervous system (brain and spinal cord). Although heterogeneity and gradients of temperature may exist between different body parts, it is the ‘core’ temperature that is principally defended against undue variation. Regional differences of temperature are greater in larger animals and may be attributed to physiology, physical differences between different parts of the body, or behavioural mechanisms (Peterson et al. 1993). For purposes of husbandry, measurement of body temperature at a single location (for example, cloaca or mouth; trunk or head if utilising an infrared device) usually suffices for evaluation of thermal behaviour and requirements.

Thermoregulatory behaviours commonly employed by reptiles include shuttling movements between a heat source (such as sunlight or warm substrate) and a heat sink (such as shade, water, or burrow), as well as precise adjustments of body volume, shape, orientation, and posture. Postural adjustments can be subtle and

are capable of providing remarkably precise control over body temperature (DeWitt 1967). All thermoregulatory behaviours require some heterogeneity of environment in terms of the physical factors affecting heat exchange (Tracy 1982). Indeed, both mean environmental temperatures and spatial heterogeneity potentially influence thermoregulation, movement, and energetics of reptiles (Sears and Angilletta 2015).

Physiological responses that produce some control over body temperature include metabolic heat production in muscle tissues of a few species, colour change in squamates (especially lizards), circulatory adjustments, and ventilatory changes to increase evaporative water loss from mucous membranes (Bartholomew 1982). Some reptiles may respond to higher temperatures by gaping or panting. Such responses are associated with heat stress, and captive animals should not be kept in conditions where they are exposed to high temperatures without the possibility of behavioural avoidance. On the other hand, at lower temperatures below the regulated range, reptiles become inactive or torpid and digestion ceases (Stevenson et al. 1985; Ultsch 1989). If animals are provided with a meal at lower temperatures and subsequently denied access to higher temperatures requisite for digestion, the ingested, potentially incompletely digested food can putrefy and kill the animal, although characteristically it is regurgitated before this can happen.

Conscientious care of reptiles requires knowledge of a species' thermal requirements, including mean selected (= 'preferred') or activity temperatures (Pough and Gans 1982), thermoregulatory behaviours, and characteristics of the physical environment normally utilised by a species. Thus, many temperate diurnal species may need a radiant heat source, whereas nocturnally-active species may avoid a photothermal resource and prefer to exploit a thermally variable substrate or hiding area. However, in most cases, a daily thermal cycle or behavioural access to thermal variation is desirable. The availability of infrared heat lamps and heating tapes now makes it feasible to arrange basic and inexpensive thermal gradients for reptiles held in enclosures. An alternative to thermal gradients is a thermal mosaic in which shelter devices or other elements of the enclosure provide an array of discrete temperatures (Gibson et al. 1989). In any case, heat availability can be either coupled to, or independent from, light cycles.

2.2.3 Variation of Body Temperature

Many reptiles experience variation of body temperature during a season and even during a single day. Tropical or aquatic species may experience comparatively little temperature variation and can be sensitive to temperature changes readily tolerated by temperate, terrestrial, and amphibious species (Inger 1959; Ruibal 1961; Hertz 1992). Indeed, non-basking species constitute a major component of the diversity of lizards in the neotropics (Huey et al. 2009). The marine file snake (*Acrochordus granulatus*), for example, thrives at water temperatures near 30 °C, but does not tolerate prolonged exposure to temperatures below about 25 °C (Lillywhite 1996). Tuataras (*Sphenodon punctatus*) are active at body temperatures well below those of most other reptiles and have a temperature for peak aerobic activity much lower than

that of turtles, lizards, and snakes (see Avery 1982, for review). On the other hand, some terrestrial species inhabiting the tropics actually experience and may require greater microclimatic variation of temperature than might be presumed solely from macrogeographic considerations (Hertz 1992).

Many factors determine or modify selected body temperatures; the need for a particular temperature can change with time and is dependent on the physiological state of an animal. Important parameters affecting thermoregulation include feeding or digestive state, lean mass or body condition, reproductive status, acclimation, disease, parasitism, trauma, dehydration, hypoxia, acid-base status, ecdysis, and seasonal rhythms. The magnitude of change in thermal behaviour as a result of such factors can be substantial. Snakes, for example, increase body temperature voluntarily from a few to more than 8 °C following feeding (Lutterschmidt and Reinert 1990). In some cases, the selected body temperature may not change, but factors such as feeding or reproductive state can influence the amount of time an animal spends at the higher temperature. Body temperature can also modify the pattern of postprandial increase in metabolic rate (Crocker-Buta and Secor 2014), and the converse is probably true. Such patterns of behaviour should be part of considerations in the development of schemes for improving the care of reptiles. Further, because of the numerous phylogenetic as well as physiological parameters producing variation of body temperature, and the paucity of relevant information for many species, thermal regimens represent one area where oversight or management authorities should not attempt to formulate rigidly specific requirements intended for broad or universal application.

Data from both laboratory-housed and free-ranging reptiles, as well as theoretical models, suggest that shifts in thermal preferences have physiological and ecological importance (reviews in Huey 1982; Lillywhite 1987a, 2013; Peterson et al. 1993; Angilletta 2009). However, further investigations are required to establish the nature and magnitude of harmful consequences should captive reptiles be denied access to appropriate thermal variation. Clearly, the inability to cool below activity temperatures for prolonged periods can affect appetite and reproduction as well as produce deleterious physiological changes (Licht 1965). Inappropriate thermal exposure can suppress the immune systems of reptiles and can operate synergistically with other forms of stress that are imposed by captivity (Regal 1980; Lance 1992; DeNardo 2006; Zimmerman et al. 2010; Zimmerman 2016).

Bacterial infections can induce reptiles to select a body temperature that is several degrees above normal levels, termed 'behavioural fever' (Kluger et al. 1975). This phenomenon has been reported in a wide range of ectothermic vertebrates, including many reptiles (Hutchison and Dupre 1992; Rakus et al. 2017). Studies of lizards have shown that the elevated body temperature, acting in concert with reduced levels of blood iron, enhances survival of animals infected with potentially lethal pathogens (Kluger 1979) (Fig. 2.3). Thus, in circumstances where reptiles are provided with thermoregulatory options, prolonged basking behaviour and the associated elevated body temperature presumably have adaptive value and, among other things, may be an indicator of infection.

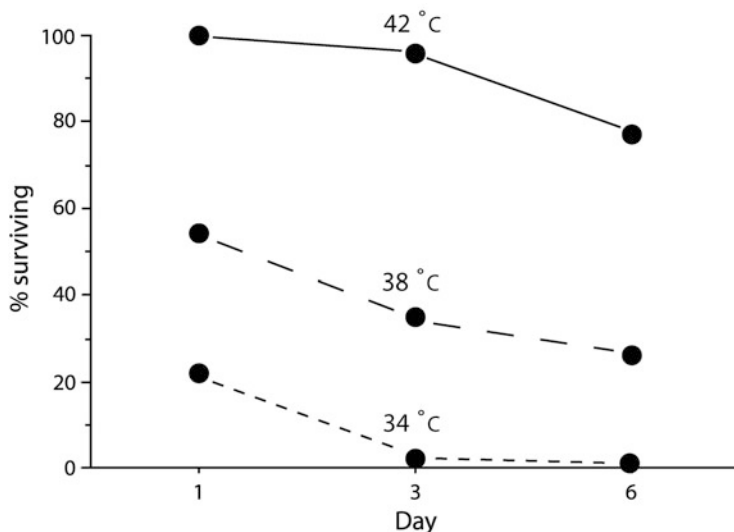


Fig. 2.3 Percentage survival of desert iguanas, *Dipsosaurus dorsalis*, injected with bacteria, *Aeromonas hydrophila*, and maintained at temperatures of 34 to 42 °C. The number of lizards in each group is 12 at 34 °C, 36 at 38 °C, and 24 at 42 °C. Adopted from data published in Kluger et al. (1975)

2.2.4 Functional Significance of Body Temperature Variation

Variation of body temperature has important functional consequences. Changes of body temperature affect biological processes and thus are important to growth, reproduction, and general health.

The thermal dependencies of biological processes are well known and have been quantified in a number of reptilian species (Huey 1982; Hochachka and Somero 2002; Angilletta 2009). In the context of husbandry, it is important to consider whole-animal functions rather than those at the cellular or molecular level. Typically, processes such as digestive rate, growth, speed of locomotion, capture of prey, and frequency of heart beat exhibit a linear or exponential increase over a broad range of temperatures, peak at one temperature or a narrow range of temperatures (plateau), and then decline, often precipitously, at higher temperatures (Fig. 2.4). Such thermal dependency curves are subject to changes in shape and position owing to thermal acclimation or acclimatisation. Therefore, the conditions in which reptiles are maintained in captivity significantly affect their metabolic functions and behavioural performance. Learning abilities of lizards are also affected significantly by temperature (Brattstrom 1978), and gestation time as well as the condition of developing or newborn offspring are influenced by gestation temperature and its variation (Peterson et al. 1993).

Temperature is very important in context of its significance to reproduction (Krohmer and Lutterschmidt 2011). Consequently, persons who keep various

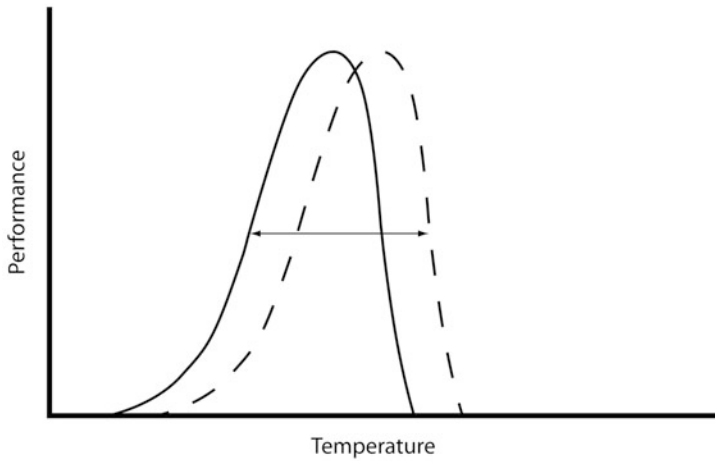


Fig. 2.4 Hypothetical ‘performance curve’ depicting how a rate variable (such as running speed, digestion) changes with temperature. The shift in the curve illustrates hypothetical changes that might be attributable to acclimation. The shift in performance could occur in either direction depending on the acclimation temperature; the horizontal dashed line represents the total change or range of possible performance breadth attributable to ‘phenotypic plasticity.’ Drawing by Rachel Keeffe

reptiles with intentions of breeding them need to be aware of thermal requirements that are compatible with reproductive cycles, including production of gametes, courtship and mating, birth or ovulation, and post-reproductive maintenance. Regimens of temperature requirements before and during reproduction can vary among species, and people who breed reptiles learn what regimens are best for a given species based on successful breeding in captivity. Such details and considerations of variation by taxa are beyond the scope of this chapter, but some publications are available to persons seeking recommendations for given species (e.g. Whittier et al. 1987; Schwarzkopf and Shine 1991; Lance 2003; Barker and Barker 2006; Krohmer and Lutterschmidt 2011; Shine 2012). There is an abundance of manuals and books that cover the breeding of the most popular pet reptiles. One of the better series is the *Proceedings of the International Herpetological Symposium*, which started in 1976 and includes many articles on captive breeding and husbandry of many reptiles (see: <https://www.internationalherpetologicalsymposium.com/proceedings>). It has proven to be relatively easy to breed many species under conditions that are not natural for the species (E.R. Jacobson, pers. com.). Those kept outdoors in areas where they are found probably do the best. Nutrition has improved dramatically, and better artificial lights for those requiring UVB have contributed to this success (see Maslanka et al. 2023).

2.3 Light and Photoreception

Both qualitative and quantitative characteristics of light have important consequences for the physiology and health of captive reptiles (Baines et al. 2016). The eyes are the principal receptors for light, whereas the pineal complex and possibly skin have secondary importance (Zimmerman and Heatwole 1990; Krohmer and Lutterschmidt 2011; Crowe-Riddell et al. 2019). The pineal organ is a neuroendocrine transducer of changes in photoperiod, and it has a functional role in many aspects of reptilian biology (Tosini 1997). Circadian oscillators may also be part of the pineal complex and are thought to be involved in the circadian organisation related to reproduction and other aspects of biology. Many functions attributable to the pineal complex are mediated by the hormone melatonin, and exogenous administration of melatonin may affect a reptile's physiology and behaviour (Tosini 1997; Krohmer and Lutterschmidt 2011).

Light reception interacts with physiology largely through centres of integration within the central nervous system (e.g. Butler 1978; Goris 2011). The periodicity of light reception is an important variable to control for captive reptiles, especially where breeding programmes are involved. Photoperiod can be a critical factor influencing reproductive cycles, although temperature is generally more important (Licht 1972; Jones 1978; Krohmer and Lutterschmidt 2011). The influence of photoperiod and its interaction with temperature or other seasonal phenomena on reproduction is known for relatively few reptilian species. Annual cycles of day length may affect appetite and metabolism, in addition to reproductive cycles.

The effects of variation in the intensity or spectral composition of light are poorly understood. Some reptiles require ultraviolet light for mineral metabolism and normal behaviour (Moehn 1974; Regal 1980; Townsend and Cole 1985; Adkins et al. 2003). Like birds and mammals, some species of reptile require UV light for cutaneous synthesis of previtamin D₃ and the maintenance of levels of the active vitamin in the blood (Pough 1991; Holick et al. 1995). Indeed, there is evidence that some lizards might adjust basking and UV exposure in relation to requirements for vitamin D₃ (Ferguson et al. 2003). On the other hand, some reptiles have been raised or maintained successfully, sometimes for multiple generations, without UV light, but with dietary supplementation of vitamin D₃ (Gehrmann et al. 1991; Pough 1991). Some reptiles may have multiple types of previtamin D₃ in their skin (Holick 1989). Neither the biochemistry of vitamin D synthesis nor the spectral qualities of UV light involved in the process are well studied in reptiles.

There is relatively little information concerning the range of irradiance that is appropriate for a given species of reptile. Ferguson et al. (2010) quantified the UV exposure of 15 species of reptiles in the field and suggested that knowledge of basking behaviour and daytime exposure to light can provide a reasonable estimate of likely UV exposure experienced or required for a species. Based on this information, species can be grouped into four zones (termed 'Ferguson zones') according to thermoregulatory behaviour and preferences for microhabitats, and each such zone can be used potentially for guidelines for UVB based on the quantitative measurements reported from the field work. The Ferguson zones extend from

crepuscular or shade-dwelling to basking in the midday sun. Further discussion of such irradiance criteria can be found in Ferguson et al. (2010, 2014), Carmel and Johnson (2014), and Baines et al. (2016).

Information about the spectral properties of commercially available light bulbs has been discussed by Gehrmann (1987), Pough (1991), Baines et al. (2016) and others. The reader is referred to these sources for suggestions regarding the use of specific bulbs for captive animals. Species of reptiles differ substantially in their requirement for, and sensitivity to, UV exposure, so a conservative approach to the use of bulbs with intense UV emission is advised. Open-habitat species have protective melanin deposits in their skin and peritoneum which limit UV light penetration, whereas species from forests may be more sensitive to UV exposure (Porter 1967). Middle wavelength UV light (bulbs designated UVB) can be injurious to the eyes of animals and their caretakers, so broad-spectrum bulbs may be advisable for the initial husbandry of species with unknown UV requirements. Care should always be taken regarding not only the duration of exposure but also the placement of lamps and irradiance intensity at varying distances from the lamps. To ensure adequate UV irradiance, a regular schedule for changing bulbs is necessary (Townsend and Cole 1985; Baines et al. 2016).

2.4 Water Exchange and Humidity

Adequate availability of water and microclimatic humidity are two of the more fundamentally important requirements of captive reptiles. Contrary to the misconception of some, reptiles (including desert species) are not waterproof, and their small body size can promote rapid dehydration in the absence of adequate environmental humidity. In natural environments, many smaller reptiles spend much time in burrows, beneath rocks or leaf litter, or secluded in other refugia where humidity is higher and air convection lower than might be suggested by the casual perceptions of climate by humans. These considerations led Pough (1991) to recommend that ambient relative humidity be maintained at levels above 70% for nearly all species of reptile. Some species, such as chameleons, require very humid conditions in addition to periodic misting or access to water for soaking. Fossorial species from mesic habitats (e.g. Florida worm lizard, *Rhineura floridana*) will desiccate rapidly if their ambient moisture in soil or sand is inadequate. On the other hand, too frequent soaking or excess humidity causes skin blemishes or lesions (Hatt 2010), even in species that are amphibious (for example, *Thamnophis* or *Nerodia* spp.). Most reptiles require access to free water, but it may be advisable in some circumstances to remove water bowls from cages occasionally, so that continuous soaking is prevented.

2.4.1 Water Exchange

Water balance compatible with normal body function is achieved through equality of input and output (Fig. 2.5). Reptiles gain water from food—both preformed water and metabolic water produced from the oxidative metabolism of assimilated products from digestion—and drinking, as well as condensation in nasal passages and absorption across the skin. Lesser amounts of water can be acquired by absorption across buccal or cloacal membranes in some circumstances involving aquatic species. Drinking is typically voluntary, but some water can also be taken in as a minor consequence of ingestion of food in marine and aquatic species, called ‘incidental drinking’ (Dunson 1985; Dunson and Mazzotti 1989). Food and free water are the more important sources of input for most captive reptiles and the more readily controlled. Metabolic water can provide significant quantities of water for arid-adapted species that have comparatively water-impermeable skin (roughly 12% of the total water intake for a desert iguana (*Dipsosaurus* sp.): Minnich 1982). Normally, metabolic water is produced at rates that roughly balance—but do not exceed—output by evaporation (Minnich 1982) and is probably significant only during periods of drought when animals cease feeding (Nagy 1972). Except for freshwater aquatic species, uptake of water across the integument or via condensation on nasal membranes provide only minor contributions to the total water budget.

Reptiles lose water by evaporation across skin and respiratory membranes, in urine and in faeces and digestive excretions. Evaporative losses may account for more than half of the total water loss and are very significant in mesic-habitat species

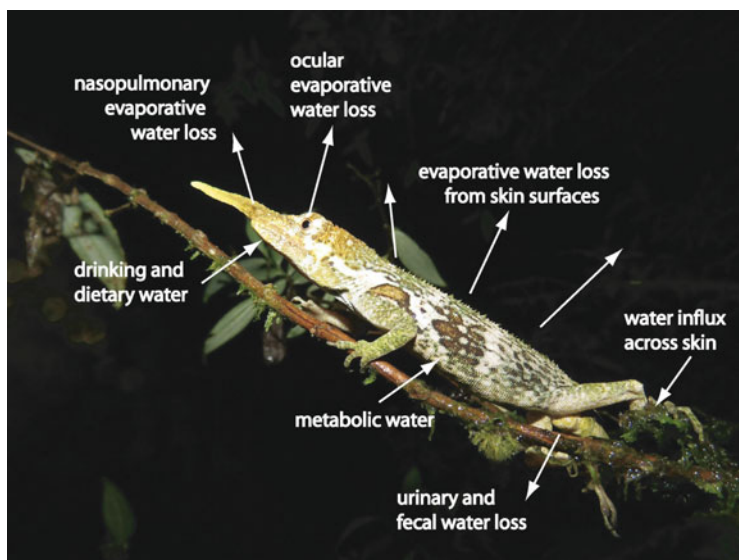


Fig. 2.5 Pathways of water exchange featuring a Pinocchio lizard, *Anolis proboscis*, climbing on a tree branch in the lower montane Andes of western Ecuador. Photograph by Michael Miyamoto

with relatively permeable skin (reviews by Lillywhite and Maderson 1982; Minnich 1982; Lillywhite 2006). Ocular water losses can account for significant fractions of evaporation from the body surface (Mautz 1982). Therefore, regimes of exposure of reptiles to dry air, convection, and radiation from lamps are important considerations in husbandry. Lighting and heating arrangements can influence water relations greatly by decreasing the vapour saturation of air whilst simultaneously raising the vapour pressure (hence evaporation) from heated surfaces. Large numbers of incandescent lights in animal rooms can elevate air temperatures and reduce relative humidities to levels that are incompatible with the well-being of captive animals. Exposure of reptiles to inappropriate levels of ambient humidity (if terrestrial) or salinity (if aquatic or amphibious) clearly can alter levels of hormones, cause loss of weight, and suppress reproduction (Lauren 1985; Summers and Norman 1988a, b; Brischoux et al. 2017).

2.4.2 Water Loss and Integument

The structure of reptilian skin strongly influences the nature and magnitude of mass transfer between animals and their environment (Lillywhite and Maderson 1982, 1988; Lillywhite 2006). Briefly, the skin consists of a deeper, fibrous dermis overlain by an epidermis of multiple layers of living or keratinised cells derived from an active *stratum germinativum* (Fig. 2.6). The keratinised tissues comprise the outermost barrier and are sloughed (shed) periodically, either as an entire unit (squamates) or in flakes or pieces (turtles, crocodylians). Species vary considerably in epidermal thickness, composition of keratin, and sculpturing of outermost surfaces. Contrary to earlier opinions, these features have little correlation with the effectiveness of the skin as a barrier to evaporative water loss (Lillywhite and Maderson 1988; Lillywhite 2006). Studies of various reptiles demonstrate that overall skin thickness does not constitute the principal barrier to diffusion of water, although it can be a secondary factor in some species.

The resistance of reptilian skin to passage of water (and possibly solutes) is determined principally by a discrete layer of lipids in a sheet-like array just beneath the keratinising cells of the epidermis (Lillywhite 2007). These cutaneous lipids—organised in a precisely layered pattern—invest successive layers of keratin in a sandwich or ‘bricks and mortar’ manner, and comprise the so-called ‘mesos’ layer of squamates (Fig. 2.6). This specialised layer of epidermis is the water permeability barrier and has been studied in some detail in squamate reptiles in which cutaneous resistance to passage of water correlates with habitat and appears to be attributable to quantitative or qualitative features of the lipid layer, as in mammals and arthropods (Landmann 1979; Landmann et al. 1981; Roberts and Lillywhite 1980, 1983) (see Table 2.1). Therefore, the external nature of the integument (such as tubercles and perceived thickness of scales) is not a reliable guide to the susceptibility of a species to evaporative dehydration. As a beginning point in husbandry, knowledge of an animal’s habitat and behaviour is a better guide to humidity requirements than are judgments based on the superficial appearance of the skin. Thus, a small desert snake

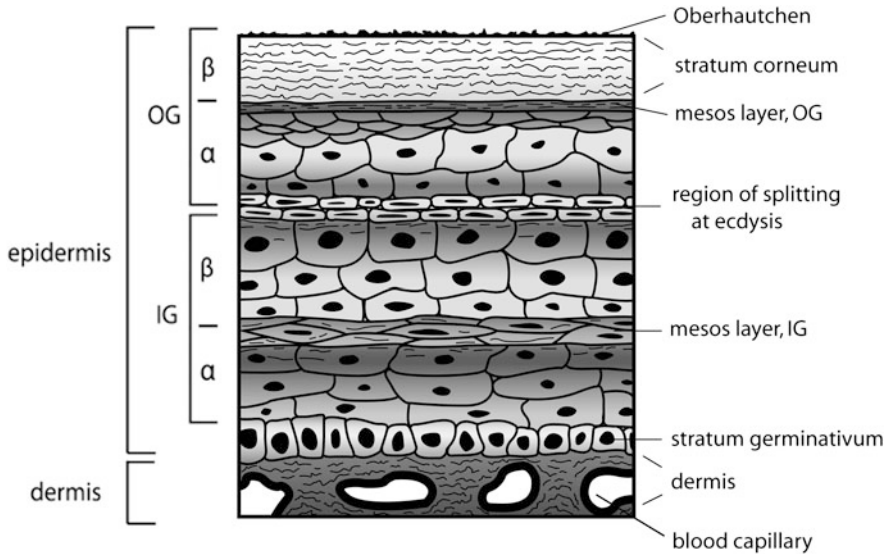


Fig. 2.6 Schematic illustration of a cross section through skin of a generalised squamate reptile, with emphasis on details of the epidermis. Two generations of epidermis are illustrated. The outer generation (OG) represents ‘skin’ (*stratum corneum*) that will be shed from the body during ecdysis, whilst the inner generation (IG) depicts renewed epidermis that will be formed before the OG is shed. Specialised cells separate the IG and OG which split apart during ecdysis. The *stratum corneum* consists of keratinised cell layers including the ‘mesos’ layer, which separates α - and β -keratin, contains stratified lipids surrounding keratin, and provides the permeability barrier to water exchange. The two types of keratin, α and β , are vertically stratified and are derived from a living *stratum germinativum* that overlies the thicker dermis below (not shown to scale). The outermost layer of OG β -keratin is termed *Oberhautchen* and bears a pattern of micro- and nano-‘microsculpturing’ on its outer surface. Drawing by Rachel Keeffe

or lizard with a very thin epidermis may have a far greater resistance to water loss than does the relatively much thicker epidermis of an alligator, which lives in a much wetter habitat. The various species of reptiles that have been investigated appear to have a skin resistance that is suitable to the potential evaporative stress of its habitat (Lillywhite 2006; Table 2.1).

Compared with terrestrial reptiles, aquatic species may experience the reverse problem of water transfer across the skin. In fresh water, the greater solute concentration of the body fluids compared with the external medium will promote osmotic movement of water from outside to inside the animal. Normally, such osmotic intake of water is eliminated effectively by the kidneys. In saline water or seawater, animals will dehydrate as in dry air if the solute levels in the external medium exceed that of the body fluids. Dehydration is therefore a potentially serious problem in marine species in natural habitats or maintained in saline water (Lillywhite et al. 2014a, b). As an example, the total water efflux of the sea snake (*Hydrophis* [= *Pelamis*] *platurus*) in sea water is $6.1 \text{ ml } 100 \text{ g}^{-1} \text{ h}^{-1}$, with 92% of the loss being across the skin (Dunson 1979). Osmotic dehydration is much more rapid in individual

Table 2.1 Values for whole skin resistance^a in selected, representative reptiles from different habitats. Data from Lillywhite (2006)

Family, species	Habitat	Resistance, s·cm ⁻¹
Trionychidae		
<i>Apalone spiniferus</i>	Aquatic	~ 3–5.4
Emydidae		
<i>Terrapene carolina</i>	Mesic terrestrial	78
Iguanidae		
<i>Anolis carolinensis</i>	Mesic arboreal	196
<i>Sauromalus obesus</i>	Xeric terrestrial	1360
Scincidae		
<i>Sphenomorphus labillardieri</i>	Mesic terrestrial	248
Xantusiidae		
<i>Xantusia vigilis</i>	Xeric terrestrial	2150–3310
Viperidae		
<i>Vipera palaestinae</i>	Mesic terrestrial	706–878
<i>Crotalus atrox</i>	Xeric terrestrial	1011
<i>Cerastes cerastes</i>	Xeric terrestrial	~1200–1400

^aValues represent the reciprocal of water vapor conductance and express the difference of water vapor density between saturated skin and external environment per unit of evaporative flux

snakes that have skin ulceration or lesions caused by infections or ectoparasites. Some reptiles (e.g. certain snakes) bruise easily: rubbing, bumping, or rough handling can injure the skin, thereby disrupting the permeability barrier and normal water balance as well as producing chronic stress related to injury.

Provided that aquatic reptiles are feeding and are in water balance at an appropriate temperature, the health of captive reptiles is often challenged by abrasions and disease involving the skin. For example, in the file snake (*Acrochordus granulatus*), the single greatest threat to the health of captive animals is multifocal epidermitis. The causes of this condition are not well understood, but they potentially relate to the quality of water, stress, or immune conditions, and skin abrasions that provide sites for viral, fungal, or bacterial infection. The initial condition is diagnosed by the presence of small white or pinkish spots on the skin, which have the appearance of chalky encrustations. Whatever the initial cause (conceivably fungal), the advanced condition produces larger patches involving lesions that harbour bacterial colonies (Lillywhite 1996).

Fungal hyphae have been collected from cutaneous lesions of *A. arafurae*, and various bacteria (including *Aeromonas* spp., *Salmonella* spp., and *Pseudomonas* spp.) have been cultured from skin lesions of aquatic snakes in general (Banks 1989). Infections can involve the lips or mouth, and these conditions become more life-threatening. If advanced cases are not treated successfully, snakes will gradually weaken and die. Ulcerative conditions increase cutaneous permeability, and osmotic insult may contribute to the stressed conditions of affected snakes, especially in cases where the buccal tissues are exposed to infections or lesions involving the mouth (T. Ellis and H. Lillywhite, unpublished observations).

The skin of reptiles is relatively non-glandular in comparison with some other groups of vertebrates. Nonetheless, there are exocrine organs and natural products of reptilian skin that are important for defence against predators, microorganisms, ectoparasites, and pheromonal communication, in addition to the role of the skin for physical protection. A review of these features can be found in Weldon et al. (2008) who summarised the natural products from exocrine organs of the reptilian integument and described their known or suspected activities. It is very important to view the skin as a complex organ with multiple integrative functions, whilst at the same time realising that the functional integrity of skin has important dependence on its role as a permeability barrier (Lillywhite 2006, 2007).

2.5 Ecdysis

All reptiles shed the outer stratum corneum of skin that is renewed periodically as animals grow throughout life. The shedding process—ecdysis—may involve pieces or patches of skin (chelonians and lizards), or as a quasi-diagnostic feature of snakes, is represented by periodic, pan-body genesis of a new inner epidermal generation and the shedding of an older, outer epidermal generation (Fig. 2.6) that is sloughed (shed) from the body as one entire sheet of keratin (Lillywhite 2014). The renewal and shedding of the stratum corneum are related to cycles of cellular events that are controlled by factors that remain little understood. How often an animal sheds its skin can be related to food consumption, growth, and metabolic rate, but other factors are important as well. In snakes, these potentially include environmental influence related to temperature (Semlitsch 1978), wear and damage of the skin surfaces, or attachment of ectoparasites (Loomis 1951; Heatwole 1999), exposure to dry air that increases cutaneous evaporative water loss (Lillywhite and Maderson 1982; Maderson 1984; Lillywhite 2006), hormones, and reproductive cycles (Kubie et al. 1978; Nilson 1980). Early postnatal shedding in newborn snakes establishes the permeability barrier within the *stratum corneum* and is probably important for lowering cutaneous evaporative water loss in dispersing individuals that become active in open, arid, or semi-arid habitats (Tu et al. 2002; Lillywhite 2006).

Keepers of captive reptiles, especially snakes, need to be aware of physical conditions—including human contact and handling—that might compromise successful ecdysis on the part of captive individuals. Snakes may become reclusive or less active during periods preceding ecdysis, and for sensitive species, a keeper might wish to add a water vessel or moist ‘hide box’ that can assist successful shedding if the air is dry. These factors, as well as pheromonal influence, might serve to synchronise ecdysis among individual snakes that are kept in close vicinity—either same cages or multiple cages that are kept in the same room (Lillywhite and Sheehy 2016).

2.6 Osmoregulation and Nitrogen Metabolism

Maintenance of the volume and composition of body fluids primarily entails regulation of the water budget, with requisite solutes (primarily ions) being derived from the diet. The kidney is the principal organ and pathway for the removal of excess water, salts, and metabolic waste products. Kidney function depends on adequate hydration (blood volume) and diminishes or ceases at low body temperature. Unlike mammalian nephrons, the tubules of reptilian kidneys lack a loop of Henle and cannot concentrate urine beyond osmotic values found in the blood plasma (Dantzler and Braun 1980). Water can be further conserved by reabsorption in the cloaca or rectum. However, this phenomenon needs further study, and the role of the hindgut in osmoregulation is not well understood (Wyneken 2013).

Fully marine reptiles and some terrestrial species possess salt glands that are anatomically distinct from the kidney and eliminate concentrated secretions of salts (principally Na^+ , K^+ and Cl^-) that might be ingested in excess (Dunson 1976). Salt glands help to eliminate excess salt and maintain ion balance, but do not permit some marine reptiles (sea snakes, file snakes) to maintain water balance by ingestion of sea water (Lillywhite et al. 2008). Contrary to earlier assumptions, recent studies have demonstrated that sea snakes do not drink seawater; they drink fresh water to maintain water balance when dehydrated; and they dehydrate at sea during periods of drought (Lillywhite and Ellis 1994; Lillywhite et al. 2008, 2012a, 2014a, b, 2015, 2019). Previous assumptions concerning sea snakes drinking seawater were based largely in the fact that sea snakes possess salt glands. However, Dunson and Dunson (1974) described the sublingual salt gland of sea snakes as being small with comparatively low rates of secretion. Interestingly, the skin of sea snakes appears to be impermeable to sodium, but passes water (Dunson 1979, 1984; Dunson and Robinson 1976). Moreover, the skin of amphibious sea kraits (*Laticauda* spp.) is more sensitive to evaporative water loss than to cutaneous efflux of water when in seawater, and the relative sensitivities to either medium (air or water) correlates with the relative degree of terrestriality (Lillywhite et al. 2009). Marine and estuarine reptiles, with or without salt glands, cannot survive for indefinite periods in saline water (Dunson 1984; Dunson and Mazzotti 1989). Reptilian salt glands function sporadically, and their role in physiological adaptation is not well understood. Some terrestrial reptiles from arid habitats are reputed to survive without a source of free water, but most species require access to water for long-term health and survival.

Excretion of nitrogenous wastes that result from metabolism of protein comprises an important component of the overall water budget of animals. Terrestrial reptiles excrete nitrogenous wastes largely in the form of urates or uric acid, which readily precipitates from solution and can be excreted with comparatively small losses of accompanying water. The white to yellowish semi-solid material characteristic of reptilian excreta consists largely of urates together with co-precipitated salts. On the other hand, nitrogenous wastes of aquatic or amphibious reptiles are excreted largely in the form of ammonium ions (with lesser amounts of urea), which are very soluble in water and require substantial water efflux for elimination. High concentrations of

ammonium ions are cytotoxic, and the ion cannot be concentrated by the kidney. Urea is more soluble in water than ammonia and is less toxic.

Urine in the reptilian kidney tubules is dilute, and uric acid is in solution. However, when urine enters the bladder or cloaca, water is reabsorbed, and some of the uric acid precipitates as the urine becomes increasingly concentrated. Thus, salts of uric acid become solidified usually with enough water to render a pasty consistency. The urine then becomes semi-solid (white to yellow in colour) and usually remains largely separated from faeces, which are also concentrated and 'dried' by reabsorption of water in the cloaca or rectum. The urine and faeces are eliminated together through the cloaca.

Catabolism of protein produces a large and rapid nitrogen load following feeding, especially in carnivorous reptiles that consume prey such as fish (Coulson and Hernandez 1983). Therefore, the use of water that is acquired in the diet or by drinking must offset the volume of water that is required for the elimination of nitrogenous waste. Previously, all squamate reptiles were considered to be uricotelic (Minnich 1979). However, it appears that ammonium ion may be an important component of nitrogenous wastes excreted by marine and estuarine reptiles (Grigg 1981; Yokota et al. 1985; Lillywhite and Ellis 1994).

With regard to husbandry of estuarine and marine reptiles, if the water requirements are not known, it is advised that keepers provide these animals with access to fresh water—at least from time to time. This can be achieved most easily by periodically immersing an animal in fresh water. Marine snakes will drink from a freshwater lens that establishes on the surface of marine waters during periods of intense rainfall (Lillywhite and Ellis 1994; Lillywhite 1996; Lillywhite et al. 2019). Snakes in general—marine or terrestrial—tend to increase the drinking of fresh water following the ingestion and digestion of a meal (Lillywhite 2017). Contrary to popular belief, there is emerging evidence that food consumption has negative rather than positive effects on water balance because the water requirements for digestion and excretion of wastes exceed the free water content and metabolic water associated with intake of food (Lillywhite et al. 2008; Wright et al. 2013; Lillywhite et al. 2014a, b).

2.7 Digestive Physiology and Nutrition

In addition to temperature and water, adequate intake of energy and nutrients is of foremost importance to captive reptiles. The quality of food and rate of feeding should ensure adequate growth or maintenance of normal weight; breeding animals will have additional nutritional requirements. The subjects of digestive function and nutritional needs of reptiles are poorly understood for many species and invite a great deal of attention in future research. The reader is referred to the following for a current summary of recommendations regarding nutritional requirements of reptiles (Frye 1991a, b; Donoghue 2006; Kischinovsky et al. 2017; Maslanka et al. 2023). The present chapter emphasises aspects of nutrition that are relevant to digestive function and the anatomy of the digestive tract (hereafter referred to as the gut).

The reptilian gut is compartmented and complex, similarly to that of many other vertebrates, including mammals (Parsons and Cameron 1977). Digestion depends on gut motility and an array of hydrolytic enzymes that require appropriate pH and temperature. The importance of mastication or reduction of particle size in the pre-treatment of food varies among species but is generally much less than in mammals. In the case of some snakes, envenomation of prey may aid digestion significantly because digestive agents in the venom circulate and initiate the process of digestion internally in the prey, whereas the gut enzymes must act upon the external surfaces of the intact prey (Bottrall et al. 2010).

Reptiles are either carnivores, herbivores, and some are omnivores (see also Maslanka et al. 2023). Snakes are almost exclusively carnivores, whereas herbivory has evolved numerous times in different clades of lizards. Herbivorous lizards typically have large heads, stout bodies, high bite forces, bladelike teeth, long guts, and partitioned colons (Herrel 2007). Herbivorous lizards and turtles are phylogenetically diverse. In general, herbivorous reptiles are relatively large and inhabit warm-climate environments, but lizards in the family Liolaemidae have evolved numerous small herbivorous species with distributions concentrated in cool climates (Espinoza et al. 2004). The success of these small species evidently is related to abilities to heat rapidly and attain body temperatures comparable to larger species in warmer habitats. Herbivorous reptiles are characterised by microbial digestion in elongated or enlarged colons with partitioning by valves or ridges, increased surface area for absorption of nutrients, and digestive efficiencies similar to herbivorous mammals with hindgut fermentation such as rabbits or horses (Bjornadal 1985). Although the overall percentage of reptiles that are strictly herbivores is relatively small, numerous reptiles are omnivorous and consume plant materials, at least occasionally.

As indicated earlier, because of the low metabolic rates and high conversion efficiencies characteristic of ectotherms (Pough 1980), reptiles may not require frequent feeding. Some species will thrive with daily feeding, whilst others (such as large snakes) can be maintained with much longer intervals between meals. The rate of feeding should vary with temperature, activity, age, reproductive status, season and parasite load, in addition to a variety of other factors affecting health or behaviour. Generally, in terms of husbandry, if a healthy animal that has 'adjusted' to captivity refuses to accept offered food, the item(s) should be removed until the next scheduled feeding (Pough 1991).

The digestibility and assimilation of energy and nutrients from food vary with the nature and size of food particles and are generally higher for carnivorous than herbivorous diets (Johnson and Lillywhite 1979; Bjornadal 1989, 1991; Bjornadal and Bolten 1990). Passage rates of food through the gut vary greatly. Some snakes and lizards will produce faeces within hours or days of feeding, whereas some viperid snakes may retain digestive excreta for months. Passage of material is greatly assisted by warm temperatures (generally $>25\text{--}35\text{ }^{\circ}\text{C}$) and activity, especially climbing or swimming. Retention of digested material in the lower gut for minimal periods may be a requirement for the efficient absorption of water from faeces across the lower intestine or cloaca, especially in xeric-adapted species. Stout,

heavy-bodied terrestrial snakes such as vipers and pythons tend to accumulate and store faeces in the hindgut for long periods, sometimes exceeding a year (Lillywhite et al. 2002). Such conditions can cause intestinal obstruction, even in wild snakes and sometimes associated with drought or brumation (Corbit et al. 2014). Thus, once again, provision of adequate water for captive reptiles is important.

Many species of reptile are herbivores or include some plant material in their diets. Most of these species exhibit morphological specialisations of the gut and depend on fermentative, symbiotic digestion (Iverson 1982; McBee and McBee 1982; Troyer 1984a; Bjorndal and Bolten 1990). As in mammals, herbivorous reptiles may select vegetation having high ratios of nutrient (for example, protein) to fibre (Troyer 1984b). Juvenile folivorous reptiles hatched in captivity may be isolated from a source of the species' characteristic complement of fermentative microorganisms (which are usually transferred from adults) (Pough 1991). Although these individuals may survive on laboratory diets that do not require the fermentation of plant cell walls, their digestive physiology may not be similar to that of wild individuals. Such situations have considerable applied significance for husbandry programmes that rear juvenile folivores for release. Such programmes (including captive breeding strategies for endangered species) should include methods for inoculating hatchlings with the species' characteristic gut symbionts (Pough 1991).

The fundamental challenge in husbandry is to provide animals with a nutritionally balanced diet compatible with availability and behavioural acceptance of the food items. Single item or prepared diets are, in general, less satisfactory than is a varied diet of natural or preferred items. Efforts should be undertaken to facilitate prompt and natural acceptance of food because forced or unnatural feeding can induce stress. To achieve these goals, the caretaker should have a thorough knowledge of the sensory cues and behaviours used by a species to detect, capture, and swallow prey. Attention should also be given to aspects of the physical and biological (social) environment in relation to season and the lean mass or fat condition of captive animals. Recently fed individuals may seek warmer temperatures and prefer seclusion or inactivity. Juvenile animals, in particular, may require higher temperatures for optimal rates of digestion, assimilation and growth (Lillywhite et al. 1973; Troyer 1984b, 1987). Observations of snakes suggest that maximal size and growth rates are achieved only when ample food and temperatures are provided during early growth stages that evidently reflect a requisite 'window' for the action of growth-promoting hormones (E. Bessette, pers. comm.).

2.8 Respiration and Circulation

All living reptiles are lung-breathers and depend on a 'closed' type of circulatory system for blood transport of respiratory gases (O_2 and CO_2) between respiratory surfaces and body tissues. Oxygen is transported largely in combination with haemoglobin contained within erythrocytes. With the possible exception of cold and dormant animals, reptilian metabolism depends on a functional cardiopulmonary system, especially in support of behavioural activities. As in other advanced

vertebrates, the blood circulation serves a variety of transport functions and assists in the regulation of acid-base balance in body fluids.

Generally, routine activities of reptiles are supported by aerobic metabolism involving generation of ATP energy by oxidative reactions requiring oxygen. However, very intense activities (e.g. sprint running, digging) may require ATP energy at rates that exceed delivery via oxidative mechanisms, and in these cases, ATP is generated very rapidly by anaerobic metabolism involving glycolytic pathways without the requirement for oxygen. This energy is additive with that from aerobic sources, but usually comprises a significantly larger proportion of the total energy used (e.g. up to about $\frac{3}{4}$ in some lizards; see discussion in Pough et al. 2016). However, intense activities enabled by anaerobic energy production are limited in duration by accumulation of lactic acid and depletion of glycogen stores in muscle. Animals become exhausted and must eventually rest whilst lactic acid buildup is dissipated and metabolised by means of aerobic processes that also replenish the stores of ATP. Keepers of reptiles should be aware of this aspect of physiology related to energetics and behaviour, although few issues are expected to arise directly related to anaerobic metabolism. Activity of reptiles tends to be intermittent, and they seldom engage in behaviours that require sustained high levels of synthesis of ATP.

2.8.1 Lung Structure and Function

All reptiles possess paired lungs, except for a number of limbless species in which one of the lungs has become greatly reduced or is absent. Reptiles vary considerably in lung structure, and the evolutionary context of such variation has been summarised by Duncker (1978). The functional parenchyma consists of elaborated membrane surfaces that form simple ‘honeycomb’-like cells or exhibit secondary and tertiary divisions leading to terminal air spaces termed faveoli by Duncker (Fig. 2.7; Duncker 1978; Perry 1989). These enlarged respiratory surfaces, analogous to the alveoli in birds and mammals, are thin and highly vascular. The remaining lung may be saccular in structure and considerably less vascular, as are the conducting airways.

Snakes exhibit perhaps the greatest variation of structure in terms of regional differentiation of functional surfaces (Fig. 2.7). In many terrestrial (and especially arboreal) species, the functional vascularised surfaces are restricted to a relatively short lung segment close to the heart (Lillywhite 1987b; Lillywhite et al. 2012b). The remaining length of ‘saccular lung’ serves a number of functions in addition to ventilating the vascular exchange parenchyma (e.g. storage of oxygen, use in defensive displays, and others; see Brattstrom 1959 for a more extensive list of putative functions). In reptiles generally, the conducting airways and respiratory surfaces are not as elaborate as comparable structures in mammals, a condition that correlates with the lower metabolic rates of ectotherms.

The complexity and diversity of reptilian lung structure, together with considerations of habitat and behavioural specialisations, possibly predispose

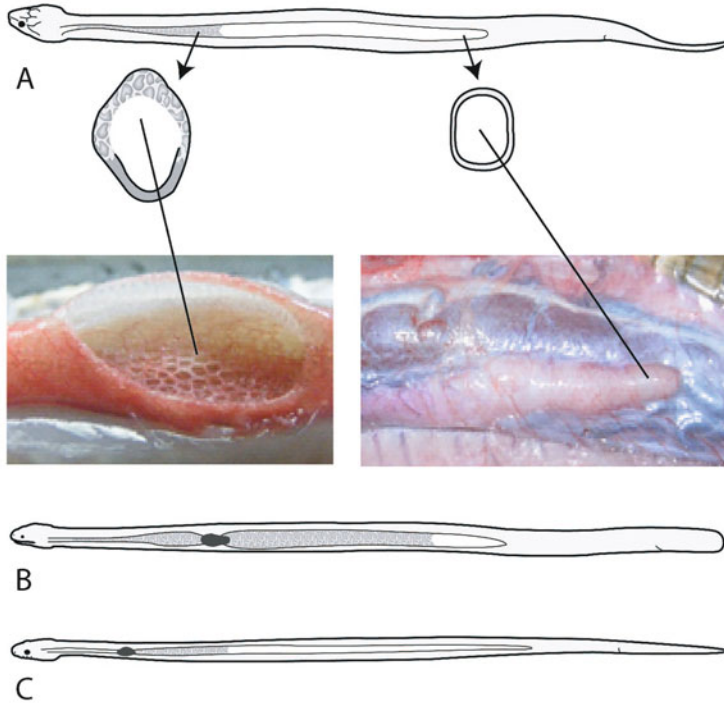


Fig. 2.7 Lung structure and heart position in snakes. **(a)** A schematic snake modeled after a Florida cottonmouth (*Agkistrodon conanti*) illustrating the extent of lung, consisting of a 'tracheal' vascularised segment (gray fill) and posterior 'saccular' lung (no fill). Cross sections below each lung segment illustrate the honeycomb nature of 3-dimensional compartments where gas exchange occurs in the wall of the lumen above the tracheal cartilage (dark gray) of the vascular lung (left), and the simple saccular nature of the posterior lung segment (right). Below the schematic cross-sections are (left) a photograph of vascular lung in a cottonmouth with an open cut to show the 'faveoli' (gas exchange units) within, and (right) the terminal saccular lung of a sea snake, which is relatively thick as well as simple and non-vascular. **(b)** A schematic sea snake illustrating a relatively mid-body position of heart (black), elongated vascular lung (gray fill), and short posterior segment of saccular lung (no fill). **(c)** A schematic terrestrial, semi-arboreal rat snake illustrating a relatively anterior position of heart and comparatively short segment of vascular lung. For further comparative details of anatomy see Lillywhite (1988), and Lillywhite et al. (2012b). Drawings by Rachel Keeffe; photographs by the author

reptiles to infection by lung parasites. Reptilian lungs frequently contain parasites. Severe parasitic pulmonary lesions can lead to lethal haemorrhage or oedema if blood pressures are increased by activity or gravitational stress (as in upright posture) (H.B.L., unpub. obs.). For information related to the diversity of parasites infecting reptiles, see Walden et al. (2021).

Lung ventilation is powered by muscular expansion and contraction of the thoraco-abdominal space; and, in some species of turtles and squamates, pulmonary smooth muscle may contribute to air movements within the lung spaces. Both the

depth and frequency of lung ventilations vary greatly, even within a species or in individual animals. Therefore, changes in ventilatory behaviour (aside from extreme alterations such as panting) are not usually reliable indicators of serious changes in health. Numerous factors such as changes of temperature, excitement, activity, diving, and skin shedding can produce marked changes in lung ventilation.

The skin, pharyngeal lining, and cloacal bursae of aquatic snakes and turtles may serve as accessory respiratory surfaces (Graham 1974; Feder and Burggren 1985; Gordos et al. 2006). However, the majority of species exchange virtually all O₂ and most CO₂ across the lung. Except for hibernating turtles, most aquatic reptiles depend on lung breathing and require periodic access to air. For reptiles that are kept in underground burrow systems, precaution should be taken to provide adequate ventilation that prevents accumulation of high levels of CO₂ (Ultsch and Anderson 1986). Reptiles that burrow in sand, soils, or leaf litter behaviourally achieve adequate O₂ uptake and CO₂ release (Pough 1969a, b). If reptiles become hypoxic, they tend to seek lower temperatures when choices are available (Hicks and Wood 1985; Wood 1991).

2.8.2 Blood Circulation

All reptiles circulate blood by means of a central heart which, except in crocodylians, consists of a single anatomical ventricle that is filled with blood from two atria. The crocodylian heart consists of four chambers (two atria and two ventricles) similar to birds and mammals. All species appear to have the capacity for shunting blood between the systemic and pulmonary circuits according to physiological requirements (Hicks et al. 1996). Furthermore, blood flow varies substantially between periods of apnoea and periods of active ventilation of the lungs (Burggren 1977, 1987; Burggren and Shelton 1979; Lillywhite and Donald 1989). Thus, one should expect blood flow in both the systemic and pulmonary circuits to fluctuate considerably over time. Heart rates of reptiles are generally lower than those of mammals, except when reptiles have achieved high body temperatures, and rates can exceed 100 beats per min (Lillywhite et al. 1999). Arterial blood pressures vary with species, activity and physiological state, with values for mean pressure ranging typically from 15–20 mm Hg to 50–70 mm Hg (Seymour and Lillywhite 1976; Burggren 1977; Burggren and Johansen 1982; Axelsson et al. 1989). In snakes, both the position of the heart (anterior in arboreal or scansorial species) and the length of vascularised lung (short in arboreal or scansorial species) vary interspecifically in relation to gravitational stress related to habitat and behaviour (Lillywhite et al. 2012b) (Fig. 2.7).

As in most vertebrates (and all ‘higher’ taxa), fluid, respiratory gases and other metabolically important molecules are exchanged between blood and tissues at the level of fine capillary networks. The capillary interface with interstitial fluids appears to be comparatively ‘leaky’ and fluids shift readily between the vascular and extravascular compartments, subject to physiological controls. Partly because of these attributes, reptiles can regulate blood (plasma) volume quite well (Lillywhite and Smith 1981; Smits and Kozubowski 1985). On the other hand, animals may be subject to oedema owing to excess capillary filtration when capillary pressures are

high because of arterial hypertension or gravity stress. Large snakes should not be held in vertical positions for long periods ($>2\text{--}3$ min) because gravitational pooling of blood and oedema in dependent tissues compromise adequate blood circulation (Lillywhite 1988; Lillywhite and Smits 1992).

The lymphatic system is not well studied but is extensive and important, at least in some reptiles (Ottaviani and Tazzi 1977; Hedrick et al. 2013). Lymphatic spaces may provide significant stores of body fluid in some species (Smits 1985).

Circulating blood volumes of reptiles vary from a few per cent to about 14% of body mass, with most values typically around 6% of body mass (Thorson 1968; Pough and Lillywhite 1984). Blood volume, as a proportion of body mass, decreases as body size increases, at least in some turtles (Hutton 1961). The plasma fraction comprises roughly two-thirds to three-quarters of the total blood volume, but values vary with species, activity, temperature and health (Thorson 1968; Lillywhite and Smits 1984). Unusually low values for haematocrit are indicative of haemorrhage or poor health. Few studies have examined how blood or plasma volume change, or how well blood circulates, in dormant or hibernating reptiles with low body temperature, reduced heart rate and increased blood viscosity (due to the low temperature) (Huggins 1961; Huggins and Percoco 1965; Snyder 1971; Ultsch 1989).

Blood can be sampled for clinical or research purposes from veins or various sinuses that are accessible by needle (for example, orbital sinuses of lizards, ventral caudal vein of snakes) (Olson et al. 1975; McDonald 1976). Whenever a needle is inserted into an orbital sinus or cardiac chamber, this should be carried out under sedation or general anaesthesia. Only trained persons should attempt to obtain blood samples by cardiac puncture because of the potential for extensive damage to the heart. Furthermore, blood drawn by cardiac puncture may be inadequate for precise measurement of blood gases (Kerr and Frankel 1972). In addition, samples of blood taken from cut tissue (for example, tail tip) are likely to be diluted with interstitial fluids and may yield erroneous values for measurements such as haematocrit. Handling of crocodylians induces glycolysis and results in blood lactate values that remain elevated for up to 24 hours (Coulson and Hernandez 1964; Seymour et al. 1985); experimenters should not assume that an animal that has been handled is truly 'at rest'.

The pH or acid-base status of the blood and interstitial fluids depends on metabolic acid production, respiratory gas exchange, ion levels and kidney function. Unlike the case in mammals, which regulate constant pH, the plasma pH of reptiles varies with changes in body temperature (approximately -0.016 pH unit per 1°C increase in temperature) (Howell and Rahn 1976). Such shifts of pH in relation to temperature appear to be regulated largely by adjustments of ventilation (and thus CO_2 levels) (Ackerman and White 1980; Shelton et al. 1986; Stinner 1987; Truchot 1987; Lutz et al. 1989). Thus, it seems possible that behaviours associated with changing temperature may, in some circumstances, be causally related to acid-base regulation rather than thermoregulation per se.

2.9 Pain and Stress

The perception of pain and the physiological consequences of acute and chronic stress are only beginning to be understood in reptiles. The term ‘nociception’ is often used interchangeably with ‘pain’ and is defined as the neural process of encoding noxious stimuli. However, the word pain is generally accepted to imply something more—a sensory and emotional experience associated with actual or potential damage to tissue (Millan 1999, Paul-Murphy et al. 2004). Comparatively, little is known about pain perception in reptiles (Lance 1992; Millan 1999; Machin 2001; Paul-Murphy et al. 2004; Mosley 2011; Sladky and Mans 2012); most of our understanding is derived from anthropomorphism, indirect observations of responses to pharmacological agents and anaesthetics, and transfer of understanding from humans and other mammals (Morton et al. 1990; Frye 1991a; Burghardt 2016). Both pain and stress are difficult to objectively quantify in any vertebrate animal, even though we possess significant knowledge regarding the mechanisms of nociception and the transmission and processing of painful stimuli (Defrin et al. 2002; Paul-Murphy et al. 2004; Sneddon 2015). In the absence of more quantitative understanding of these subjects, one should assume that all reptiles feel pain and can become stressed by exposure to unnatural conditions or insult to which an animal exhibits defensive behaviour.

As one example for consideration here, rough handling of snakes can obviously inflict pain (as judged from behavioural responses) and is always stressful. If a large snake is held vertically, writhing movements, or the mere mass of the animal can damage the vertebral column; in addition, the gravitational stress of upright posture can impair blood circulation. Similarly, overly tight handling of venomous species such as rattlesnakes by inexperienced handlers can result in physical damage to underlying tissues (Arena et al. 1995). There are anecdotal reports among zookeepers and veterinarians that larger pythons used for handling in zoos or educational institutes may suffer more frequently from spinal disease (e.g. osteopathy; Maas 2018).

Stress can be reduced significantly, and any pain or bodily damage associated with handling can be avoided, if a captured snake is lifted gently on a hooked stick and deposited slowly into a container rather than being grabbed behind the neck with a force-grip instrument. It may not be possible to follow these recommendations during capture of all species, but most viperids, for example, can be handled in this way. Tubing of snakes also is a commonly practiced procedure, and methods that avoid ‘pinning’ or holding of snakes are less stressful and also safer with respect to ‘hands on’ with venomous species. Reptiles that are procured in a non-aggressive manner are more likely to better adapt to captivity because the experience of a traumatic capture conceivably induces chronic stress. Handling stress can cause dramatic hormonal changes even in reptiles that are habituated to humans (Lance 1992). Improper handling, as well as crowding and poor sanitation, produce physiological deterioration leading to reduced growth, suppressed reproductive capacity and increased mortality from disease.

Further research is needed to understand the physiological basis of, and interactions with, stressful states and to evaluate how stress can be ameliorated in captive animals (see also Gangloff and Greenberg 2023). Again, considerable variation of requirements is expected among species in order for reptiles to live, thrive, and reproduce in captivity. A common failure in providing appropriate care of captive reptiles is the assumption that sympatric species, closely related species, or subspecies of a nominate species, have identical or similar requirements for environment and physical external stimuli.

2.10 Animal Welfare Considerations

In recent years, issues of animal welfare have produced the broad application of prescribed common guidelines for the care of domesticated and laboratory mammals. Although reptiles have become increasingly subject to such regulation, many aspects of their biology are not sufficiently known or appreciated to guarantee an appropriate formulation of common guidelines for their care and use. In most cases where regulatory oversight is in force (for example, at academic research institutions), optimal care depends largely on the knowledge and experience of individual investigators rather than requirements and restrictions that are rooted in biomedical research with mammals or urban-based ideologies of pet care. A generalised set of guidelines for husbandry or research is not uniformly applicable to all reptilian species and thus may not promote the best care possible (Pough 1991; Beaupre et al. 2004). Guidelines for optimal care vary not only among higher order taxa but also between closely related species. The variability of husbandry requirements becomes increasingly evident as the goals of the care-giver become more ambitious or complex. Hence, practices for temporary maintenance or exhibit might be far less stringent than those for scientific investigation or captive breeding in zoological facilities.

On a long-term basis, there are multiple factors related to physical, behavioural, and physiological requirements that must not be neglected. Generally, cleanliness and the provision of an appropriate physical environment are of foremost importance. Temperature, light, and ambient humidity are attributes of the environment that strongly influence the health of reptiles. The presence of appropriate stimuli, and the absence of excessive harmful stimuli, are necessary to prevent deterioration of the immune system of animals, which often precedes the onset of disease (see Gangloff and Greenberg 2023). Attention to these factors requires some knowledge of the physiological requirements, in addition to the behaviour and ecology, of the species in question.

This chapter has provided a general overview of reptilian physiology and discuss those aspects of structure and function that are most relevant to the care and well-being of captive reptiles. The subject matter is broad and interrelated with many aspects of behaviour, life history, and veterinary care. In cases where the limitations of space curtail adequate discussion of topics, the reader has been provided with relevant references to literature wherein further information can be found. This

information will hopefully provide both a perspective and roadmap that are useful to future research, synthesis, and understanding of the requirements of reptiles that are necessary for health and vigour whilst in captivity or subjected to experimental investigation.

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Abstract

Behaviour is shaped by the perception of the surrounding world, which is created by the senses. Reptilian sensory systems are shaped by the varied ecologies and complex evolutionary histories of reptiles. In this chapter, we outline the major senses of reptiles: photoreception (vision, parietal eyes, cutaneous), mechanoreception (hearing, balance, and touch), chemoreception (gustation, olfaction, vomeronasal), thermoreception (cutaneous, heat-pit), and magnetoreception. We give general descriptions of the sensory anatomy, including relevant examples of how senses relate to the behaviour and sensory evolution of these animals. We also focus on how major senses mediate intraspecific communication in reptiles, focusing on visual communication via colouration and other visual displays, acoustic communication through calls and songs, and chemical communication using specialised scent glands. Among the diverse sensory specialisations of reptiles, we also outline some of the rare senses for select taxa including magnetoreception navigation in archosaurs, and heat-pit foraging in snakes. Although these unusual senses can be directly related to important behaviours, reptiles do not rely solely on one sensory system for any behaviour, and almost all stimuli are integrated in the brain to inform immediate decision-making. Thus, all sensory capabilities should be considered when attempting to understand the relative importance of sensory systems to reptilian behaviour. We aim to impart an appreciation for how different stimuli may be perceived by reptiles in captivity. Further, signals salient to various reptiles may be invisible to humans (e.g. UV colouration, pheromones), and different reptiles may have

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heightened or impoverished sensory abilities. Thus, an understanding of reptilian sensory systems is vital for ensuring animal health and welfare in captivity.

Keywords

Behaviour · Chemoreception · Communication · Magnetoreception ·
Mechanoreception · Photoreception · Thermoreception

3.1 Introduction

Understanding how reptiles sense their environment is key to understanding reptilian behaviour. The perception of the surrounding environment is created by the senses, which detect and convert stimuli into bioelectrical impulses that neurons in the brain can interpret. Each of the senses uses sensory receptors attuned to specific types (modalities) of physical stimuli such as light, vibration, chemical, pressure, and heat. For example, photoreceptors in the eye are attuned to light, mechanoreceptors in the ear and skin receive vibrations, and chemoreceptors in the nose and tongue detect chemicals. Once stimuli are transduced into bioelectrical impulses, they provide information about the surrounding environment that can be used to maintain homeostasis, trigger seasonal activities such as hibernation, find food and avoid predators, and communicate with others. In this chapter, we outline the major senses of reptiles and give general descriptions of their associated anatomy, including relevant examples of how senses relate to the behaviour and sensory evolution of these animals.

Reptiles are part of a larger group of terrestrial vertebrates (tetrapods) called amniotes. Amniotes evolved approximately 340 million years ago, leaving aquatic habitats and giving rise to modern reptiles, birds, and mammals, characterised by having an amnion during the embryonic stage (Clack 2012). The ancestors of amniotes were thought to have general sensory capabilities in the terrestrial environment, but soon diversified as they adapted to new habitats and foraging strategies, and developed social communication (Müller et al. 2018). Modern reptiles can be divided by their phylogenetic relationships: the Lepidosauria includes the modern Rhynchocephalia (tuatara) and Squamata (lizards, amphisbaenians and snakes), and the Archosauria includes Aves (birds), Testudinata (turtles), and Crocodylia (crocodiles, alligators, caimans, and gharials) (Table 3.1; Modesto and Anderson 2004). Table 3.1 contains an overview of sensory capabilities among these major groups (excluding birds), but with over 11,000 currently recognised species of non-avian reptiles (Uetz et al. 2020) there are many exceptions to these broad generalisations. We have also indicated unique sensory specialisations such as magnetoreception for compass navigation in sea turtles. However, it is important to note that even if a sense is unique, reptiles do not rely solely on one sensory system for any behaviour. For example, a rattlesnake can detect the body heat of its prey using pit organs, but must also integrate this information with other visual and chemical cues if it is to calculate how and when to perform a successful predatory

Table 3.1 Overview of major sensory developments among the major groups of reptiles

Group	No. species ^a	Major sensory systems			
		Photoreception	Mechanoreception	Chemoreception	Thermoreception
General comments applicable across the major groups of reptiles	11,050	This sense includes lateral and parietal eyes and skin photoreception. Intra- and inter-specific visual communication is prevalent in lizards and snakes. A few groups have very reduced eyes due to burrowing habits. Parietal “third” eye is important for circadian cycles in Lepidosauria	This sense includes hearing, touch, and balance systems. Many reptiles were presumed to be deaf (e.g. snakes) and silent (e.g. turtles), but this is generally not the case. All reptiles can hear and geckos, crocodiles and some turtles have sophisticated acoustic communication. The importance of touch is often overlooked but many groups have specialised cutaneous receptors, some aquatic reptiles can sense vibrations underwater	This sense includes taste, smell, and vomeronasal system. Almost all reptiles have taste buds on the tongue and/or mouth. Most reptiles have specialised glands that emit secretions and other chemical signals for intra- and inter-specific communication. The vomeronasal organ is used to detect pheromones and other odorants and often used in conjunction with tongue-flicking (in squamates). Used for multiple and complex behaviours including exploration, foraging and detection of prey, trailing of struck prey, feeding, detection of	All reptiles are ectotherms and so generally must bask to gain enough energy for feeding, locomotion, and other vital functions. Sensory receptors are likely located in peripheral nerve endings within the skin
					Magnetoreception A mysterious and rare sense; experimentally demonstrated in sea turtles; thought to be used by other reptiles that have complex navigation abilities

(continued)

Table 3.1 (continued)

	Group	No. species ^a	Major sensory systems				
			Photoreception	Mechanoreception	Chemoreception	Thermoreception	Magnetoreception
Archelosauria	<i>Testudinata</i> Sea turtles, freshwater turtles, terrestrial turtles and tortoises	353	Flatter corneas for underwater vision in sea turtles. All visual opsins expressed in the eyes; retina have both cone (with oil droplets) and rod photoreceptors. Polarised light patterns may help aquatic turtles orient to the surface of the water	Nerve endings are present in the shells of turtles, conferring some level of touch-sensitivity Turtles have good underwater hearing and are sensitive to frequencies from 50 Hz to 1500 kHz. Some turtles have complex vocalisations during aggregations for mating and migration	pheromones and mating, detection of predators, thermoregulation, and drinking Turtles can actively pump air/water into the nasal cavity (gular pumping), which is important for foraging and navigation Turtles lack a well-developed vomeronasal system, but a vomeronasal epithelium is present inside the nasal cavity, which may be used to detect volatile and non-volatile chemicals underwater	See general comment	Sea turtles use magnetoreception for compass navigation and for recognising feeding and natal habitats, although the sensory receptors and neurobiology of this sense are unknown. Some other terrestrial turtles are thought to also use magnetoreception for compass orientation

Lepidosauria	<i>Crocodylia</i> Alligators, crocodiles and gharials	25	Retina has rods and cones (with oil droplets). Vision adapted for both water and air. Elliptical pupils and inner reflective layer of the eye help increase visual acuity at night	Specialised receptors on the skin (ISOs) confer sensitivity to water motion, allowing for precise orientation towards prey moving in the water Crocodylians have a broad range of hearing sensitivity (50 Hz to 2.5 kHz) and complex acoustic communication. Distinct vocal repertoires have been recorded in many species and are used in a variety of social situations and habitat types	Crocodylians have complex nasal passages and use gular pumping to suck in airborne chemicals The vomeronasal system is absent in post-embryonic crocodylians	ISOs touch receptors are also sensitive to thermal gradients	Many crocodylians have complex navigation abilities and 'homing' behaviours that are likely to involve magnetoreception
	<i>Rhynchocephalia</i> Tuatara	1	Rods and cone photoreceptors and fovea. Parietal eye can detect overall light levels used in circadian cycles and compass orientation	Limited range of hearing sensitivity (100 to 800 Hz)	Functional vomeronasal system but does not use tongue-flicking	See general comment	See general comment
	<i>Amphisbaenia</i> Worm lizards, <i>Bipes</i>	195	Eyes appear degenerated in many burrowing species	Limited hearing sensitivities (50 to 700 Hz); Hearing of ground-borne	Sophisticated vomeronasal system involving tongue-flicking.	See general comment	See general comment

(continued)

Table 3.1 (continued)

	Group	No. species ^a	Major sensory systems			Thermoreception	Magnetoreception
			Photoreception	Mechanoreception	Chemoreception		
			(e.g. <i>Bipes</i>), but all opsins are present	vibrations using jaw bones connected to inner ear (convergent with snakes)	used in habitat selection, recognising predator, prey, and mates		
	<i>Lizards</i> Lizards including (e.g.) geckos, skinks, gila monsters	6687	Advanced visual capabilities in many diurnal lizards (e.g. anoles, chameleons) linked with finding and catching prey. Complex evolution of photoreceptors causing many cone-like rods and vice versa. All visual opsins are typically present, except RH1 is missing in geckos. Parietal eye can detect overall light levels used in circadian cycles and compass orientation. Changing of skin colour (background adaptation) likely linked to localised	Numerous cutaneous mechanoreceptors on the head and body of lizards confer a sense of touch. Some species (e.g. chameleons) may use these for vibrational communication along substrate. Although lizards are generally silent, acoustic communication is very important for a few groups. Geckos emit barks and calls for social functions. Lizards generally have very good hearing abilities (500 Hz to 4 kHz; up to 20 kHz in some	Sophisticated vomeronasal system that can involve tongue-flicking. Varanid lizards have bifurcating tongues used to follow prey odour 'trails'. Lizards have epidermal follicular glands that secrete chemicals for intra-specific communication	See general comment	See general comment

[illegible]

^aSpecies estimates taken from the Reptile Database (Uetz et al. 2020)

strike (Safer and Grace 2004; Bakken and Krochmal 2007; Goris 2011). All senses are integrated in the brain to inform immediate decision-making. Thus, all sensory capabilities should be considered when attempting to understand the relative importance of sensory systems to reptilian behaviour. Because it is not possible to truly perceive and understand the world as might a reptile (or any other individual), paying close attention to the known sensory attributes of animals allows us to at least estimate what they can detect and thus by what they may be positively or negatively affected.

3.2 Photoreception

Eyes are at the centre of reptilian visual systems; they are complex organs that receive energy in the form of photons, converting them into bioelectrical impulses that can be interpreted as an image by the brain. The visual systems of reptiles are incredibly diverse owing to their varied ecologies and evolutionary histories (e.g. nocturnal, aquatic, fossorial habits) and specialised methods of prey acquisition (e.g. projectile tongues of chamaeleons). Visual systems typically provide the ability to form an image from visible light information that is relayed to the brain from the optic nerves of eyes, but many reptiles have other light sensing abilities as well, such as the parietal ‘third’ eye and cutaneous (skin) photoreception (see Lillywhite 2023).

3.2.1 Eyes and Vision

Light enters the eye via a transparent layer of tissue (cornea) and is focused by the lens onto an intricate layer of sensory cells (the retina) at the back of the eye (Fig. 3.1). The shape of the eye is supported by a ring of dense fibres, bone, and/or cartilage (sclerotic ring), which is ubiquitous among vertebrates except for crocodylians, snakes, and mammals. Behind the cornea is a ring of smooth muscle and pigment (iris) that surrounds the pupil (Fig. 3.1). When the iris is constricted, it controls the aperture of the pupil influencing the amount of light that can enter the eye. The eyes of reptiles also have many peculiarities compared to mammals, such as internal protrusions like the conus in lizards, the function of which is still being researched.

The retina contains two types of light-sensitive cells, or photoreceptors: cones, which have tapered outer segments used in daytime vision, and rods, which have longer cylindrical-shaped outer segments used in night vision (Fig. 3.1) (Fu 2015). Both rods and cones contain opsins, which are proteins that become light sensitive due to the binding of a chromophore, a derivative of vitamin A (Fu 2015). Most reptiles have four or five opsins expressed within their photoreceptors (Fig. 3.2) (Simões and Gower 2017). These opsins have different spectral sensitivities, allowing reptiles to differentiate wavelengths of light. Rods contain rhodopsin, and different cone types contain a combination of opsins sensitive to different colour

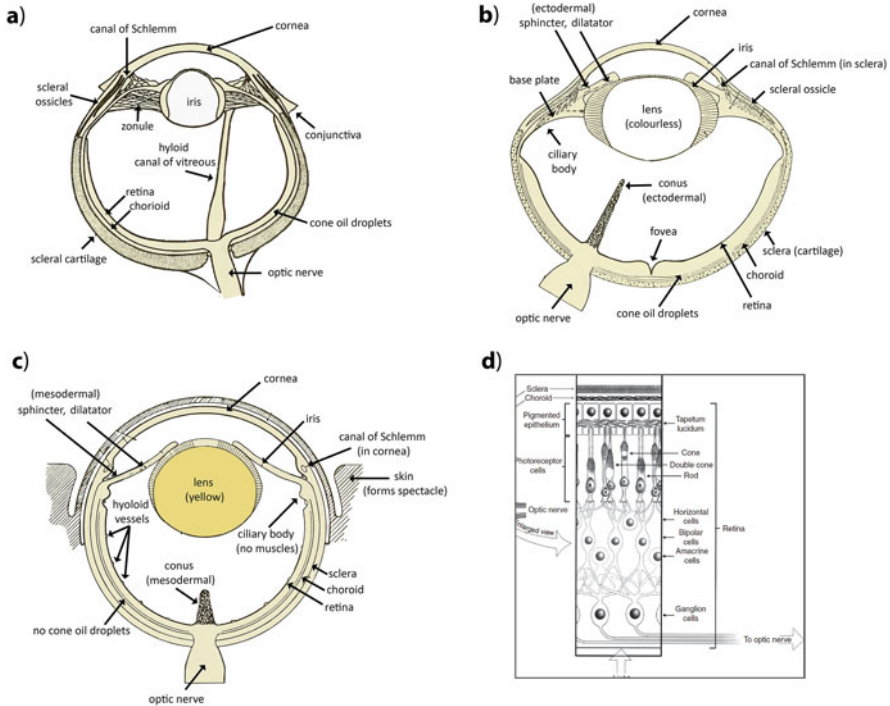


Fig. 3.1 Comparison of eye anatomies in (a) turtles, (b) lizards, and (c) snakes, and enlarged view of a generalised retina (d). Note that many features of the snake eye have evolved independently from the lizards, e.g. the conus, sphincter, and dilator are derived from different tissue types (mesodermal versus ectodermal), and the ciliary body applies force onto the lens from different directions. The retina is a layer of cells at the back of the eyeball which includes the photoreceptors, pigmented epithelium, and neuronal cells (Horizontal, Bipolar, and Amacrine cells); photoreceptor cells are found in variable proportions and anatomies among major reptile groups, e.g. solely cone photoreceptors are seen in turtles and highly diurnal snakes, rods are found in crocodiles, rod-like cones in geckos, and cone-like cells in some crepuscular snakes. Image credit: eye diagrams modified from Walls (1942) and retinæ provided by E. Jacobson

spectra including short, medium, and long wavelengths (Fig. 3.2) (Lamb et al. 2009; Simões and Gower 2017).

Generally, the proportions of rods or cones in the retina signify the nocturnal or diurnal habits of various species: lizards have variable proportions of both rods and cones; turtles have primarily cones, whereas the primary visual cells are rods in crocodylians and tuatara (Walls 1942). Most colubrid snakes have retinæ with only cones, although these cones are not homologous with those in other vertebrates and evidently evolved from rods (Bhattacharyya et al. 2017). In tuatara and lizards, cones are densely packed into small depressions within the retina (fovea). These ‘pockets’ of cones expand the size of the image when it is projected onto this part of the retina, which increases visual acuity. Anoles (*Anolis* sp.) have two foveae per eye, and other

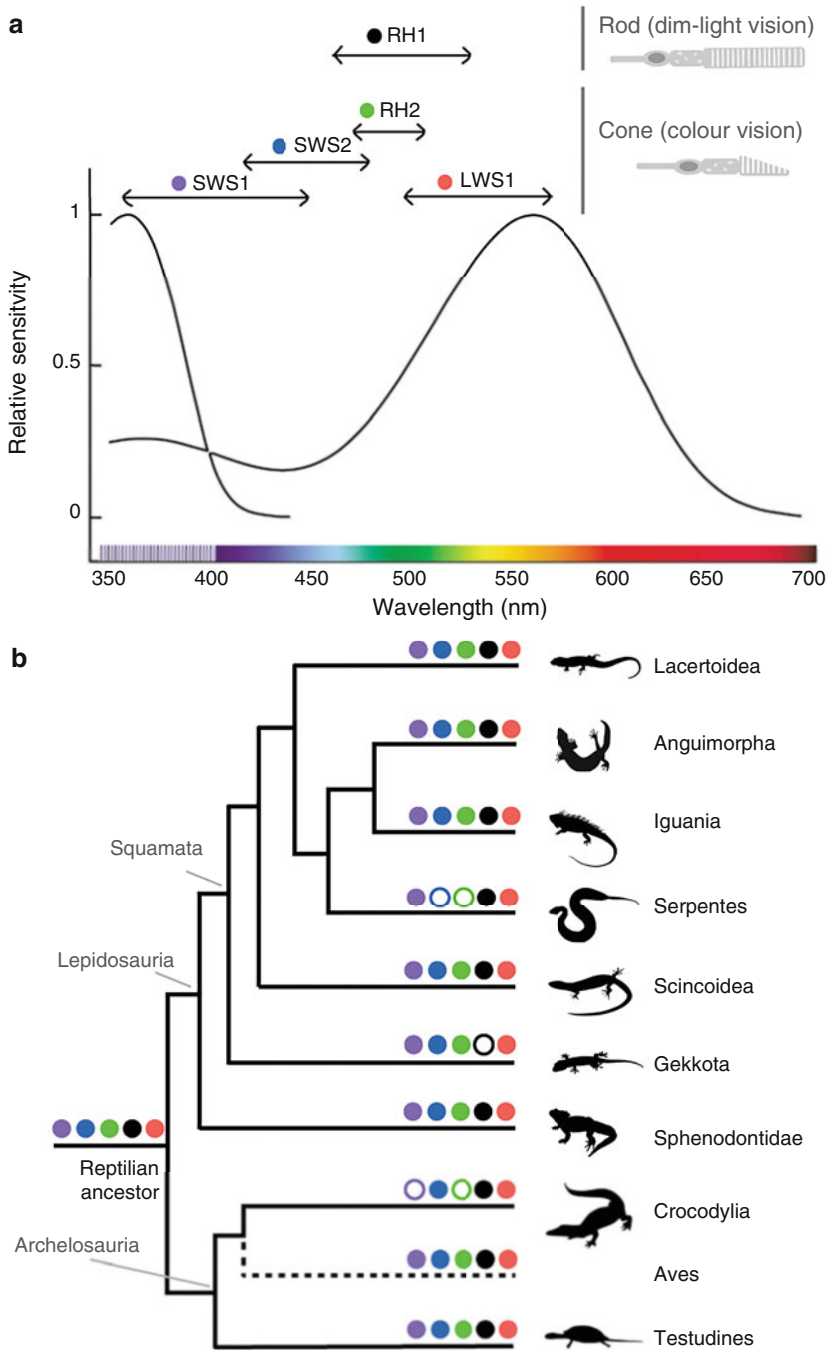


Fig. 3.2 The spectral sensitivities of reptilian visual opsins. **(a)** The cone opsins are sensitive to short- (SWS1 and SWS2), medium- (RH2), and long-wavelengths (LWS) used in daytime vision; the rod opsin is sensitive to medium-wavelengths used in night vision. **(b)** The opsins and phylogenetic relationships among reptiles; some groups (snakes, geckos, and crocodylians) have

highly visual lizards such as chamaeleons have deeper foveae to create greater visual acuity (McDevitt et al. 1993).

Also contributing to colour sensitivity in reptiles are pigmented oil droplets inside the cones, present in many diurnal lizards and turtles (Goede and Kolb 1994), but not snakes and crocodylians. These oil droplets likely function as mini light filters, and these groups are sensitive to a broad colour spectrum including ultraviolet (UV) (Bowmaker 1998; Stavenga and Wilts 2014; Simões et al. 2016a). Some reptiles can also sense light polarisation patterns, which relates to the direction and angle of light waves. For example, freshwater turtles use polarisation patterns produced by light scattering at the surface of the water (Meyer-Rochow 2014), but the anatomical and physiological mechanisms underlying this sensory capability are unknown.

The ancestors of snakes were thought to be highly fossorial, which resulted in limbless and elongate bodies for underground locomotion, and a reduced reliance on the visual system in a dim-light environment (but see Caprette et al. 2004 for discussion on eye anatomy and aquatic origins in snakes). As snakes transitioned above ground and out of the darkness, they effectively ‘re-evolved’ vision. Snakes, therefore, have very different photoreceptor and eye anatomies compared to lizards and tuatara, and notably modern snakes are missing fovea, oil droplets, and some cone opsins and phototransduction genes (Figs. 3.1 and 3.2) (Walls 1942; Underwood 1967, 1970; Simões et al. 2016a). True cones were probably lost in the putatively fossorial ancestors of modern snakes. Despite the limited complement of eye anatomy, many modern snakes are highly visual foragers, which is a testament to the power of selection and ingenuity in evolution.

The opsins and photoreceptors of reptiles are incredibly variable owing to their diverse ecologies and complex evolutionary history. The typical photoreceptor configuration in mammals is a ‘duplex’ retina of rods and cones, but adaptations to specific habitats and ecologies have resulted in dramatic shifts in spectral sensitivities and visual abilities in many groups of reptiles. For example, the ancestor of geckos is thought to have been diurnal causing them to have a ‘simplex’ retina solely of cones. However, many present-day species of geckos are nocturnal and have simplex retinæ of rods, implying their photoreceptors ‘flipped’ from cones into rod-like cells during evolution (Schott et al. 2019). This process of switching back and forth between cell types was originally proposed by Walls (1942) to explain the diversity of photoreceptor types among reptiles and has subsequently become well-supported by anatomical and genetic studies (Underwood 1963; Simões et al. 2016b;



Fig. 3.2 (continued) lost some opsins, but may compensate by shifting the visual sensitivities of the retained opsins. Note that the duplex photoreceptor configuration (cones and rods) is an oversimplification of the reptilian visual system (see discussion in ‘eyes and vision’). Modified from Simões and Gower (2017); relationships among reptiles based on Modesto and Anderson (2004) and Pyron et al. (2013). Animal silhouettes available from Phylopic under creative commons license (CC BY-NC-SA 3.0), image credits: G. Mützel, N. M. Koch, J. M. Wood, C. N. Zdenek, O. Griffith, S. Traver, O. B. Kimmel and S. Hartman

Bhattacharyya et al. 2017; Schott et al. 2019). Changes in opsin genes have also evolved to shift the spectral sensitivity to dominant light spectra in the environment, e.g. blue light penetrates better in water so some aquatic reptiles can sense a wider range of blue wavelengths of light (Hart et al. 2012; Simões et al. 2020).

In addition to the range of opsins and photoreceptors, reptiles have a plethora of eye anatomies. Different sizes and shapes of pupils can alter the way that light enters the eye, which may be correlated with certain activity patterns and foraging strategies. Vertical pupils are generally associated with predators such as ambush vipers, which have vertical slit-like pupils that allow fine control over how much light enters, also enhancing depth perception whilst foraging (Murphy and Howland 1986; Brischoux et al. 2010; Banks et al. 2015). Vertical pupils can also help correct colour aberrations. Horizontally elongated pupils are more common in prey because this shape allows panoramic view and horizontal contours, which may help detect the movement of an approaching predator in the distance (Banks et al. 2015). Generally, among lizards the shape of the pupil is correlated with diurnal (round) or nocturnal (vertically elliptical) habits (Fig. 3.3). Turtles generally have round

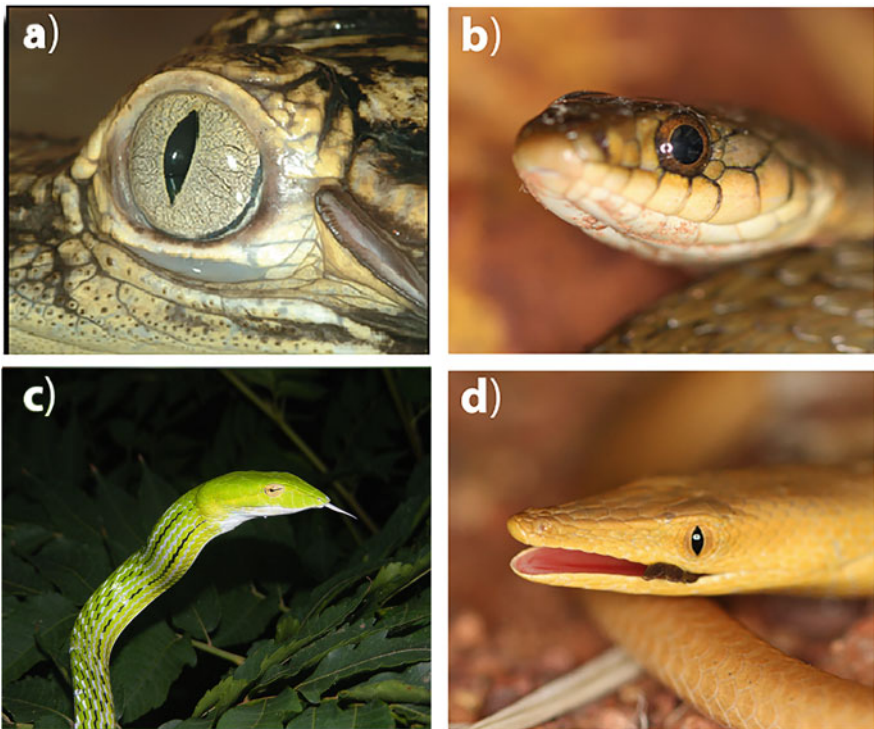


Fig. 3.3 Pupil shape in reptiles. (a) vertical ‘slit’ pupils in an alligator (*Alligator mississippiensis*), (b) round pupils in a keelback snake (*Tropidonophis mairii*), (c) horizontal keyhole pupil in an Oriental whip snake (*Ahaetulla prasina*), and (d) a vertical pupil in a Burton’s legless lizard (*Lialis burtonis*). Image credits: K. Vliet, J. M. Crowe-Riddell, H. B. Lillywhite

pupils, whereas crocodylians have vertically elliptical pupils that are responsive to a range of light intensities (Fig. 3.3). In snakes, the shape of the pupil is variable, and some arboreal species have a horizontal ‘keyhole pupil’ that is considered to confer very acute vision with excellent abilities to judge distance and detect movements (see Lillywhite 2014) (Fig. 3.3). Crocodylians have a reflective layer at the back of the eye (*tapetum lucidum*), which increases visual acuity at night and creates a mirror-like ‘eye shine’ when illuminated by a flashlight. The aquatic medium alters properties of light refraction, which can also influence the anatomy of eyes in aquatic reptiles. Crocodylians and turtles, for example, have anatomy that is convergent with the eyes of some fishes, which tend to have flatter corneas to compensate for the altered light properties underwater (Fleishman et al. 1988).

High visual acuity is predominantly associated with terrestrial and arboreal species of reptiles, and many diurnal lizards with high visual acuity have deep foveae within their retinæ, which likely helps focus light to form a sharp visual image (McDevitt et al. 1993). Chamaeleons are one of the more impressive examples of eye evolution with opposite shaped lens (concave) and cornea (convex) that increase each eye’s field of view (Ott and Schaeffel 1985). Chamaeleons can independently focus each eye, allowing optimal depth perception whilst targeting prey and scanning for potential predators (Ott et al. 1998; Ott 2001). Many diurnal snakes have a tinted lens, often appearing yellow in colour, to filter out UV and blue light which increases visual acuity during the day (Simões et al. 2016a). The eyes of arboreal snakes also exhibit features that help to detect and target prey, including horizontal ‘keyhole’ pupils in some species that provide ‘wraparound’ vision and together with slenderised cones enhance acuity; a wide binocular field of vision; eye lines and attenuated snouts that help to target prey; and head-swaying behaviour that likely helps to gain additional parallax (Lillywhite and Henderson 1993; Lillywhite 2014).

Although all reptiles have eyelids, some lizards and all snakes have a transparent spectacle covering the eye that is formed by fusion of the eyelids embryologically. In some other lizards, certain scales of the lower eyelid—which is typically more moveable than the upper eyelid—have become transparent. Most species of turtles, crocodylians, and lizards also have nictitating membranes, which are semi-opaque third eyelids that slide horizontally over the cornea to keep it moist (Wyneken 2012). In snakes, blood vessels inside the transparent spectacle can obstruct vision. When threatened, snakes can constrict blood flow to effectively remove it from the visual field (Van Doorn and Sivak 2013). The spectacle can also impair vision during skin shedding because it loosens and becomes opaque; snakes will often hide or may become defensive during this time.

Finally, Harderian and lacrimal glands are variably present accessories to the eyes of reptiles and secrete lubricating fluids. Harderian glands are present in all major groups and are well developed in snakes. Lacrimal glands are lacking in some lizards (geckos, chamaeleons), tuatara, and snakes. In marine turtles, the lacrimal glands are enlarged and function as extrarenal salt glands. Smaller Harderian glands lubricate the eyes of sea turtles. There is histochemical and ultrastructural evidence that orbital glands (Harderian and lacrimal) change during acclimation of a freshwater turtle to

seawater (Baccari et al. 1993). Harderian glands also appear to provide the fluid that fills the lumen of the vomeronasal organ in lizards and snakes (Rehorek et al. 2000). The mixing of Harderian-derived fluid within the vomeronasal organ in snakes may function as a solvent for lingually transferred pheromones and prey chemicals (Huang et al. 2006).

3.2.2 Visual Communication

Many reptiles use visual signals for intra- and inter-specific communication. Rapid movements can serve to attract attention of visually oriented animals. For example, male jacky dragons (*Amphibolurus muricatus*) attract female attention by whipping their tails and waving their arms (Peters and Evans 2003). Some freshwater turtles (e.g. *Chrysemys* spp., *Graptemys* spp., *Pseudemys* spp. and *Trachemys* spp.) will swim parallel to another turtle, bobbing their head and batting their foreclaws in an underwater display known as the ‘titillation sequence’. This behaviour is thought to be important species-specific courtship, but has also been reported as ‘play’ in juvenile turtles (Kramer and Burghardt 2010; Vogt 1993; Gillingham and Clark 2023). Many lizards have brightly coloured tails that attract attention, acting as a decoy to enable a quick escape from attacks by predators (Bateman et al. 2014) (Fig. 3.4a). Juvenile boas and pythons (as well as other species) often have colourful tails, which they move in hypnotic undulations to lure in curious prey (Heatwole and Davison 1976). Colour can also enhance the visual signals of reptiles with elaborate territorial and courtship displays. For example, the colourful throat patches of anole lizards (*Anolis* spp.) are advertised when extending a modified throat flap (dewlap) (Fig. 3.4a, b) that is otherwise hidden from view (Nicholson et al. 2007). Similarly, male lizards of some species such as tawny dragons (*Ctenophorus decresii*) and side-blotched lizards (*Uta stansburiana*) have distinctive throat patches that are sometimes associated with types of male behaviour; e.g. aggressive tawny lizards have bright orange to yellow, whilst meek males have blue to grey colours (Olsson et al. 2013). Colour can also be used by lizards in defence. Many lizards have bright blue tails to distract predators (Fig. 3.4c). Blue-tongued skinks (*Tiliqua* spp.), for example, ‘overload’ the visual system of an attacking predator by dramatically unfurling their bright UV-blue tongues (Fig. 3.4d) (Badiane et al. 2018). Colourful displays can also signal danger, such as the red and black bands of venomous coral snakes (*Micurus* spp.) (Fig. 3.4e), which are so effective at deterring avian predators that many ‘harmless’ colubrid snakes (e.g. *Lampropeltis*) mimic their colour patterns and thrashing defensive behaviour (Fig. 3.4f) (Savage and Slowinski 1992). Visually perceived human presence is known to influence behaviour in wild and captive reptiles, and such frequent visual disturbances cannot be ruled out as a factor in welfare (see Warwick 2023).



Fig. 3.4 Examples of visual signals in reptiles. (a) Bright orange dewlap of the brown anole (*Anolis sagrei*) and pale cream of the (b) bark anole (*Anolis distichus*); (c) Decoy tail colouration in the blue-tailed skink (*Nucras caesicaudata*); (d) Defensive display in the Australian sleepy lizard (*Tiliqua rugosa*); the black and yellow banding pattern of the (e) venomous Eastern coral snake (*Micrurus fulvius*), and (f) harmless scarlet king snake (*Lampropeltis elapsoides*). Attribution 4c): CC BY 2.0, <https://creativecommons.org/licenses/by/2.0/deed.en>, G. Peters. Image credits: G. Peters, C. Nitschke, B. Kircher, J. D. Curlis, H. B. Lillywhite

3.2.3 Non-Visual Photoreception

Light detection that is not directly involved in image-forming vision is known as ‘non-visual photoreception’ and often occurs independently of the photoreceptors in the eye (Kelley and Davies 2016). Non-visual photoreception is a ubiquitous sense across animals used to regulate vital physiological and behavioural functions (Wolken 1995). Among reptiles, non-visual photoreception can involve ‘extraocular’ pathways of the pineal system in the brain, parietal ‘third’ eye, and

cutaneous photoreception (Foster and Soni 1998; Peirson et al. 2009; Kelley and Davies 2016).

3.2.3.1 The Parietal Eye and Circadian Rhythms

Circadian rhythms are an animal's internal clock that regulates the timing of daily or seasonal biological events (e.g. when to sleep, feed, reproduce) according to the day/night light cycle. Mammals 'keep the time' via a non-visual opsin (melanopsin) expressed in specialised neuronal cells in the retina of the eye (Campbell et al. 2001; Davies et al. 2014). However, in reptiles, the brain and other extraocular organs are also responsible for a circadian clock, and these organs are rendered sensitive to light by a different type of melanopsin as well as a plethora of other non-visual opsins (Campbell et al. 2001; Bertolucci and Foá 2004; Peirson et al. 2009; Davies et al. 2015).

Tuatara and some lizards have a parietal eye on top of their heads in addition to the lateral eyes (Gundy and Wurst 1976). The parietal eye typically consists of a simplified retina, lacking in a lens and corneal structures that connects to the pineal gland in the brain. Photoreceptors within the parietal eye transduce light using special opsins (e.g. parietal opsin) and phototransduction pathways that are distinct from those of the lateral eyes (Su et al. 2006). Light stimuli received by the parietal eye likely do not produce a visual image; instead, parietal eyes are thought to detect overall light levels in the environment informing the animal about day-night cycles. The parietal eye may also detect polarised light and may be used as a 'compass' for navigation (Bertolucci and Foá 2004). For example, the parietal eye of ruin lizards (*Podarcis sicula*) can detect sky polarisation patterns; these lizards become completely disoriented when the parietal eye is painted over (Beltrami et al. 2010). The role of the parietal eye in reptilian behaviour is not yet fully understood, and more research is needed to uncover how light information received by the parietal and lateral eyes is integrated in the brain.

3.2.3.2 Skin and Photoreception

Lacking in feathers or fur, the scales of reptiles are thought to be a prime site for cutaneous photoreception (Kelley and Davies 2016). Among squamate reptiles, cutaneous photoreception has been linked to basking behaviour in wall lizards (*Podarcis muralis*) whereby they are sensitive to both visual and infrared wavelengths of light (Tosini and Avery 1996a, b). Cutaneous photoreception can also aid in concealment from predators. For example, blindfolded Moorish geckos (*Tarentola mauritanica*) darken their skin colour in response to dimmed light, which is linked to pigment-cells in the skin (melanophores) that appear to be directly sensitive to light without the aid of eyes (Fulgione et al. 2014; Avallone et al. 2018). The paddle-shaped tails of some sea snakes (*Aipysurus* spp.) are sensitive to light, which helps them hide their vulnerable hind-body and tails under dark crevices whilst resting during the day (Zimmerman and Heatwole 1990; Crowe-Riddell et al. 2019a). The dorsal caudal skin of sea snakes is sensitive to blue and green light and likely involves a melanopsin light-detection pathway. It is unknown whether cutaneous photoreception is involved in concealment behaviours of other

reptiles, but this might be attributable to the dearth of studies explicitly testing response to light on the skin in other reptiles (although note that Young and Morain (2003) found that Saharan horned vipers [*Cerastes cerastes*] do not use cutaneous photoreception whilst burrowing). The evolution of cutaneous photoreception is poorly known, and further research is needed to understand the physiology and biological importance of this sense in reptiles.

3.3 Mechanoreception

The ability to sense tactile, pressure, and vibratory stimuli is based on ‘mechanoreception’ and is used in three major sensory systems: touch, hearing, and balance/equilibrium. Mechanoreceptors within the inner ear respond to airborne vibrations (i.e. sound), which provide perception of hearing and can also detect body movement contributing to the sense of balance. Cutaneous mechanoreceptors respond to direct deformation of the skin and convey information such as texture, location, intensity, and duration of stimuli, which contribute to the sense of touch. Mechanoreception may thus hold an important role in a welfare context where animals are subject to excessive vibrational disturbances (see Mancera and Phillips 2023).

3.3.1 Cutaneous Mechanoreceptors and Touch

The scales of reptilian skin are made of corneous proteins that create a hardened epidermis. Despite this cornified exterior, reptilian skin is rendered sensitive to touch by numerous, small cutaneous mechanoreceptors. Reptiles show considerable variation in cutaneous mechanoreceptors, which tend to consist of a bristle-like protrusion from the skin in tuatara and some lizards (e.g. geckos, anoles, chamaeleons, agamids) or dome-shaped ‘tubercles’ in snakes, varanid lizards, and crocodiles (Fig. 3.5) (Landmann 1975; von Düring and Miller 1979; Matveyeva and Ananjeva 1995; Ananjeva et al. 2010). Cutaneous mechanoreceptors are typically concentrated on areas of the head or limbs that are most likely to be in contact with surrounding substrate (Underwood 1967). There is some evidence that the density, distribution, and morphology of tactile organs correlate with species’ ecology or habitat (see below; Crowe-Riddell et al. 2016; Riedel et al. 2019). The outer epidermis of cutaneous mechanoreceptors tends to be thinner to allow underlying sensory cells to detect and relay information about the vibration, texture, location, intensity, and duration of stimuli (von Düring 1973; Landmann 1975; von Düring and Miller 1979). Turtle shells are vascularised and presumably innervated, but lack cutaneous mechanoreceptors, so are likely not highly sensitive to touch.

Mechanoreception provides important cues for navigating substrate, sensing prey, and intra-species interactions. Mechanoreceptors have been described in the mouth of crocodiles, snakes, and turtles that likely aid in handling prey, chewing and jaw movement (Burns 1969; Nishida et al. 2000; Buchtová et al. 2009; Di-Poi and Milinkovitch 2013). Cutaneous mechanoreceptors on the adhesive toepads of

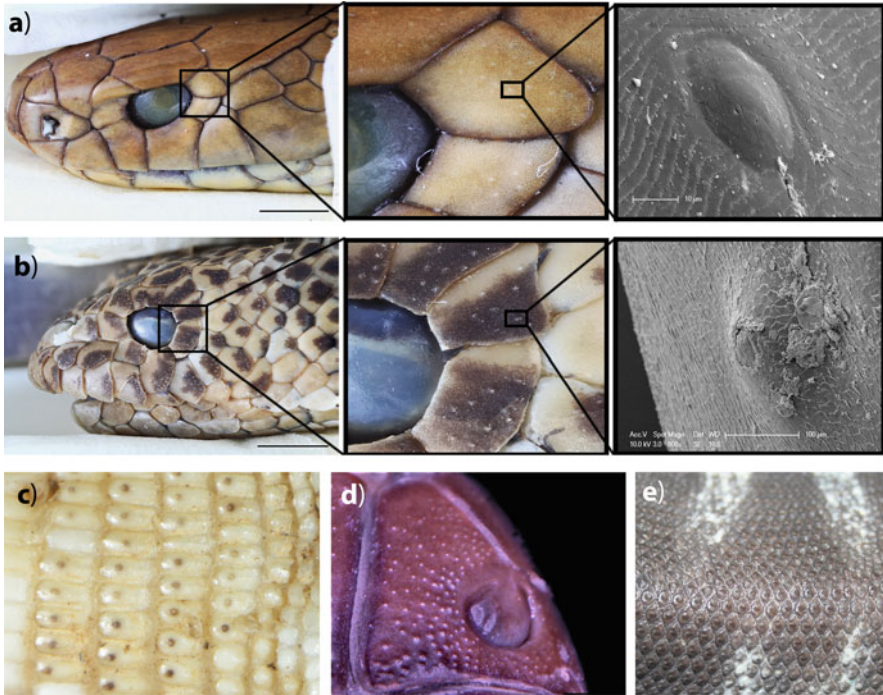


Fig. 3.5 Comparison of cutaneous mechanoreceptors in (a) terrestrial land snake (*Pseudonaja textilis*) and (b) a fully-aquatic sea snake (*Aipysurus duboisii*). Other examples of cutaneous mechanoreceptors in squamates: (c) northern ridge-tailed monitor (*Varanus primordius*), (d) bar-bellied sea snake (*Hydrophis major*) and little file snake (*Acrochordus granulatus*). Image credit: *A. granulatus*, H. B. Lillywhite; all other images, J. M. Crowe-Riddell

geckos may be useful for correcting grip whilst climbing (Lauff et al. 1993), and those on their tails might sense breakage sites after tail loss (autonomy) (Russell et al. 2014). Many burrowing snakes and lizards appear to have higher densities of cutaneous mechanoreceptors on their heads compared to surface-dwelling relatives; these might be used to ensure body submergence, navigate inside burrows, or sense prey (Underwood 1967; Hetherington 1989; Young and Morain 2003). Some blind snakes (Typhlopidae, e.g. *Rhinotyphlops* spp.) have extremely protruding tactile organs concentrated on their curved rostral scale, but other burrowing snakes with similar rostral structures used for digging (Colubridae, e.g. *Lytorhynchus* spp.) lack tactile organs on their snout entirely (Landmann 1975; Young and Wallach 1998). Chamaeleons are thought to detect vibrations generated by other chamaeleons moving along the same branch by using cutaneous mechanoreceptors in their feet or legs, allowing for a ‘private communication channel’ between neighbours (Barnett et al. 1999).

3.3.1.1 Tactile Communication

In addition to using tactile cues for navigating substrate and sensing prey or predators, mechanoreception is important for intraspecific interactions such as parental care, combat, courtship, and mating behaviours in reptiles. Male lizards will often lie on top of females and use their claws to cling to or scratch females. Snakes receive tactile cues along their entire body in sinuous interactions such as male–male combat that involves wrapping forebodies and using their chin to press opponents' head down to the ground (Carpenter 1977, 1984; Gillingham et al. 1977; Barker et al. 1979; Greene 2000). During courtship and mating, male snakes will lie on top of females and may bite and press and/or rub the chin along the female's body (Noble 1937; Gillingham et al. 1977; Gillingham 1979). Snakes with 'pelvic spurs' such as pythons and boas may use these vestigial limbs to scratch and poke at soft tissue between the female's scales which induces cloacal gaping (i.e. lifting the anal scale) (Stickel and Stickel 1946; Gillingham and Chambers 1982). Given that snakes lack limbs, cutaneous mechanoreceptors on the chin and tail are vital for body and cloacal alignment (Noble and Schmidt 1937; Mason et al. 2000). Evidence suggests that tactile cues are essential to inducing hormonal changes that lead to vitellogenesis (i.e. follicle development) in females (Mendonça and Crews 1990, 2001).

3.3.1.2 Hydrodynamic Sense

Many aquatically-foraging reptiles have specialised mechanoreceptors to sense vibrations in water, which is known as a 'hydrodynamic sense'. Crocodylians have cutaneous mechanoreceptors called 'integumentary sensory organs' (ISOs) scattered over their skin; these organs are concentrated on the jaws in alligators and caimans, but extend to cover much of the body and tail in crocodiles and gharials (Soares 2002; Leitch and Catania 2012). ISOs are small convex organs, measuring approximately 1 mm in diameter, consisting of specialised 'light touch' receptors (Merkel cells) that connect to free nerve endings in the outer epidermis and underlying dermal neurons and lamellated corpuscles (von Düring 1973; Jackson et al. 1996; Leitch and Catania 2012). As an alligator waits at the surface of the water, the position of the ISOs on their jaws receive incoming ripples caused by falling prey or other objects (Leitch and Catania 2012; Grap et al. 2015). Behavioural experiments of captive alligators in a dark room showed that these predators can orient towards the source of ripples with incredible accuracy and speed just by using their ISOs (Leitch and Catania 2012). Studies of fossil crocodylians have revealed the indentations of ISOs as well as large cranial foramina (openings in the skull) that link the large trigeminal nerve to ISOs, indicating that underwater mechanoreception is an ancient innovation of crocodylians (Soares 2002; George and Holliday 2013). Finally, in addition to exquisite mechanoreception, ISOs are also chemoreceptive and probably sensitive to water pH and temperature, making them unique multi-sensory organs (Brooks and Jackson 2007; Di-Poï and Milinkovitch 2013).

Some snakes are also sensitive to water motion: file snakes (*Acrochordus* spp.), tentacled snakes (*Erpeton* spp.), and marine snakes (Hydrophiinae family) (Lillywhite 2014). File snakes are ambush predators that live in fresh, brackish, and marine waterways of south-east Asia (Murphy 2012). The scales of file snakes

have tiny hair-like cutaneous mechanoreceptors (sensillae) that are concentrated on the head and are sensitive to water motion generated by the movement of fish (Povel and VanDerKooij 1997) (Fig. 3.5). Tentacled snakes have conspicuous tentacle-like organs on their snout, measuring approximately 3 mm in length and densely innervated, which act as enlarged mechanoreceptors (Winokur 1977). These snakes live in freshwater swamps in Asia and use their tentacles to detect the movement of prey and orient their strike towards the fleeing fish (Catania 2010; Catania et al. 2010). The hydrophiine sea snakes and sea kraits are thought to detect water motion and pressure changes using scale organs (sensilla) concentrated on the head. Although these scale organs have underlying cells and innervation patterns comparable to their terrestrial snake relatives (i.e. Meissner corpuscles), these tiny organs are more protruding and typically cover a higher portion of the scales in marine snakes (Crowe-Riddell et al. 2016, 2019b) (Fig. 3.5). What appear to be sensory structures occur on the body scales of the yellow-bellied sea snake (*Hydrophis platurus*), and these have filamentous extensions (Lillywhite and Menon 2019). How marine snakes use these enhanced scale organs has not been thoroughly investigated, but might involve detection of potential prey, predators or mates, or sensing pressure changes associated with weather events (Westhoff et al. 2005; Lillywhite et al. 2009; Liu et al. 2010). Both sea snakes (Liu et al. 2010) and sea turtles (Wilson et al. 2017) change behaviour in relation to approaching tropical storms.

Other ambush foraging aquatic reptiles may also benefit from a hydrodynamic sense, e.g. freshwater turtles such as alligator snapping turtles (*Macrochelys temminckii*) from North America and mata mata (*Chelus fimbriata*) from South America. Indeed, the latter species have sensory ‘barbels’ on their chin and upper jaw that may be mechanoreceptors. However, whether scale organs have been co-opted for sensitivity to water motion in aquatic-associating reptiles needs to be examined.

3.4 Ears and Hearing

The anatomy of the ear can be divided into three parts: the outer or external ear (lateral surface of head to tympanic membrane), middle ear (structures for transmitting sound), and the inner ear (otic capsule). Crocodylians and lizards have an external opening as part of their outer ear (external auditory meatus), but the outer ear structures are absent in most other reptiles including turtles, tuatara, snakes, amphisbaenians, and earless lizards. The tympanic membrane or ‘ear drum’ has evolved at least five times during the evolution of tetrapods and connects with an air-filled tympanic cavity (middle ear) that facilitates the transmission of airborne sound (Clack 1997). The ancestor of the Lepidosaurians had a well-developed tympanic membrane that became secondarily lost in snakes, amphisbaenians, tuatara, and some lizards. Most lizards and crocodylians still have a tympanic membrane, whilst turtles have a cartilaginous tympanic disc (Evans 2016). Airborne vibrations cause the tympanic membrane to vibrate, which in turn moves the columella

(homologous to the mammalian stapes) and creates vibrational waves in the fluid-filled cavities of the inner ear (Dehnhardt and Mauck 2008). Thus, airborne vibrations are transduced into vibrational movements in liquid.

The intricate anatomy of the inner ear has a dual function: the basilar papilla (homologous to the cochlear duct in mammals) is involved in hearing whilst the semi-circular canals are involved in equilibrium (sensing body position, movement, and balance) (see below). The basilar papilla contains many elastic fibres embedded within a specialised basilar membrane. The fibres are of varying lengths and tensile strength that resonate with specific frequencies of sound, analogous to the strings on a piano. Shorter, stiff fibres are most responsive to high-frequency sounds, and longer, flexible fibres respond to lower-frequency sound waves. Hair-like cells are triggered by the movement of these elastic fibres and generate neuronal impulses that travel to the brain via the auditory nerve. However, geckos are unique among all amniotes in that some of the hair-like cells lack innervation, and the elastic fibres within the basilar papilla are arranged in reverse pattern to other amniotes, a perplexing anatomy that is the subject of active research (Manley et al. 2013). The overall shape and volume of the basilar papilla is positively associated with sensitivity or range of hearing frequency in reptiles and can be used to predict the complexity of vocalisations in some species (Walsh et al. 2009). Localising the source of a noise is achieved by the auditory system simultaneously comparing the intensity and arrival time of a sound stimulus as it impinges on different sides of the body. Lizards have an improved ability to localise sound because the middle ear cavity opens directly into the pharynx, creating a hearing system that is highly directional (Christensen-Dalsgaard and Manley 2005).

Crocodiles and most lizards hear quite well, whereas tuatara, turtles, and snakes sense lower-frequency vibrations. Most lizards can hear a broad frequency of sound (500 Hz to 4 kHz, and over 20 kHz in some gekkonids), crocodylians hear a relatively broad range (50 Hz to 2.5 kHz), whilst turtles (50 Hz to 1.5 kHz), tuatara (100 to 800 Hz), amphisbaenians (50 to 700 Hz), and snakes (40 to 1000 Hz) have relatively lower sensitivities (Gans and Wever 1972; Manley and Kraus 2010; Young et al. 2013; see also Mancera and Phillips 2023). Among lizards, geckos have an impressive hearing ability that corresponds to their highly distinctive inner ear structure and diverse vocal repertoire (see below). Both crocodylians and turtles can hear underwater. Turtles have much better sensitivities in water versus air, whilst crocodylians can hear equally well in either medium (Christensen-Dalsgaard et al. 2012). Although much is known about the hearing capabilities of many reptiles, we have relatively little understanding of how vibrational stimuli and hearing influence behaviours of various taxa.

Snakes were once thought to be functionally deaf because they do not have an outer ear opening or tympanic membrane (e.g., Young 2003). However, recent physiological studies show that snakes are sensitive to ground-borne vibrations and to some degree airborne vibrations. Snakes have an inner ear cavity and cochlear duct that connects to a middle ear bone (columella), which is modified to attach to the quadrate bone and lower jawbone (mandible) (Fig. 3.6). Because the head of snakes may directly contact the ground, they are able to transduce vibrations via

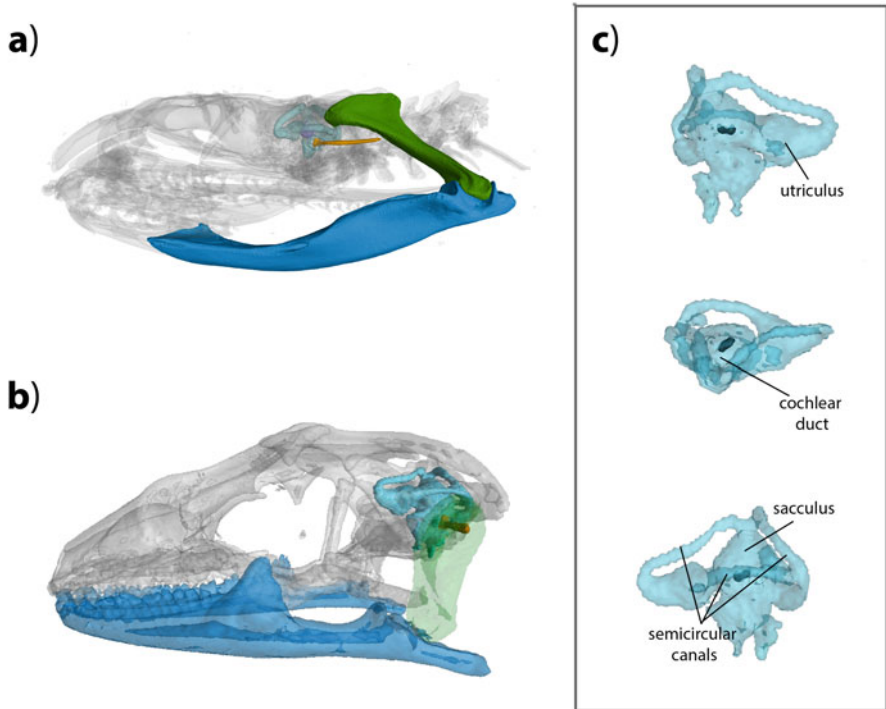


Fig. 3.6 Anatomy of the reptilian ear. (a) The hearing structures of a snake, the air-filled chambers of the outer and middle ear are absent; instead, vibrations are conducted by bones: the mandible (blue), quadrate (green), and columella (orange) connect to the inner ear space. (b) Some of the hearing structures in a lizard, the columella (orange) connects the inner ear (light blue) to the tympanic membrane (not pictured); note that the lower jaw and quadrate are not part of the hearing system of lizards and most other reptiles. (c) The anatomy of the inner ear space in a gecko from different rotational planes. The inner ear consists of three semi-circular canals, sacculus, utriculus, and cochlear duct, which is used in the vestibular system and hearing across reptiles. Image credit: Auckland green gecko (*Naultinus elegans*) from the University of Michigan Museum of Zoology (UMMZ-129352) segmentation by R. Nagesan. Olive sea snake (*Aipysurus laevis*) segmentation by J. M. Crowe-Riddell

conduction through tissue and bone to the inner ear. Interestingly, amphisbaenians also have a columella-quadrate connection (via specialised cartilaginous attachments) indicating that detection of ground-borne vibrations may be a convergent adaptation to burrowing lifestyles (Gans and Wever 1972).

Auditory brain responses to ground-borne vibrations have been recorded in ball pythons (*Python regius*) and demonstrate sensitivity to low-frequency vibrations (50 to 1000 Hz; peak sensitivity 80 to 160 Hz). When vibrations are airborne (i.e. sound), these auditory brain responses are abolished (Christensen et al. 2012). However, rattlesnakes (*Crotalus atrox*) have been demonstrated to perceive and respond to airborne vibrations that are frequency-modulated within the range 200 to 400 Hz (Young and Aguiar 2002). Mid-brain and auditory responses have been

recorded at similar sensitivity in boas and vipers, and at lower sensitivities in sea snakes (40 to 600 Hz; peak 60 to 100 Hz) (Hartline 1971; Wever 1978; Westhoff et al. 2005; Chapuis et al. 2019). Although this is a relatively narrow range of sensitivity compared to other vertebrates (e.g. humans, 20 to 20,000 Hz), it is still enough to show that hearing is important for feeding and presumably fleeing behaviour in snakes (Young and Aguiar 2002; Young and Morain 2003). Saharan horned vipers (*Cerastes cerastes*) that are partially buried in sand can localise and accurately strike live mice by detecting vibrations (via the inner ear) caused by the footfall of the mice (Young and Morain 2003). Sounds and airborne and substrate vibrations are also shown to be detected via the auditory nerve in several species of snakes (Hartline and Campbell 1969). Vibrational stimuli and pressure changes are also detected by snakes in water (see 'Hydrodynamic sense' above and Lillywhite 2014).

3.4.1 Acoustic Communication

Reptiles use hearing to detect objects and predators in their environment, but most species do not create noise or communicate socially by sound in general. Some species do use sound to communicate, and vocalisation occurs in crocodylians, turtles, and many gekkonids as well as occasional species from all major lizard families (Gans and Maderson 1973; Manley and Kraus 2010). Gekkonid lizards, potentially due to their highly nocturnal lifestyles and thus limited ability for visual communication, produce a range of sounds that are used in courtship displays, territorial disputes and to deter potential predators (Manley et al. 2013). They are unique among lizards in possessing vocal cords, which produce complex sounds, sometimes with tonal or harmonic qualities (Gans and Maderson 1973; Marcellini 1977; Rittenhouse et al. 1998). For examples, Australian barking geckos (*Underwoodisaurus* spp.) emit a loud 'bark' whilst aggregating in the breeding season, whereas tokay geckos (*Gekko gecko*) emit distinctive and high-pitched 'squeaks' and short 'clicks' as distress calls (Young et al. 2013). The common barking gecko (*Ptenopus garrulus*) is highly vocal, and the sounds produced have social function that sometimes involve choruses at the entrance of burrows (Haacke 1975; Rittenhouse et al. 1998). Gekkonids that vocalise have an enlarged basilar membrane, enhanced hearing sensitivity, and can produce high-frequency sounds of over 20 kHz (Marcellini 1977; Manley and Kraus 2010). Although other lizards do not vocalise, hearing ability is still very good. Experiments on plated skinks (*Zonosaurus laticaudatus*) and collared iguana (*Oplurus cuvieri cuvieri*) from Madagascar revealed that these lizards 'eavesdrop' on nearby bird songs. When a flycatcher alarm call is heard, these lizards will cease foraging and be vigilant for predators (Ito and Mori 2010; Ito et al. 2017).

Crocodylians have an impressive repertoire of vocalisations that are used in social situations, and different species can have distinct calls that convey specific meanings (Young et al. 2013). Hatchling alligators, for example, emit synchronised calls to communicate with their parents and facilitate social interactions with their siblings

(Vergne et al. 2009). Adult crocodylians use ‘hissing’ sounds during defence that contrast with the guttural bellows and growls, and the soft ‘chumph’ exhalations that are emitted during courtship and mating (Lang 1989; Vergne et al. 2009). Gharials can also modulate their vocalisations using a distinctive bulb-like organ on the end of their snouts (Lang 1989). Bellowing will often be synchronised among groups of crocodylians with roaring choruses that can last up to 10 min in alligators and up to 1 min in caimans (Dinets 2013). Crocodylians are also thought to hunt cooperatively (Dinets 2015), which might require social communication using acoustic signals. Crocodylians also have an impressive array of non-vocal acoustics that are used to communicate: slapping and snapping their jaws at the surface of the water to create loud popping sounds, or ‘jawclaps’, as well as exhaling through their nares whilst submerged to create a steady stream of popping bubbles (Lang 1989). Headclaps and roars are associated with dominance displays in male crocodylians, but females have been known to headclap in captivity, especially when males are absent (Dinets 2011). In addition to roars, claps, and bubble popping, some alligators and caimans create low-frequency vibrations underwater (<10 Hz) by rapidly contracting their body muscles, which create long-range acoustic signals undetectable to the human ear (infrasound). The social situation, complexity of habitat and continuity of waterways often dictates which type of acoustic signal is used in crocodylians (Dinets 2013). Thus, it is important to consider how the captive environment might influence vocal behaviour in crocodylians.

Finally, the acoustic communication of turtles is just beginning to be understood, but their vocalisations can be many and varied in contexts of reproduction and other social situations (Ferrara et al. 2014a, b). Males often make vocalisations whilst mounting females during mating (Galeotti et al. 2004, 2005a, b), and some freshwater species (e.g. *Chelodina oblonga*) communicate using distinctive underwater calls (Giles et al. 2009). Female sea turtles will also vocalise whilst laying eggs (Cook and Forrest 2005). Giant South American turtles (*Podocnemis expansa*) have an impressive range of vocalisations, used in a variety of social contexts including hatchling communication with adults, and are possibly important for congregating during mass migrations (Ferrara et al. 2013). Hatchling vocalisations have also been documented in many species of sea turtles, but it is unknown whether these are used for a social purpose (Ferrara et al. 2014b, 2019; McKenna et al. 2019). Although acoustic communication in turtles is still not fully understood, it is clear that many species of freshwater and marine species are affected by underwater noise created by boat traffic, infrastructure development, and oil and gas exploration (McCauley et al. 2000; Willis 2016). Similarly, anthropogenic acoustic-vibrational factors must be regarded as relevant to captive conditions, environmental disturbance issues, and stress (see Mancera and Phillips 2023).

3.4.2 Vestibular System and Equilibrium

The inner ear contains the vestibular system, which contributes to the sense of motion and where the body is oriented in space. The integration of orientation and

balance underlies many motor reflexes and compensatory behaviours to stabilise the head, neck, eyes, and limbs, and is vital for locomotion. The mode of locomotion and the anatomy of the vestibular system have been relatively understudied in reptiles.

The reptilian vestibular system includes three structures in the inner ear: the sacculus, utricle, and three semi-circular canals (Fig. 3.6). The two chambers are contiguous with the canals and contain a membrane filled with endolymphatic fluid. Generally, the sacculus and utricle are responsible for sensing changes in linear acceleration caused by motion or a change in body position: the sacculus is sensitive to vertical movement (e.g. snake climbing up a tree), and the utricle is sensitive to horizontal movement (e.g. a lizard moving forward). Sensing movement in other directions (i.e. angular acceleration) is imparted by the semi-circular canals, which are oriented orthogonally, allowing perception of rotational movement in three different planes. At the base of each canal is an expanded area containing a patch of sensory cells (ampullae). Hair-like projections of the cells are embedded in a gelatinous mass called the cupula. When the head rotates, inertia of the endolymph and the cupula causes them to lag behind the head motion, causing the sensory hairs to bend and thereby transduce action potentials in associated neurons. Variations in the size and length of the semi-circular canals are correlated with the general mode of locomotion among mammals, but have been comparatively understudied in reptiles. Anatomical variations have been noted among reptiles; for example, turtles, burrowing lizards and snakes have short canals whereas some lizards, that need higher manoeuvrability during locomotion, have elongated and rounder canals (Palci et al. 2017; Müller et al. 2018). One study that investigated the vestibular system in lacertid lizards found anatomical variation was connected to differences in micro-habitat and skull shape. For example, lizards with wide, flat skulls (sand-diving spp.) have a wider vestibular system than species with a more rounded head shape (Vasilopoulou-Kampitsi et al. 2019).

3.5 Chemoreception

Chemicals provide vital cues for reptiles, and chemoreception is one of the more important reptilian sensory systems. Chemicals also tend to linger in the environment and thus can be used to track odours over large distances or over long periods of time, making chemoreception a 'long-range' sense. Chemoreceptors contain membrane-embedded proteins that bind to specific chemicals. Internal chemoreceptors are vital for monitoring internal changes in chemical composition of the blood and other body fluids. Externally, chemicals produced by reptiles that induce behavioural change in other individuals of the same species are known as 'pheromones'. These are used in a plethora of social interactions involving 'chemical communication'. Reptiles can detect pheromones and other chemicals using three main chemical senses: olfaction (smell), associated with the nasal cavity; gustation (taste) associated with taste buds within the oral cavity; and vomeronasal olfaction (vomeronasal), associated with the vomeronasal (Jacobson's) organ within the

nasal cavity. These sensory systems are mediated by separate cranial nerves: i) olfaction; ii) three branches of gustation nerves; and the iii) vomerolfaction. Given the known sensitivity of reptile olfaction in environmental perception (e.g. Chiszar et al. 1995) it is important to consider what sensory disturbances may be imposed on captive reptiles by the myriad of atypical chemicals used for cleaning and other regular purposes in captive settings.

3.5.1 Tongue and Gustation

Taste is conveyed by gustatory chemoreceptors (taste buds) in the oral epithelium of the tongue and mouth and is important for distinguishing between palatable and unpalatable food. Taste buds are composed of support and sensory cells within the oral epithelium that are clustered together to form distinctive bulbs. At the tip of the bulb is a small pore with hair-like projections (cilia) exposed to chemicals that have been dissolved in saliva. The cilia bind to specific chemicals to convey different taste sensations. For example, studies in mammals and birds have shown that the binding of sodium ions conveys the perception of saltiness, alkaloids can convey bitterness, and glucose gives a sweet taste. Taste buds have been described on either tongue, mouth, pharynx, and/or palate for the major groups of reptiles (Korte 1980; Schwenk 1985, 1986; Nishida et al. 2000; Berkhoudt et al. 2001; Putterill and Soley 2003; Heiss et al. 2008), but can be variably present or even absent in some species. Furthermore, some reptiles have co-opted the tongue for non-gustatory functions, which has likely reduced the total number of taste buds present in the mouth and impoverished their taste perception. For example, chamaeleons have a prehensile tongue for grabbing prey, and snakes and varanid lizards have forked tongues involved in the vomeronasal sense (see below) (Schwenk 1993; Young 1997).

3.5.2 Nose and Olfaction

Reptilian olfactory systems consist of a specialised extension of the brain (olfactory bulb) that innervates the epithelium of the nasal passages, which opens up externally (nostrils) and internally inside the mouth (choanae) (Parsons 1970). The anatomy of the nasal passages is quite diverse among reptiles, ranging from a relatively simple cavity in turtles to convoluted sinuses and bone protrusions (conchae) in crocodylians (Parsons 1970). Nasal cavities also tend to vary in aquatic species, with sea turtles, sea snakes and some aquatic lizards possessing a long, straight vestibulum and nostrils that can be sealed by vascularised erectile tissue. In these aquatic species, the nostrils tend to be positioned dorso-medially on the head (as opposed to laterally) to facilitate breathing at the surface of the water (Schwenk 2008). Interestingly, the number of olfactory genes has decreased in fully-aquatic sea snakes, which seal their nostrils, and thus likely rely more heavily on their vomeronasal sense for detecting chemicals underwater (Kishida and Hikida 2010; Kishida et al. 2019). Crocodylians and turtles actively suck air into their nose in an

olfactory behaviour called ‘gular pumping’, although crocodylians do not exhibit this behaviour underwater like turtles do (Weldon and Ferguson 1993; Schwenk 2008). Sea turtles can also discriminate airborne chemicals associated with land and may use smell to aid foraging and navigation (Endres and Lohmann 2013).

3.5.3 Vomeronasal System

The vomeronasal organ (VNO) is a chemoreceptive structure (also called Jacobson’s organ) located in the roof of the mouth at the base of the nasal septum in many terrestrial vertebrates (Fig. 3.8) (Halpern 1987). Among reptiles, the VNO is functional in turtles, tuatara, lizards, and snakes, whilst being absent (vestigial) in post-embryonic crocodylians and reduced in some lizards (Burghardt 1970). The VNO is best developed in lizards and snakes, where it is separated from the nose by an extension of the palate. The VNO contains cell bodies of sensory neurons representing receptors that largely detect specific organic compounds that are conveyed to them from the environment. Vomeroolfaction is closely linked with olfaction and is activated by tongue-flicking for chemoreception of chemical cues produced by predators, prey, or sexual pheromones from potential mates. The sense is presumed to be lost in crocodylians, but detection of pheromones is still possible through olfaction (Schwenk 2008). In turtles, a vomeronasal epithelium is located inside the nasal cavity that can detect volatile and non-volatile chemicals in the air or water; however, there is not a clear consensus concerning the exact nature of the VNO, or its homologue, in Testudines (Burghardt 1970; Parsons 1970; Schwenk 2008). In squamates, vomeroolfaction is generally well developed and may be the predominant sense underlying many behaviours, especially chemical communication within and among species. Sensory deprivation and other studies indicate generally that tongue-flicking is positively associated with use of VNO chemoreception in various behaviours of amphisbaenians, lizards, and snakes (e.g. Burghardt 1970; Graves and Halpern 1990; Schwenk 1995). Tuatara do not tongue-flick, but likely use the VNO whilst foraging (Besson et al. 2009).

Squamates have paired VNO located in the roof of the mouth and at the base of the nasal cavity (Fig. 3.7). Uniquely among tetrapods, the VNO is completely separated from the nasal cavity, opening only into the mouth through narrow ducts (Schwenk 1993). Each VNO contains an innervated sensory epithelium that receives chemicals via a duct that opens into the mouth. Odours are collected by protruding, oscillating, and then retracting the tongue in a behaviour collectively known as ‘tongue-flicking’ (Filoramo and Schwenk 2009). Tongue-flicking is important for detecting and discriminating between different types of prey and is more frequent in species that are active foragers (as compared with opportunistic ambush predators) (Cooper 1997). Amphisbaenians have limited eyesight, but use tongue-flicking and the VNO to discriminate between live prey and predators, mate recognition, and choosing appropriate soil for burrowing (López and Salvador 1994; López and Martín 2001). Tongue flick-attack scores in response to cotton swabs wetted with test solutions have been used to investigate prey preferences and to document geographic variation of ingestively naïve snakes (Burghardt 1970, 1993).

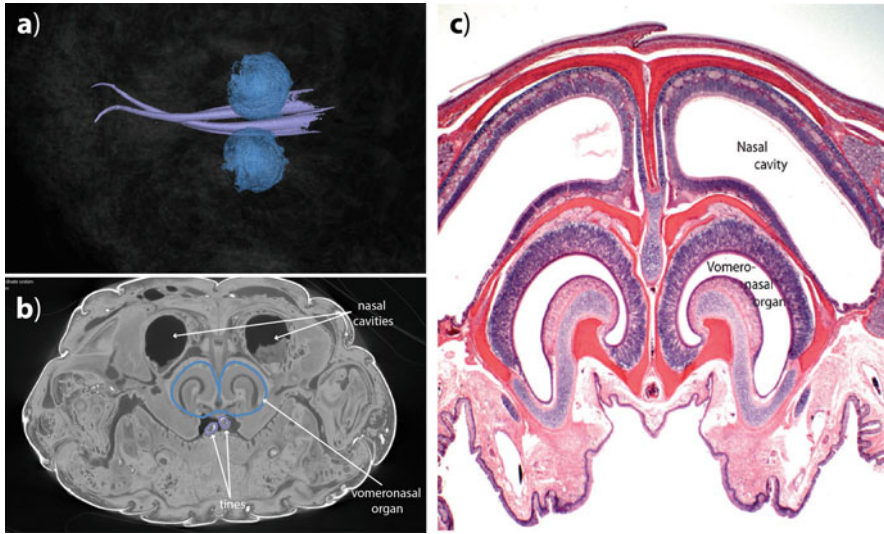


Fig. 3.7 Chemosensory systems in snakes. (a) Dorsal view of 3D segmentation of the vomeronasal system and (b) transverse slice of a CT scan showing the paired vomeronasal organs, tongue tines and nares in the olive sea snake (*Aipysurus laevis*). (c) Transverse histological section showing sensory epithelium in the vomeronasal organs and nasal cavities of a corn snake (*Pantherophis guttatus*). Photo credit: sea snake segmentation, J. M. Crowe-Riddell; corn snake, E. Jacobson

The distinctive bifurcated or ‘forked’ tongues of snakes and some lizards (e.g., varanids, teids) is an adaptation to collect odorants and determine in which direction a chemical signal is stronger (Schwenk 1994). The anatomy of the forked tongue is such that the tongue tips (tines) can be separated widely during tongue-flicking and thus simultaneously sample differences in odorant strength at two points (Schwenk 1994) (Fig. 3.7b). Similar to how hearing works in the ear (see above), the two sources of stimuli can be compared to deduce the direction of the odour source or ‘stereo-olfaction’ (Schwenk 1995; Filoramo and Schwenk 2009), which is most useful in following scent trails left by prey and potential mates. The sensitivity of the vomeronasal sense is exemplified in Komodo dragons (*Varanus komodoensis*) that can track the odour trails of injured prey over several kilometres (Auffenberg 1981). In addition to finding prey and mates, vomerolfaction plays an important role in detecting predators (Miller and Gutzke 1999; Amo et al. 2004).

Studies of rattlesnakes illustrate the use of VNO in chemosensory searching during predatory episodes (Chiszar and Scudder 1980). Detailed studies of predatory behaviours of rattlesnakes, as well as early research with European vipers (*Vipera berus*), indicate that tongue-flicking occurs with greater frequency and precision if a snake has first struck a rodent than if it has not. Indeed, striking prey appears to activate chemosensory searching and chemical input to the VNO. Studies suggest that envenomation alters chemical aspects of the prey, especially in the oral and nasal tissues, and these changes in stimuli are detected by a snake (Chiszar and Scudder 1980; Kardong and Smith 2002). This feature of strike-induced chemosensory

behaviour may also be involved with the well-known inclination of snakes to swallow prey headfirst (Ashton 2002; Mori 2006), as well as the tendency of rattlesnakes to fail at striking a second live mouse. It is very probable that other squamate reptiles exhibit similar strike-induced chemosensory searching behaviours involving increased tongue-flicking and use of VNO, even in naïve animals at birth or hatching (e.g., Burghardt and Chmura 1993; see also Ford and Burghardt 1993).

Changes in rate of tongue-flicks correspond with associated neural activity in the accessory olfactory bulb, with neural firing following retraction of the tongue and activity in the tongue retractor muscle (Meredith and Burghardt 1978). How a given behaviour is mediated by VNO chemoreception is not always entirely clear (however, see Graves and Halpern 1990). Indeed, the tongue itself is likely to mediate chemoreceptive sense (see Lillywhite 2014). There are at least six hypotheses related to transfer of chemical stimuli from tongue to sensory epithelium of the VNO (Young 1993). One of the most commonly cited mechanisms is direct insertion of the tongue tips into the openings of the VNO in the palate (Broman 1920). However, morphological and X-ray cinematography data refute this scenario (Young 1990; Oelofsen and Van den Heever 1979; Filoramo and Schwenk 2009). Most authors agree that the transfer involves suction of odorant molecules through the duct and into the lumen of the VNO, generated by pressure from the tongue and perhaps the anterior lingual processes (Broman 1920; Young 1993). The anterior processes are directly aligned with the VNO in the roof of the mouth and are elevated following tongue retraction. The ventral surfaces of the tongue make contact with these processes on each retraction. Hence, it was proposed that the anterior lingual processes provide the vehicle for transfer of stimuli to the VNO during chemoreception by snakes (Gillingham and Clark 1981). However, Filoramo and Schwenk (2009) showed that this explanation could not account for chemical transfer in squamates other than snakes. They showed that it is much more likely that transfer occurs when the retracted tongue is compressed within the mouth and chemical-laden salivary fluid is transported hydraulically from the tongue tips to the VNO.

Sensory input from the VNO to the brain is integrated with inputs related to olfactory, visual, and infrared receptor systems. However, when the brain is deprived of vomeronasal input, strike performance and trailing behaviour following a strike are both diminished. Hence, chemosensory information from the VNO appears to be very important with respect to multimodal sensory systems related to complex behaviours involved with foraging and procurement of prey (see further discussion in Lillywhite 2014). Although there is no consensus for generalisation among squamate reptiles, chemosensory information from the VNO may be important for multiple and complex behaviours (at least in squamates) including exploration, foraging and detection of prey, trailing of struck prey, feeding, detection of pheromones and mating, detection of predators, thermoregulation, and drinking (see Burghardt 1970, 1980; Graves and Halpern 1990; Halpern 1992; Ford and Burghardt 1993; Schwenk 1995; Lillywhite 2014).

3.5.4 Chemical Communication

Reptiles have incredibly sophisticated chemosensory (olfaction and vomerolfaction) capabilities and almost all species engage in chemical communication. However, chemical communication has been largely overlooked in behavioural research, potentially because chemical detection is a relatively impoverished sense in humans (Doody et al. 2013). Reptiles produce pheromones via the epidermis and specialised glands in the skin and elsewhere, and each individual likely produces its own personal ‘lexicon’ of chemicals that other reptiles can use to recognise and assess each other (Aragón et al. 2001; Shine et al. 2003a). Thus, chemical communication is at the centre of many reptilian social behaviours (reviewed in detail in Mason and Parker 2010; see also Gillingham and Clark 2023).

Reptiles can produce and deposit odorants into their environment in multiple ways. Crocodylians have a paired paracloacal gland—used in territorial behaviour, especially during the breeding season—and paired gular glands that are rubbed against females during courtship and mating. Turtles (except tortoises) have specialised Rathke’s glands that connect to pores on the outer edge of their shell (Weldon et al. 2008). In some species, the Rathke’s gland fluids can be sprayed when handled by humans and are likely to play a defensive role (Mason and Parker 2010). Many turtles also have a complex array of mental glands on the chin and throat. These mental glands are often enlarged in male tortoises (e.g. *Gopherus* spp.) and their secretions are linked to territorial behaviour during the mating season (Rose et al. 1969; Alberts et al. 1994). Tuatara have a paired gland, opening on both sides of the cloaca, and thought to secrete pheromones. Many turtles have specialised glands on their chins that begin producing pheromones at sexual maturity. These chin glands are larger in males and swell during the mating season (Winokur and Legler 1975). Gland secretions are also involved in inter- and intra-specific recognition. For example, secretions from non-native red-eared sliders (*Trachemys scripta*) can be detected by native Spanish terrapins (*Mauremys leprosa*) in the same habitat (Polo-Cavia et al. 2009).

Snakes have scent glands with two ducts exiting the vent that emit malodorous secretions to deter predators when they feel threatened. Snakes also secrete chemicals via their skin for intraspecific communication. Tongue-flicking directly on female skin lipids is a vital cue to initiate courtship and mating behaviours in snakes, including the turtle-headed sea snake (*Emydocephalus annulatus*) (Shine 2005). Chemical communication has been well studied in mating aggregations of common garter snakes (*Thamnophis sirtalis*) in Manitoba, Canada. After emergence from wintering dens, male garter snakes can precisely track females using the pheromone trail left by females during the mating season (Shine et al. 2003b; Mason and Parker 2010). These snakes can also chemically assess the body size and mating condition of potential mates (Shine et al. 2003a, 2004). Some male garter snakes can even mimic the scent of a female to attract males, which may increase their body temperature or distract male competitors (Shine et al. 2000). Trailing behaviour has also been observed in neonates of rattlesnakes (*Crotalus* spp.) and pine snakes (*Pituophis melanoleucus*), which appear to follow scents and discarded

skin sheds of adults to find wintering dens (Burger 1989; Brown and MacLean 1983).

Chemical communication in lizards and amphisbaenians is primarily through follicular epidermal glands (Fig. 3.8). Many lizards also exude secretions from the cloaca via the urodaeal gland. The follicular epidermal glands are located near the

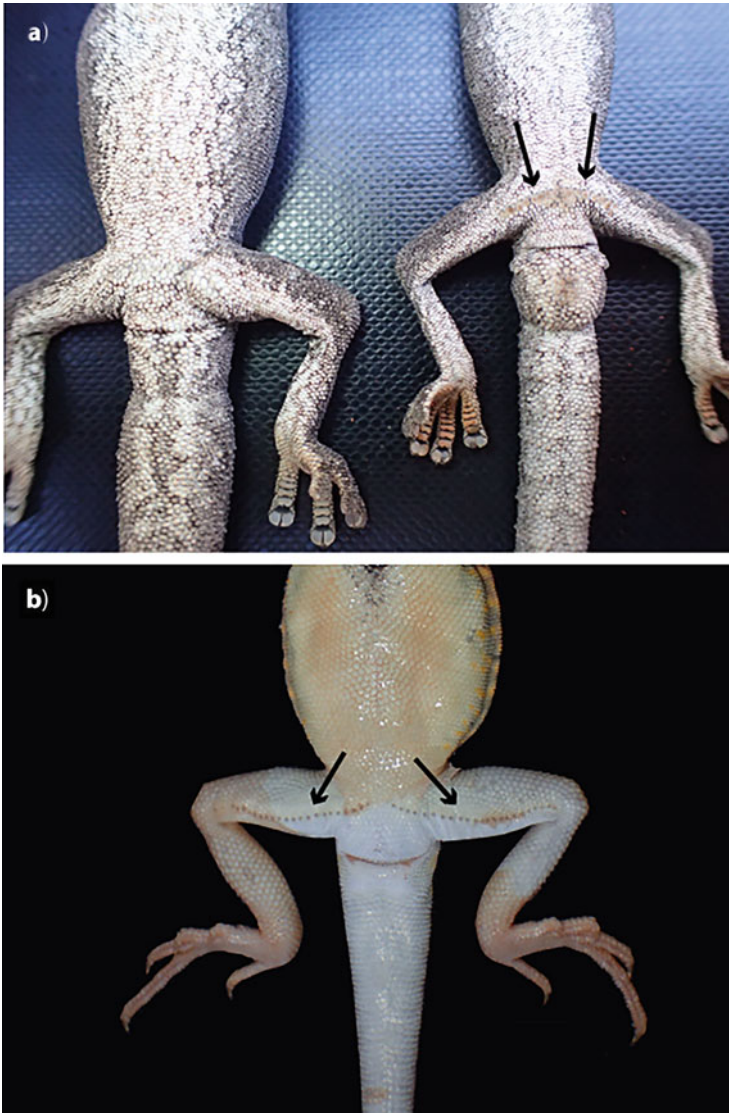


Fig. 3.8 Chemosensory glands in lizards. (a) Sexual dimorphism in a western spiny-tailed gecko (*Strophurus strophurus*) and (b) a male claypan dragon (*Ctenophorus salinarum*). Femoral pores are indicated by arrows. Image credit: M. Hutchinson

vent (precloacal) and thighs (femoral) and secrete a waxy substance of proteins and lipids (reviewed in Mayerl et al. 2015). Follicular epidermal glands are estimated to be present in a quarter of all lizard species. The groups with the highest proportions of glands are lacertids (97%), gekkonids (35%) and iguanids (27%), and lower proportions are found in dibamids (14%) and scincids (1%), and none are recorded in anguimorphans (García-Roa et al. 2017). These glands are often larger and more complex in males. Because temperature and humidity can degrade chemicals, lizards from different habitats secrete different chemicals that will linger for longer in their environment (Baeckens et al. 2018). For example, lacertids from dry 'xeric' habitats tend to have a higher proportion of fatty acids and high weight alcohols, whilst species from wet 'mesic' habitats secrete more aldehydes and low weight alcohols (Baeckens et al. 2018). Many lizards use chemical cues to recognise and assess nearby conspecifics. For example, experiments with captive wall lizards (*Podarcis* spp.) found that males can detect when gland secretions of closely-related lizard species were present (Barbosa et al. 2006). Similarly, studies on Iberian rock lizards (*Lacerta monticola*) found that males can distinguish the chemical signatures of familiar and unfamiliar males from neighbouring populations (Aragón et al. 2001). Thus, chemical signals have a huge impact on captive reptiles and these 'invisible' signals should be considered when assessing animal behaviour (Weldon et al. 1994).

3.6 Thermoreception

Thermal radiation refers to the wavelengths of the electromagnetic field that cannot be detected by photoreceptors in the eye, attributable to the heat of an object and generally in the long-wave infrared (IR) part of the electromagnetic spectrum. Reptiles respond to thermal gradients on the skin and display thermoregulatory behaviour (e.g. basking) likely by using heat-activated proteins in the peripheral nerve endings distributed throughout the skin (Seebacher and Franklin 2005; Gracheva and Bagriantsev 2015). The most well-studied thermoreceptors in reptiles are the specialised pit organs of snakes, which probably evolved for thermoregulation and have become co-opted for specialised detection of prey (Krochmal and Bakken 2003; Seebacher and Franklin 2005).

3.6.1 Heat-Sensing Pits in Snakes

Infrared reception with a distinctive pit organ anatomy has evolved in three distantly related groups of snakes: pit vipers (Crotalinae), pythons (Pythonidae), and boas (Boidae). Pit vipers have a pair of facial pits between the nostril and eye that are angled forward. A membrane is suspended inside the pit and forms an inner chamber at the bottom of the recess (Fig. 3.9). Pythons and boas tend to have relatively smaller and more numerous pits arranged in a row along the upper (and sometimes lower) labial scale rows. In pythons, labial pits are formed by an invagination in the scale, whereas pits in boas (when present) are formed by invaginations between the

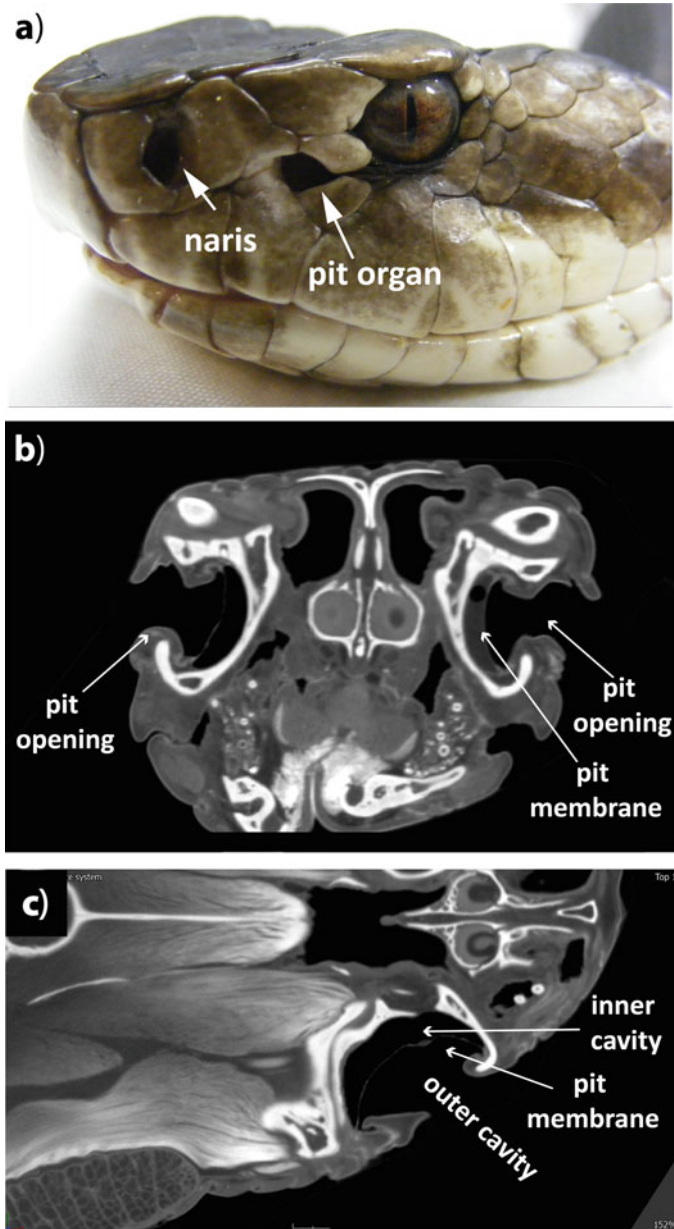


Fig. 3.9 Heat sensitive pit organs in pit vipers. **(a)** Cottonmouth head showing the location of the loreal pit organ and naris. **(b)** Transverse and **(c)** frontal slices from a CT scan of an Amazonian palm viper (*Bothrops bilineatus*) showing the pit organs and pit membrane suspended within the hollow cavity. Photo credit: Amazonian palm viper, University of Michigan Museum of Zoology (UMMZ-245084); cottonmouth (*Agkistrodon conanti*), H. Lillywhite

scales (Goris 2011). In boas and pythons, a membrane closely lines the inner surfaces of the pit and contains nerve masses and capillaries (Newman and Hartline 1982). In addition to the heat-sensitive membrane, the inner skin of the pit organs contains arrays of ‘micro-pits’ (0.5–2 μm in diameter) with complex nanostructures (Amemiya et al. 1995). The spacing of these micro-pit arrays and complexity of their nanostructures suggest that they selectively absorb photons in ambient light, which enhances detection of IR by the pit organs and protects them from ultraviolet radiation (Amemiya et al. 1996).

The membrane of pit organs can detect IR radiation between 700 nm and 1000 nm and the thermoreceptors are activated by temperatures greater than approximately 28 °C (Gracheva et al. 2010). Pit organs are more sensitive than the labial pits of boas and pythons, and they can detect minute temperature changes of 0.001 °C (Gracheva and Bagriantsev 2015), allowing even blinded individuals to target and strike prey accurately (Newman and Hartline 1982; Kardong and Mackessy 1991). The pit membrane contains a dense network of capillaries and large nerve masses (Newman and Hartline 1982; Amemiya et al. 1996), which are directly sensitive to heat and connect to the fifth cranial nerve (the trigeminal). The unique anatomy of the trigeminal nerve in snakes with pit organs integrates with the visual system somatotopically within the optic tectum, suggesting that pit vipers see a thermal image superimposed on a visual image (Hartline et al. 1978; Newman and Hartline 1981).

The blood vessels within the pit membrane carry IR heated blood away and thus serve as a cooling system that maintains the sensitivity of the pit organ (Cadena et al. 2013). The pit opening and distribution of sensory cells inside the membrane gives a field of view (approx. 100° in pit vipers) that creates a ‘heat image’ of potential prey (Goris 2011). Some authors have suggested that the evolution of pit organs has reduced the need for using vision whilst searching for prey, but many pit vipers still have a well-developed visual system (Liu et al. 2016; Gower et al. 2019). Therefore, it is more likely that those snakes with IR detection use this thermal information when visual input is limited (e.g. dark nights or burrows) and use both signals—light and heat—to improve targeting accuracy in other foraging scenarios (Cock Buning 1983; Grace et al. 2001; Goris 2011).

3.7 Magnetoreception

Magnetoreception is the enigmatic sense that allows animals to detect the Earth’s magnetic field. Although the mechanism, receptors, and anatomy for magnetoreception are unknown, many animals—including whales, migratory birds, and sea turtles—have been experimentally shown to use the Earth’s magnetic field to migrate over vast distances (Hofmann and Wilkens 2008; Nordmann et al. 2017). The magneto-sense of sea turtles was first discovered in experiments that showed hatchlings orientated towards the water post-hatching and could navigate to feeding grounds beyond the shoreline. Experimenters created a miniature magnetic field using a faraday cage and exposed captive hatchlings to different magnetic

conditions that mimicked the field of natural navigation paths (Lohmann and Lohmann 1996). The sea turtles changed their direction of swimming in response to the simulated fields, corresponding to the direction of currents in that part of the Atlantic Ocean. Hatchling turtles use the unique inclination and strength of their natal beach magnetic field to create a mental ‘image’, which can be used to distinguish their nesting site upon return in adulthood (Lohmann and Lohmann 1998; Lohmann 2007). Further research confirmed that both hatchlings and adult sea turtles use a combination of ‘compass sense’ whilst traversing the ocean and local ‘magnetic signature’ for positional information (Hofmann and Wilkens 2008). Box turtles (*Terrapene carolina*) are also thought to use a magneto-sense for compass orientation in combination with circadian and light cues (Mathis and Moore 1988). There is a strong link between magnetoreception and vision (both polarised and ultraviolet photoreception) in migratory birds, but it is unclear whether turtles use the same system (Wiltchko and Wiltchko 2006; Meyer-Rochow 2014). Finally, other reptiles such as crocodiles navigate and display ‘homing’ behaviours, which may involve magnetoreception (Rodda 1984; Meyer-Rochow 2014).

3.8 Animal Welfare Considerations

In this chapter, we hope we have conveyed an appreciation for the diversity of reptilian senses and how these might be integrated to elicit fundamental behaviours including thermoregulation, foraging, navigation, and communication. We also hope that the reader has gained an appreciation for how we, as humans, are limited by our own sensory capacity and perceptions to truly ‘know’ how another animal perceives its world. This is especially true for signals that are essentially invisible to humans such as UV colouration and pheromones.

Furthermore, the sheer diversity in sensory systems (Table 3.1) and lack of representative studies among some reptilian groups limit our understanding of how senses are integrated to influence reptilian behaviour (Burghardt 2013). However, we can make best possible decisions considering the knowledge at hand. For example, it is important to consider how one might set up an environment for a chameleon that is highly visually oriented compared to a terrestrial snake that is more chemically or heat oriented. Consider how different stimuli—light, sound, heat or odors—might make a captive animal feel threatened or stressed.

Understanding of the primary sensory capabilities of the captive reptile may also inform the type of enclosure or enrichment that should be provided (Burghardt 2013). Different sensory cues are important for stimulating appropriate behaviours in captivity, e.g. chemical cues in food are often needed for recognising prey and initiating feeding (Weldon et al. 1994). Additionally, if the captive reptile is displaying erratic or unusual behaviour, it is important to take note of potential sensory stimuli that might evoke responses, although undetectable to us (Warwick et al. 2013). Note that we are able to exercise some level of control over our own sensations, whilst this may not be the case for captive reptiles. Animals might require some capacity to make choices in seeking or avoiding sensory inputs, and we should

consider that some reptiles might have impoverished or heightened sensory abilities. Further comments that are relevant to these contexts can be found in Gillingham and Clark (2023), Lillywhite (2023), Mancera and Phillips (2023), and Warwick (2023).

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Abstract

The concept of stress is notoriously difficult to define, despite its ubiquity in both common parlance and the scientific literature. Given the clear importance of understanding how organisms deal with challenging environments in both natural and husbandry contexts, examining the relationships between internal and external stressors and the stress response is essential to working with both captive and wild animals of any species of any class. In this chapter, we outline historical and contemporary concepts of stress, with an emphasis on how these ideas can inform our approaches to caring for reptiles in captive contexts and decision-making in a management context. We include a description of the physiological stress response systems, with examples of studies that have improved our understandings of the mechanisms and indicators of the stress response in reptiles. Furthermore, we demonstrate how the stress response is manifest in other aspects of organismal function, including behaviour, social interactions, reproduction, and immunity. Identifying bioindicators of stress and how best to mitigate or manage them is central to good husbandry practice.

Given the influence of the stress response at every level of organisation, good husbandry must also be regarded as essential to good research. It should also be clear that, within limits, the stress response is a normal aspect of the functioning of healthy individuals and that clinically conspicuous pathology emerges only when stressors are repeated, sustained, or extreme. Finally, we describe new

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findings and new directions that may provide useful data and techniques to facilitate the identification of stressors and the mitigation of negative effects. Throughout this chapter, we emphasise the need to examine stress in reptiles from a reptilian point of view, adopting an ethological approach to see the world from the organisms' perspective. Of course, we will never know what it is like to be a reptile. Given the vastly different physiological needs and sensory systems of reptiles compared to humans, and the great variation among reptilian taxa, our best approximation of the reptile's experience necessitates the use of data-driven decisions based on empirical research. To inform a continuing improvement of captive reptile care, we summarise recent work on the theoretical understanding of stress and the application of that understanding in practice.

Keywords

Adaptive scope · Allostasis · Behaviour · Captive care · Catecholamines · Glucocorticoids · Homeostasis · Hypothalamic–pituitary–adrenal axis · Physiology · Reptile · Stress · Stress response · Sympathetic adrenomedullary axis · Welfare

4.1 Introduction

Stress is a protean concept representing the response of an organism to challenges evoked by real or perceived threats to meeting its biological needs, most conspicuously (but not only) attributable to changes in the environment. The phenomena that trigger these variable responses and a possible cascade of subsequent related coping mechanisms differ across levels of organisation, from cells to societies, but always occur when the normalised *adaptive scope*—tolerance to change—is exceeded (Greenberg 2002). The most urgent, but by no means the only, challenge with which organisms must cope is maintaining homeostasis (e.g. Tokarz and Summers 2011). Although compromised homeostasis constitutes an existential threat, lesser challenges often go unnoted even when they play important roles in an organism's life history or invoke relatively modest or subclinical stress responses—often a consequence of cumulative 'microstressors' (MacLean 1976). Whilst all organisms continually respond to their environments, the time scale, level of response, and flexibility of response in different systems and between individuals can vary. These responses will be shaped according to the organism in question and its previous experience, as well as the magnitude of the environmental change, the strength of the signal received by the organism, internal constraints on response, and biological limitations. These constraints all have their roots in ancestral adaptive contexts, and are also affected by development across an individual animal's lifetime. The scope and form of the stress response emerge as a result of environmental factors or the internal configuration of an organism, for example, linked physiological pathways or genetically co-determined traits. Thus, the seemingly simple question of defining when a response to an environment becomes 'stressful' has been long debated. This

problem is somewhat mitigated by conceptualising the cascade of effects through different levels of organisation within the body, each of which has more-or-less ability to cope with the stressor before passing it to another level if necessary. This tolerance for stress is *adaptive scope* and it varies at each level of organisation and depends on continuing, as well as past, experiences such as acclimation (Greenberg et al. 2002).

An additional problem for thinking about stress in reptiles is inherent in our reliance on theoretical and empirical work that emerges from an intuitive extrapolation from our understanding of human or mammalian responses. Such anthropocentric (or mammalocentric) thinking, whilst at the root of misleading biases, can nevertheless provide a launching point for our understanding of stress in reptiles. Required is an ‘ethological attitude’ (Burghardt 1977; Greenberg et al. 2002) emphasising the awareness and eschewal of implicit bias, the most obvious of which is anthropocentrism, but a profound challenge to objectivity in a multitude of less obvious habits of thinking (Greenberg 2023, Table 4.1). Very often, the environmental needs and the conditions that cause stress for reptiles are quite dissimilar to those of mammals and can easily lead to erroneous assumptions. Whilst the need to account for the physiological and sensory systems of the organism in question may seem obvious, the intrinsic biases created by our human experiences of the world make the application of this perspective challenging. This is often evident in our conceptualisation of stress in reptiles. An additional challenge to speaking across disciplines and taxa is the diverse and often conflicting terminology (e.g. Calabrese et al. 2007).

Some personal examples will help illustrate how bias, assumptions, and over-generalisations about the causes and consequences of physiological stress response may influence decision-making regarding husbandry in reptiles. As Gangloff conducted PhD research on garter snake physiology and behaviour, he often interacted with the Institutional Animal Care and Use Committee to justify how the treatment of snakes was humane under conditions unthinkable for a mammal. For example, hibernation in the dark at a few degrees above freezing without food for several months as manifested in some species each winter (e.g. Holden et al. 2021) was anathema to anyone whose paradigm for animal care was entirely mammalian. It was apparent that the committee members, whilst well-intentioned, could not perceive of animal needs so unlike the mammals with which they were most familiar. For example, hibernation (seasonal torpor, brumation) in reptiles [exemplified by the bearded dragon, *Pogona vitticeps*, described by Capraro et al. (2019)] involves distinctive adaptive strategies at multiple levels of gene expression and activation not observed in other hibernators. As a result, mammalocentric committees asked for revisions in procedure that would in fact be detrimental—for example, to ‘wake them up’ daily whilst in hibernation to verify that they were in good health. In working with green anoles, Greenberg was relentlessly urged by the relevant university animal care and use committee to abandon procedures well-tolerated by small lizards in practice (Greenberg 1992) in favour of protocols well-known to small mammal researchers, but which proved harmful to the small reptiles used in this research. Issues such as these have prompted spirited discussion amongst

Table 4.1 Paradigms for understanding and defining stress

Name	Major tenets of framework	Key References
Adaptive scope	<ul style="list-style-type: none"> • At each level of organisation (cell, tissue, organ, organism) the dynamics of stress tolerance and response are different • An incomplete resolution of stress at one level will evoke a response at the next level in a hierarchical manner that effectively conserves resources 	Greenberg et al. (2002)
Allostasis	<ul style="list-style-type: none"> • Extends concept of homeostasis to be more dynamic • Focuses on maintenance of stability through change via physiological adjustments • Primary currency is energetics • ‘Emergency life history stage’ occurs when perturbations push organisms to prioritise immediate survival over other functions 	Wingfield et al. (1998) Wingfield and Kitaysky (2002) Korte et al. (2005) McEwen and Wingfield (2003) McEwen and Wingfield (2010) Sterling and Eyer (1988)
Reactive scope model	<ul style="list-style-type: none"> • Extension of allostasis model • Mediators of stress response follow predictable cycles (predictive homeostasis) and unpredictable events (reactive homeostasis) • Homeostatic overload occurs when levels exceed reactive scope too often or too long (homeostatic overload) • Levels can also fall too low to accomplish their goals (homeostatic failure) • Focus is primarily on physiological mediators (e.g. glucocorticoid hormones) 	Romero et al. (2009) Romero (2012)
Damage-fitness hypothesis	<ul style="list-style-type: none"> • Describes relationship between damage and anti-damage regulators • Explicitly addresses the trade-off in mounting a stress response to minimise damage from external stressors and the potential for anti-damage regulators to cause physiological dysfunction themselves • Explains why variation in anti-damage regulators at cellular or organismal levels may not correlate with fitness effects of stressors 	Wada and Heidinger (2019) Wada (2019)
Adaptive calibration model	<ul style="list-style-type: none"> • Extends models of allostasis with the addition that repeated, chronic stress carries important information—this information is integrated into development • Explicitly addresses stress responses in evolutionary life-history developmental framework • Explains among-individual differences in stress response • Describes non-linear relationship between magnitude of stressors and stress response 	Del Giudice et al. (2011, 2013) Ellis and Del Giudice (2014)
Control systems definition	<ul style="list-style-type: none"> • Can be applied across levels of biological complexity (including plants and organisms lacking nervous systems) • Stress response relies on feedback and feedforward control 	Del Giudice et al. (2018)

herpetologists (Langkilde and Shine 2006; Lillywhite et al. 2017). Even so, confidence in particular husbandry, housing, and experimental procedures can be extended to less familiar species only by inference. Such inference is not always correct. These examples illustrate that it is essential to our understanding of stress in reptiles that we keep in check our taxonomic biases and understand the limits of our inferences.

4.2 Defining Stressors, Stress, and the Stress Response

Stress describes an organismal state in which individuals cope with real or perceived threats to real or perceived biological needs (Greenberg et al. 2002). Such a state can be induced by a variety of stressors, including external environmental factors, internal perturbations, or cognitive processes. Importantly, it is the organism's perception and response that define a stressor, not necessarily any intrinsic quality of the factors inducing the response (DeNardo 2006). Timing can be crucial: organisms are constantly making adjustments in response to environmental change—this is the basis of acclimation and predictable (e.g. daily, seasonal) cyclical change. However, when changes occur so quickly that they require resources that cannot be easily mobilised, we can view the stimulus as acute, unpredictable, or uncontrollable. Such stimuli can evoke different patterns of response at more complex levels of organisation (Koolhaas et al. 2011; Del Giudice et al. 2018). Unpredictability precludes an adaptive anticipatory response. Loss of control occurs when response demands exceed the capacity of the organism and are characterised by a delayed recovery of a 'typical' physiological and neurological profile (Koolhaas et al. 2011).

There is no universal prescription for dealing with stress generally nor in reptiles specifically, given the diverse and dynamic environments that they inhabit, their varied and flexible physiologies and life histories, and apparent resilience to certain stressors (Huey 1982; Busch and Hayward 2009; Dickens and Romero 2013). Studies of stress generally focus on the relationship between the magnitude of the stressor and the stress response variables that can be quantified by a number of factors or proxies which we discuss below. As we consider these concepts, it is important to recognise that certain responses are not necessarily pathological; rather, integrated responses to environmental challenges are generally adaptive in healthy individuals (Selye 1976; Korte et al. 2005; DeNardo 2006; Romero et al. 2015). Thus, we can apply some general frameworks to our understanding of stress in reptiles in a captive context although the individual thresholds for risk assessment and (clinical) intervention will vary on a case-by-case basis.

In an adaptive short-term context, the stress response will often prioritise immediate survival needs over long-term investments in fitness such as energy storage or reproduction. However, when prolonged, such a stress response may bear negative consequences. Interestingly, work in mammals demonstrates that mild stressors can energise responsiveness up to a point at which increasing stress diminishes the response. This pattern defines the famous inverted U-shaped curve of the Yerkes–

Dodson principle (Yerkes and Dodson 1908), in this case, graphically representing the behavioural consequences (vertical ordinate, y-axis; Fig. 4.1) to stressors of increasing intensity (horizontal abscissa, x-axis). This sometimes counter-intuitive non-linear relationship is often observed across a spectrum of stressor and stress responses and complicates interpretation of stress biomarkers, potentially misleading protocols for intervention. Whilst simple in its essence, it provides the scaffold for more complex processes and has thus been relevant in various disciplines where it is known by different terms (stress-response curve, adaptive response, hormesis), despite efforts to reconcile troubling semantic differences (Calabrese 2008).

Several paradigms are useful in understanding when and how a reaction to the extrinsic or intrinsic environment becomes a stress response (see Table 4.1). We first recognise that much of this work builds on early models to understand the importance of homeostasis. This was described as the maintenance of stability in the *milieu interior* by Claude Bernard in the nineteenth century (Bernard 1879; Holmes 1986). These ideas were subsequently developed by Walter Cannon, who coined the term ‘homeostasis’, described a ‘fight or flight’ response, and recognised psychological as well as physical trauma (Cannon 1932). Others then offered early descriptions of stress syndromes, notably Hans Selye (1976) who made the important point that a life without stress is not a life and that it is stress in excess that is damaging to health, echoing the Yerkes–Dodson principle described above. Currently, commonly referenced models of stress in the reptile literature are the ‘allostasis’ model (Sterling and Eyer 1988; McEwen and Wingfield 2003, 2010; Korte et al. 2005) and its extension to the ‘reactive scope’ model (Romero et al. 2009). These models build

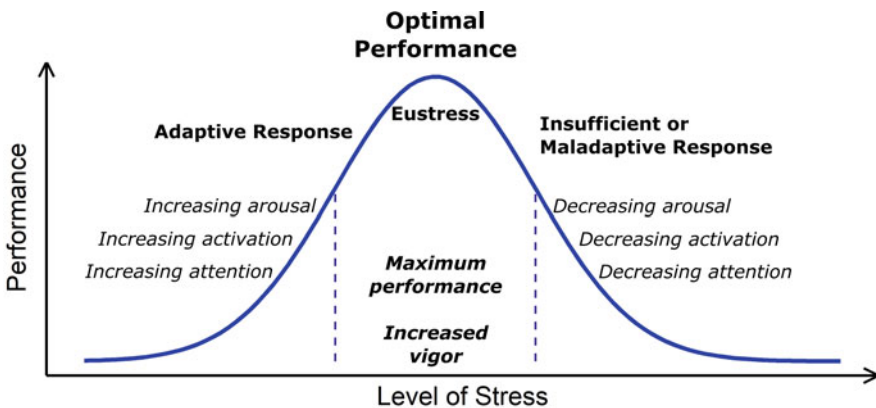


Fig. 4.1 An idealised inverted U-shaped curve illustrating the Yerkes–Dodson principle (Yerkes and Dodson 1908), representing the behavioural consequences (vertical ordinate, y-axis) to stressors of increasing intensity (horizontal abscissa, x-axis). This sometimes counter-intuitive non-linear relationship is often observed across a spectrum of stressor and stress responses and complicates interpretation of stress biomarkers, potentially misleading protocols for intervention. This concept has been relevant in various disciplines and thus is known by different terms (stress-response curve, adaptive response, hormesis), despite efforts to reconcile troubling semantic differences (Calabrese 2008)

from previous work in the biomedical field, integrating an understanding of physiological systems with ideas of environmental perturbation in a natural context (Romero 2004; Table 4.1). Both the allostasis and reactive scope models similarly describe how organismal needs may exceed ‘adaptive scope’—the range of tolerance for stress at a particular level of organisation before higher levels are triggered to help cope (Greenberg et al. 2002). This shift of coping mechanisms from lower to higher levels of organisation will ideally mitigate unpredicted or unexpectedly large perturbations, either physically experienced or perceived. Earlier models described adaptive physiological and behavioural aspects of a shift in level as an ‘emergency life-history stage’ necessitated by immediate concerns evoked by ‘labile perturbation factors’ (Wingfield et al. 1998; Wingfield and Kitaysky 2002). Such a response is optimally beneficial in maintaining short-term survival and functionality but will be detrimental to organismal health and fitness if long sustained. Just how long is too long will depend on the nature of the stressor, the internal and external contexts in which the organism is functioning, and the magnitude of the response.

The concept of allostasis describes how levels of control variables (e.g. hormones, parasympathetic activity) change in ways that maintain stable levels of less flexible internal variables (e.g. blood pH, oxygen supply). The allostasis concept utilises energy balance (demands *versus* availability) as the metric of deviation from a functional range whilst reactive scope models focus primarily on levels of physiological mediators (e.g. glucocorticoid hormones). In this context, the ‘adaptive scope’, as mentioned above (Greenberg 2002; see also Table 4.1), refers to tolerance for change at one level of organisation (such as increased metabolism or a peripheral vasomotor response) before additional higher-order coping mechanisms (such as behaviour) are evoked—the tolerance for stress before such a transition can vary significantly as animals acclimate during more gradual change (Greenberg 2002). The inherent trade-offs in mounting a stress response to mitigate the potential negative impacts of a stressor *versus* the potentially negative effects of the stress response itself are formalised in the Damage-Fitness Model put forth in recent work (Wada 2019; Wada and Heidinger 2019). Under this framework, damage to internal systems at the cellular, tissue, or organismal level can occur when either the stress response is insufficient to mitigate the external stressor or when the response molecules themselves become dysfunctional or excessive. When these responses are either exaggerated or prolonged they may themselves cause damage and impair organismal function. For example, this phenomenon occurs in the case of chronically elevated glucocorticoid levels (Sapolsky et al. 2000; Dantzer et al. 2014). To mitigate this response, anti-damage regulators operate across levels of biological organisation and may include heat-shock proteins, DNA repair mechanisms, inflammatory responses, catecholamines, or adrenocortical responses (Wada 2019).

Key to these models is that past experiences of stressors carry information that may predict future environments. In this sense, the experience of chronic or repeated stressors can be used by an organism to predict and prepare for future demands. The information theory aspect of the allostasis and reactive scope models is formalised in the Adaptive Calibration Model (ACM, Del Giudice et al. 2011, 2013). Whilst the original application was primarily to humans, this model provides a robust

framework for integrating stress responsivity and developmental plasticity. Specifically, this framework provides two important insights that build on earlier models and that may be applicable to reptiles, though little empirical data yet exist to test these ideas: (1) the ACM explains individual variation in stress perception and responsivity in an explicitly evolutionary context; and (2) this model describes a complex, non-linear relationship between external stressors and internal responsivity, another expression of the Yerkes–Dodson Law describing the relationship between stressor intensity and organismal response (Yerkes and Dodson 1908; Calabrese 2008). Such non-linear relationships may explain why there is an apparent lack of correlation between certain stress bioindicators (e.g. glucocorticoid hormone levels) and fitness (see below; Breuner et al. 2008; Bonier et al. 2009; Patterson et al. 2014; Schoenle et al. 2018). Under the ACM, individual differences in stress responsivity profiles result from previous experiences that ‘calibrate’ the stress response system to modify that individual’s physiological and life-history phenotype to better match its environment. For example, under conditions of both very low levels of external stressors and high levels of external stressors, a ‘responsive’ phenotype might be adaptive insofar as this facilitates an individual’s ability to take advantage of nurturing conditions in the first case and promotes defensiveness and self-preservation in the second case (a concept parallel to ‘coping styles’; Koolhaas et al. 1999; Korte et al. 2005). However, under intermediate levels of external stress, a less responsive phenotype may be advantageous. Indeed, the ecology and evolutionary significance of such individual variation in stress response is an active area of research (Øverli et al. 2007; Narayan et al. 2012; Cockrem 2013; Crespi et al. 2013; Dantzer et al. 2014; Wada 2015; Tanner and Dowd 2019). Importantly, the ACM framework emphasises that stress responses can be activated to cope with environmental perturbations of any valence (positive or negative); thus, such calibration reflects the functioning of a healthy individual in the context of life experiences, not pathology (Korte et al. 2005; DeNardo 2006; Romero et al. 2015).

More recently, Del Giudice et al. (2018) generalised the ACM in a way that can be applicable to an even broader range of organisms, including animals lacking a central nervous system and plants. This is the control systems paradigm, which categorises a stress response as the outcome of an inability to control a variable critical to fitness. The response to such a variable, which may be either internal or external to the organism, is reliant on either feedback (responsive) or feedforward (predictive) control. Thus, this paradigm serves nicely to generalise from the endocrine-focused models above and can be applied across a broader range of biological complexity (Del Giudice et al. 2018). It is important to note that the consequences of stress are manifest across scales of biological organisation and complexity, from subcellular responses to community-level consequences. Squamate reptiles (snakes and lizards) have been used as model species to describe how response to environmental stressors may impact populations and communities (Wake 2007; Sinervo et al. 2010; Diele-Viegas and Rocha 2018). Given the context of this book on reptiles in artificial or otherwise evolutionarily novel environments, we will intentionally focus on the stress response of organisms and biomarkers (physiological and behavioural) of the stress response as they pertain to the care

and welfare of animals in captivity (for example, in zoos and laboratories), and their continuity and prosperity in nature (Warwick 2023). In this way, we simultaneously honour their intrinsic value as fellow organisms and their place in a complex ecosystem, which we must avoid compromising in our own self-interest.

4.2.1 Stress Response Pathways

How individuals respond to stressors in natural environments is an active area of research, with implications for both the study of evolutionary processes (Palacios et al. 2012; Patterson et al. 2014; Cox et al. 2016; Dantzer et al. 2016; Vitousek et al. 2019a) and conservation (Wikelski and Cooke 2006; Busch and Hayward 2009; Angelier and Wingfield 2013; Baker et al. 2013; Cooke et al. 2014; Dantzer et al. 2014; McCormick and Romero 2017; Martin et al. 2018). Nevertheless, there is much uncertainty about how biomarkers can be used to assess the health status of individuals and, by extension, populations. Physiological biomarkers include several hormones, metabolites, or immune function parameters sampled from various body tissues or excretions; broad physiological indicators such as body mass or body condition (body mass scaled to size); or a variety of other proxies for physiological processes such as reactive oxygen species or telomere length. Additionally, quantifying changes in behaviours, especially those related to body maintenance, locomotion, searching, reproduction, feeding, or aggression, can serve as reliable stress indicators (Warwick et al. 2013; Martínez-Silvestre 2014; Gillingham and Clark 2023; Warwick 2023). Considering the great diversity of reptilian lifestyles, generalisations from one species to another about the interpretation of these biomarkers can distort our understanding and efforts to mitigate challenges to welfare. This diversity would obviously influence every area of conservation, husbandry, and captive care. This issue was pointed out for laboratory reptile surgery, in particular, by Alworth et al. (2011), who emphasised the need for informed flexibility in the implementation of familiar techniques in unfamiliar animals—another example of potentially pernicious implicit bias.

The life history of each species should be well understood before interventions are attempted. This approach is a central theme of ‘ethologically informed design’ (Greenberg 2023). Also, interpretation can be complex, as Greenberg (2002) pointed out: the orchestration of the stress response involves nested hierarchies and reciprocal interactions. Alternative coping strategies are invoked depending on what might be rapidly changing environmental challenges and circumstances, including immune challenge, aggression and social dominance, or courtship and mating. In addition, it is clear that many apparently specific effects of releasing factors and steroid hormones on behaviour are secondary to non-specific effects in the nervous system (see Summers and Winberg 2006). For example, among the consequences of social dominance in the green anole (*Anolis carolinensis*) is the suppression of behaviour of a subordinate in the presence of the dominant in ways that increase the likelihood of survival: subordinates have reduced testosterone and reproductive behaviour, select lower and less conspicuous perches, and increase

melanocyte-stimulating hormone (MSH) to invoke brown rather than green colour, presumably protecting them from further stressful interactions (Greenberg et al. 1995). Plavicki et al. (2004) observed that dominant anoles (*A. carolinensis*) exhibit a reduced stress response to non-social stressors (such as simulated predation) relative to subordinates. Interestingly, both dominant and subordinate males of this species exhibit elevated faecal corticosterone compared with solitary males (Hudson et al. 2019). In these cases, assessing the impacts of a stressor must take into account these complex pathways and social structures on organism physiology and behaviour.

An understanding of both baseline and stress-induced levels of biomarkers in wild populations is essential in applying these parameters as stress response indicators in captive animals. With such information, it is possible to utilise markers to characterise more precisely the magnitude, duration, and functional consequences in individual animals and to monitor the response to changes in their environment. Additionally, this information can be used to provide settings that are configured by the researcher to evoke selected daily or seasonal variations in biomarkers that comprise their natural life histories. For example, to maximise environmental validity, Greenberg (1978) simulated the natural habitat of the lizards studied until behavioural patterns in the lab matched reference patterns observed in the field. This approach went so far as to simulate dawn-to-dusk changes in the colour of light, as well as the more obvious variables of day length, temperature, humidity, and diverse types of prey. These laboratory conditions replicated the natural habitat (e.g. Jenssen et al. 1995) to the extent possible and evoked behavioural biomarkers comparable to those seen in nature as indexed with a detailed ethogram (as in Greenberg 1977). This environmental context matters because the acute stress response may shift with exposure to previous stressors. For example, as discussed below, elevated glucocorticoids characteristic of chronic stress can alter the threshold and intensity of an acute stress episode, characterised by a change in ratios of epinephrine to norepinephrine. Animals may become acclimated or habituated to a stressor resulting in a downregulation of the stress response even as the stressor remains. Exposure to a stressor may also increase the individual's stress response, known as sensitisation (Fig. 4.2; Busch and Hayward 2009; Angelier and Wingfield 2013).

There are two primary axes of physiological stress response: the sympathetic adrenomedullary (SAM) axis and the hypothalamic–pituitary–adrenal axis (HPA axis; sometimes referred to as the hypothalamic–pituitary–interrenal axis in reptiles). Broadly, the SAM axis is the first response system, releasing catecholamines (e.g. adrenaline) within seconds of a perceived stressor to instigate behavioural and physiological responses that promote survival. The HPA axis responds more slowly, generally within minutes, but may be sustained for hours or days (reviewed in Sapolsky et al. 2000; Romero and Gormally 2019). Because the vast majority of research on the physiological stress response in reptiles concerns the HPA axis—often using the upregulation of these hormones as synonymous with stress response—we begin our discussion of these response pathways here.

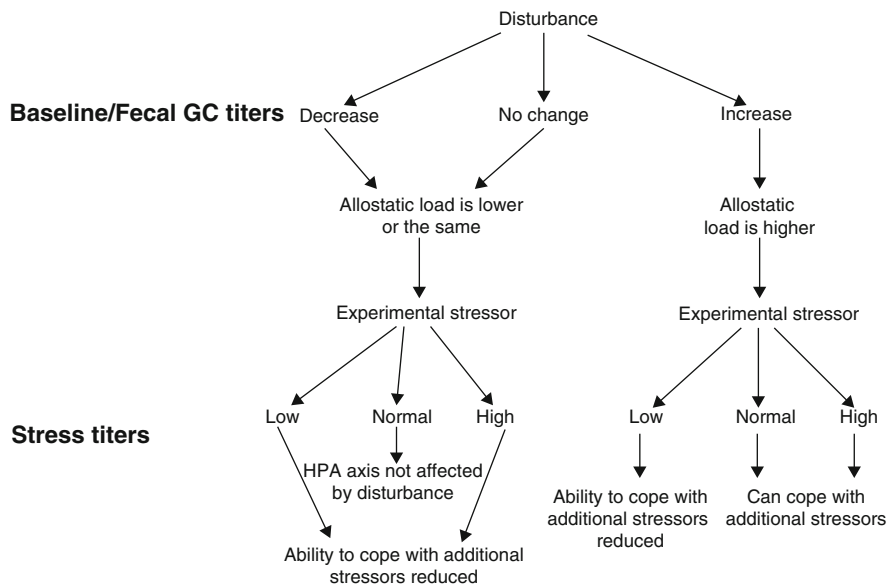


Fig. 4.2 Flow chart indicating how results from field studies on baseline, faecal, and stress-level GC titers could be interpreted in relation to allostatic load and ability to cope with additional stressors. Stress-level titers can be induced via a standardised protocol (e.g. capture and restraint) or chemical challenge (e.g. injection with the releaser hormone adrenocorticotrophic hormone, ACTH) (Reprinted from Busch and Hayward 2009 with permission from Elsevier)

4.2.1.1 The HPA Axis

The hypothalamic–pituitary–adrenal (HPA) axis maintains organismal energy balance generally and modulates energetic allocation during and after an encounter with a stressor specifically (Sapolsky et al. 2000; Wingfield and Kitaysky 2002). This hormonal pathway is evolutionarily ancient, dating to before the origin of vertebrates, with important roles in osmoregulation, development, and the response to environmental challenges (reviewed in Denver 2009; Tort and Teles 2011). Historically, the activation of the HPA axis has been used as a proxy for stress responsivity, if not the sole metric. This hormonal axis responds to various environmental cues and, through a signaling cascade involving the hypothalamus and pituitary gland, ultimately results in the release of the glucocorticoid (GC) hormones (Norris and Jones 1987; Denver 2009).

In reptiles, the HPA response generally results in elevated circulating corticosterone concentrations after several minutes of handling stress. To indicate baseline levels of corticosterone, blood samples must therefore be obtained within 2.5–15 min of handling, depending on the species and immediate environmental conditions (Palacios et al. 2012; Cockrem 2013; Tylan et al. 2019). Although we are accustomed to associating the stress axis with its powerful end-product, glucocorticoid hormones, the intermediate trophic hormones may have their own independent

actions, and likely so in the brain. For example, corticotrophin-releasing factor (CRF) is released in several central and peripheral tissues and has autonomic, homeostatic, and cognitive consequences and is involved in the endocrine and behavioural responses to stress (reviewed in Bale and Vale 2004; Smith and Vale 2006), though we lack sufficient data to assess this in reptiles. The molecular origin of two important stress-related peptides, adrenocorticotrophic hormone (ACTH) and melanocyte-stimulating hormone (MSH), is pro-opiomelanocortin (POMC). Several physioactive and possibly psychoactive peptides are derived from variations of cleaving POMC, sometimes by tissue-specific post-translational processing. When POMC is configured to produce ACTH the classic stress axis is activated, but sibling POMC-derived peptides may also be created, such as β -endorphin and α -MSH. These molecules may present in the brain of reptiles (Dores et al. 1984) and should not be discounted. Indeed, they may contribute to mitigating chronic stress directly or by means of psychoactive actions in the nervous system (e.g. Swaab and Martin 1981; Datta and King 1982; Eberle 1988). Whilst there are many unknowns related to the function of these molecules in reptiles, levels of circulating α -MSH were negatively correlated with circulating corticosterone and positively correlated with circulating testosterone across populations of the western fence lizard (*Sceloporus occidentalis*), suggesting an allocation trade-off of POMC to produce hormones in either the melanin or HPA pathways (Seddon and Hews 2019). Further, POMC-derived peptides are likely also released in the brain where they have effects that appear independent of trophic actions in the body. Indeed, the physiology and behaviour of subordinate male *A. carolinensis* suggest that POMC-derived α -MSH can have protective and restorative actions as well as suppress testosterone-dependent high-risk behaviour (reviewed in Greenberg et al. 1995; Tokarz and Summers 2011).

The most often measured indicators of stress response are the primary GC hormones, cortisol (in most mammals and fish), or corticosterone (in amphibians, reptiles, and birds). GC hormones are generally measurable from a variety of tissue samples (blood, faeces, saliva, skin, feathers). In addition to being the most commonly used physiological biomarker of the stress response, changes in GC hormones are difficult to interpret, being pleiotropic and possessing permissive, suppressive, stimulatory, and preparative actions (Sapolsky et al. 2000). Nonetheless, GCs play a central role in many pathways integral to energy balance maintenance generally and the stress response specifically. This makes glucocorticoid measurements important providers of useful information about the current physiological status of an individual, if interpreted in the relevant context (McEwen and Wingfield 2010; Angelier and Wingfield 2013; Vera et al. 2017). Historically, it has often been assumed that high corticosterone concentrations indicate that an individual is more 'stressed' (e.g. Guillelte et al. 1995). However, the complex role of corticosterone in regulating energetic balance in both day-to-day functions and stressful situations belies such simple interpretation and has been debated extensively in the literature (Bradshaw 2003; Johnstone et al. 2012; Breuner et al. 2013; Cockrem 2013; Schoech et al. 2013; Romero et al. 2015; Vera et al. 2017; MacDougall-Shackleton et al. 2019).

Across taxa, data suggest that baseline and stress-induced levels of circulating glucocorticoids have been shaped by different selective pressures (Vitousek et al. 2019a). Corticosterone levels cycle within individuals at daily, seasonal, and yearly time scales in a wide range of taxa, including reptiles (e.g. Summers and Norman 1988; Moore et al. 2000a; Ott et al. 2000; Romero 2002; Romero and Wikelski 2006; Lutterschmidt et al. 2009; Eikenaar et al. 2012; Palacios et al. 2012; Selman et al. 2012; Dayger and Lutterschmidt 2016; West and Klukowski 2018; Zena et al. 2019). This precludes simple interpretations of baseline levels. The relationship between stressor intensity and stress response profiles can also be non-linear, which again complicates interpretation (Yerkes and Dodson 1908; Busch and Hayward 2009; Del Giudice et al. 2011). Finally, corticosterone plays a central role in both the stress response and the recovery from an encounter with a stressor, to the extent that it can be thought of as an ‘anti-stress’ hormone that facilitates return to the normal sequence of life-history stages (Sapolsky et al. 2000; Wingfield and Kitaysky 2002; Johnstone et al. 2012). For example, the activation of the HPA axis can counter-regulate the actions of the sympathetic (SAM) stress response, prevent damage due to overshooting of immune and inflammatory responses, and regulate post-stressor metabolism. The actions of the HPA axis serve to both facilitate recovery from short-term stressors and mitigate the potential negative consequences of long-term stress response (Wingfield and Kitaysky 2002; Del Giudice et al. 2011). The variability of the corticosterone response within and between individual animals further disallows any simple generalisations from absolute levels of circulating hormones (Cockrem 2013; Romero and Gormally 2019).

At a molecular level, corticosterone interacts with two intracellular receptors that translocate to the cell nucleus and act as transcription factors following ligand activation: a mineralocorticoid receptor (MR) present at high density and a glucocorticoid receptor (GR) present at lower density (Sapolsky et al. 2000). These receptors form homodimers or heterodimers before then acting as transcription factors, but may even dimerise with receptors for other steroid hormones (reviewed in MacDougall-Shackleton et al. 2019). Furthermore, an additional lower-affinity MR receptor is located in the plasma membrane and binds corticosterone when corticosterone is circulating at high concentrations. This receptor mediates non-genomic cellular responses in neurons of the hypothalamus and hippocampus that amplify the effect of other stress hormones and can produce rapid behavioural responses (reviewed in Breuner et al. 1998; de Kloet et al. 2008; Groeneweg et al. 2011). At basal levels, corticosterone primarily binds with intracellular MRs, but at increased stress-induced concentrations it binds with GRs and plasma membrane MRs to mediate various aspects of the stress response (Landys et al. 2006; de Kloet et al. 2008; Busch and Hayward 2009). Generally speaking, at low levels corticosterone has anabolic effects through MR pathways, whereas at higher circulating concentrations it promotes catabolic effects in service of immediate energy mobilisation through GR pathways (reviewed in Guillelte et al. 1995; Korte et al. 2005). This non-linear dose-dependent response resonates with the Yerkes–Dodson principle, as discussed above. Changes in the expression levels of the different receptor types provide an additional mechanism to modulate the downstream effects

of circulating corticosterone in a tissue-specific manner (Busch and Hayward 2009; Angelier and Wingfield 2013). Further, these receptors possess pleiotropic effects on additional pathways (Ratman et al. 2013).

In addition to changes in receptor densities, HPA stress responsivity is modulated at a number of additional levels (Moore and Jessop 2003; Wingfield 2013; Romero and Gormally 2019). For example, corticosterone in blood plasma is bound to corticosterone-binding globulins (CBGs) or other proteins such as albumin, which regulate the amount of corticosterone that is available to tissues (Mendel 1989; Breuner and Orchinik 2002; Breuner et al. 2013, 2020). CBGs bind on average about 90% of circulating cortisol or corticosterone in vertebrate tetrapods, rendering these molecules unavailable to tissues, though few data exist for reptiles (Desantis et al. 2013). The proportion of bound *versus* unbound corticosterone can then be important in determining the downstream effects of the stress response (e.g. in birds, Malisch and Breuner 2010; in mammals, Edwards and Boonstra 2015). The only study to our knowledge measuring CBG in reptiles in an ecological context found that these proteins may play a role in moderating differences in stress responsivity of territorial vs. non-territorial male tree lizards (*Urosaurus ornatus*, Jennings et al. 2000). Additionally, steroidogenic enzymes expressed in target cells can affect the end outcome of corticosterone signalling. For example, the two forms of 11- β -hydroxysteroid dehydrogenase can either convert corticosterone to inactive deoxycorticosterone or enhance corticosterone's ability to bind to receptors (reviewed in Wingfield 2013). Recent work in biomedical fields suggests that the cochaperone molecule FKBP5 may play an important role in regulating the flexibility of HPA response to stressors by modulating the actions of glucocorticoids within cells. Variation in the expression of FKBP5 can affect the magnitude of response and ability to return to baseline after a stressor. Further, variation in methylation of the FKBP5 gene can possibly drive variation in HPA flexibility across generations, though virtually nothing is known about this molecule's actions in non-avian reptiles (Zimmer et al. 2020). To further complicate interpretations of corticosterone, some environmental conditions that are clearly stressors do not elicit a response from the HPA axis. For example, lizards and snakes under conditions of dehydration or restricted water availability do not show increased circulating corticosterone (Capehart et al. 2016; Moeller et al. 2017; Dupoué et al. 2018a). Taken together, it is clear that great care must be made in interpreting measures of total corticosterone concentrations, including consideration of both the extrinsic and intrinsic context in which the measurement was made.

Because of the complex role of corticosterone in energy regulation, there is no clear relationship between either basal or stress-induced corticosterone concentrations and fitness in diverse taxa (Breuner et al. 2008; Bonier et al. 2009; Crespi et al. 2013; Schoenle et al. 2018; Romero and Gormally 2019). Nevertheless, some studies in reptiles do demonstrate a clear relationship in specific contexts. The best examples come from studies in Galápagos marine iguanas (*Amblyrhynchus cristatus*), in which individuals exhibiting higher levels of stress-induced corticosterone were more likely to survive periods of severe food shortage (Romero and Wikelski 2001; Romero 2012) and a fouling of the environment (Wikelski et al.

2002). In contrast, increased survival was associated with higher baseline corticosterone in wild side-blotched lizards (*Uta stansburiana*, Comendant et al. 2003) and in common lizards (*Zootoca vivipara*) with experimentally augmented corticosterone (Cote et al. 2006). Furthermore, different theoretical models of the maintenance of homeostasis across both life-history stages and unpredictable environmental stressors do not agree on a common measure of the stress response or even which biological parameters should be the focus of such studies (Romero et al. 2009; McEwen and Wingfield 2010). Interestingly, recent work in both lizards and birds suggests that the responsiveness of the HPA axis to negative feedback (that is, its ability to 'turn off' after 'turning on') may be closely tied to fitness (Romero and Wikelski 2010; Vitousek et al. 2019b; Zimmer et al. 2019; Lattin and Kelly 2020). This responsiveness varies across populations in a garter snake species (*Thamnophis sirtalis*, Gangloff et al. 2017a), perhaps in response to local ecological conditions. Whilst the importance of negative inhibition of the HPA axis fits the general expectations based on work with mammals (Sapolsky et al. 1986), additional tests of the consequences of this variation in HPA termination after the initial stress response are much needed in reptiles.

Overall, the state of affairs of general principles and theories of organismal stress response across taxa can be described as in the 'natural history' phase (Breuner et al. 2013), especially in regard to ectothermic vertebrate tetrapods (amphibians and non-avian reptiles). For example, much work is specifically needed for studies of behavioural neuroendocrinology in reptiles (Kabelik and Hofmann 2018). Additional research to describe and catalogue aspects of stress response in natural populations will then inform our understanding of responses to artificial or novel environments (Wingfield 2008, 2013; Vera et al. 2017). Notwithstanding, many studies have shown significant associations between circulating levels of total corticosterone and stress-related physiological and behavioural phenotypes. Thus total corticosterone titres generally remain an important bioindicator of stress response (Angelier and Wingfield 2013; Jessop et al. 2016; Taff and Vitousek 2016), especially when combined with additional indicators of physiological and behavioural response (see below; Mormède et al. 2007; Schoech et al. 2013). We emphasise that the HPA axis response to extrinsic and intrinsic stimuli is part of the normal functioning of healthy individuals. Further, corticosterone plays a role in other axes of homeostatic maintenance. For example, corticosterone exhibits mineralocorticoid actions important in maintaining water balance (reviewed in de Kloet et al. 2008), as demonstrated in reproducing Children's pythons deprived of water (*Antaresia childreni*; Brusch et al. 2020). Corticosterone also plays a role in modulating levels of circulating catecholamines. Corticosterone lengthens the half-life of the enzyme phenylethanolamine N-methyltransferase (PNMT), which catalyses the conversion of epinephrine (EPI) to norepinephrine (NOREPI) and effectively changes the ratio of these catecholamines released in response to an acute stressor (Wurtman 2002). Next, we turn to these catecholamines and their role in the stress response.

4.2.1.2 The SAM Axis

Whilst the activation of the HPA axis is often treated as synonymous with the stress response, it is in fact the sympathetic adrenomedullary (SAM) axis that first reacts to perceived stressors. This includes the famed ‘flight or fight’ response, whereby an organism mobilises its energetic capacities to either endure a stressor (‘fight’) or remove itself from potential danger (‘flight’). Following activation of the sympathetic nervous system, the adrenal chromaffin cells release the catecholamines epinephrine (EPI) and norepinephrine (NOREPI), in varying proportions depending on circumstances. Chromaffin is condensed in the adrenal medulla of mammals, but in reptiles it is less compact and more diffuse. Catecholamines increase heart rate and ventilation, increase blood flow to skeletal muscle, and promote hyperglycaemia via glycogenolysis and glycolysis (reviewed in Stevenson et al. 1957; Akbar et al. 1978; Coulson and Hernandez 1979; Norris and Jones 1987; Janssens and Giuliano 1989; Keiver and Hochachka 1991). They act by stimulating alpha and beta adrenergic receptors, which can have opposite effects: alpha receptors tend to evoke stimulation and constriction of targets, whereas beta receptors cause relaxation and dilatation. The extent of stimulation determines outcomes and depends on the relative amounts of circulating EPI and NOREPI; whilst NOREPI can stimulate alpha receptors, EPI preferentially stimulates beta receptors and tends to override alpha effects. Some NOREPI is always present as the end-product of sympathetic neurons, whereas additional EPI is synthesised in acute stress under the influence of circulating corticosterone. However, it is likely that in reptiles, as in other vertebrates, the ratios of EPI and NOREPI are variable depending on the activity of a metabolic intermediary and ‘... on the magnitude and type of stimulus that initiates neural activation of the medulla’ (Vollmer 1996). Some of the dynamics of this system are represented in the chromatophore model in *Anolis* (Fig. 4.3).

As mentioned above, because background levels of corticosterone can act on chromaffin tissue to increase synthesis of EPI from NOREPI, chronically stressed individuals produce a more intense acute stress response. This may determine at least part of the variability in observations of the timing of release and relative concentrations of these two catecholamines in different individuals. For example, in American alligators, (*Alligator mississippiensis*) subjected to restraint stress and removal from water, plasma concentrations of EPI peaked immediately and NOREPI after 1 h, whereas corticosterone did not peak until after 4 h (Lance and Elsey 1999). Both EPI and NOREPI increased dramatically within seconds in response to handling stress and to interactions with a conspecific in male tree lizards (*Urosaurus ornatus*), though the increase in NOREPI was more pronounced (Matt et al. 1997). The circulating levels of these hormones quickly reached asymptote and remained elevated for several minutes. The pattern was slightly different in response to a staged aggressive encounter with a conspecific: whereas both EPI and NOREPI were elevated, the NOREPI levels quickly decreased after the encounter whilst EPI remained elevated (Matt et al. 1997). A similar pattern was found in desert iguanas (*Dipsosaurus dorsalis*) run to exhaustion, whereby after 2 h NOREPI had returned to baseline, but EPI remained elevated (Gleeson et al. 1993). In painted turtles (*Chrysemys picta*), circulating EPI and NOREPI increased during forced submersion in water and dropped rapidly during recovery. However, corticosterone was not

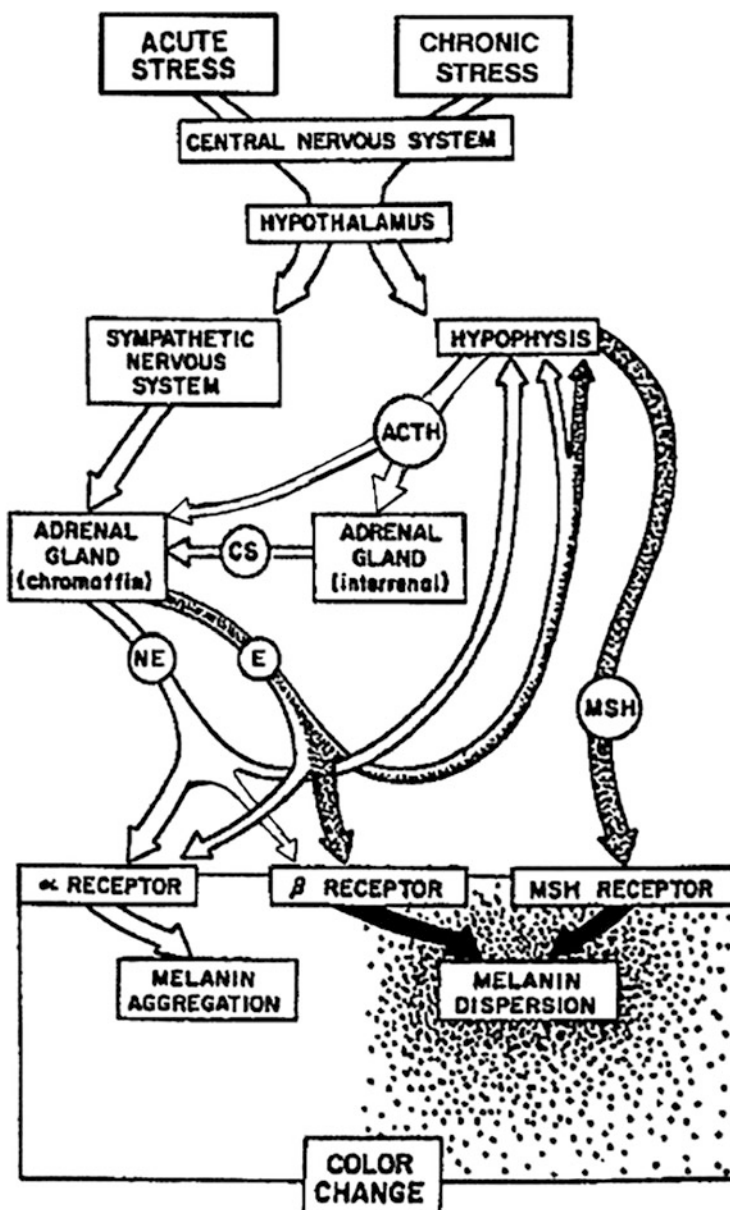


Fig. 4.3 The putative effects of stress hormones on a dermal chromatophore of *Anolis carolinensis*. Acute and chronic stressors are integrated to cause the release of hormones that interact with each other and converge in affecting the darkness of a chromatophore. *ACTH* adrenocorticotropic hormone, *CS* corticosterone, *E* epinephrine, *MSH* melanocyte stimulating hormone, *NE* norepinephrine. *CS* can elevate the ratio of *E* to *NE* by facilitating a key enzyme within the adrenal gland. *E* stimulates beta receptors preferentially and then alpha receptors resulting in opposing effects (Adapted from Greenberg and Crews 1983)

elevated during this forced anoxia, but rapidly increased when the turtles were released (Keiver et al. 1992). Energy stores are rapidly mobilised by EPI and NOREPI in response to a stressor, but such actions, such as the elevation of circulating glucose, are detrimental in the long term. The actions of GCs serve to modulate this energetic response and return individuals to normal functionality (Sapolsky et al. 2000). These findings provide strong support for the idea that catecholamines comprise the initial stress response, whereas GCs, such as corticosterone, serve to aid in recovery after the encounter with a stressor (*sensu* Wingfield and Kitaysky 2002).

A model of interactions between corticosterone, EPI, NOREPI, and MSH was developed with the benefit of the unique chromatophores of the green anolis lizard, *A. carolinensis* (Fig. 4.3; Taylor and Hadley 1970; Greenberg 2002). Unlike chamaeleons and other lizards investigated, body colour changes are, perhaps uniquely in *A. carolinensis* (Norris and Carr 2013), attributable only to circulating hormones. The chromatophore is not innervated (Kleinholz 1938a, b), thus allowing body colour in green anoles to serve as a partial *in situ* assay of the endocrine tone of the chromo-active hormones. A unique patch of beta-only chromatophores (Hadley and Oldman 1969) just caudal to the eye (the post-orbital 'eyespot') is an indication of highly elevated levels of circulating EPI. An individual's pattern of colour change indicates its ability to cope in agonistic encounters; when quickly appearing (within several seconds) relative to an adversary, animals were more likely to prevail in agonistic interactions. When sampled 30 s into a fight, plasma catecholamine levels are significantly elevated, but at 30 s following a fight, winning male lizards have more NOREPI relative to EPI, suggesting greater resilience (Summers and Greenberg 1994).

The SAM axis response to stress is clear and provides several potential metrics of short-term stress response. Yet, the rapidity with which this axis produces and releases catecholamines, such as EPI or NOREPI, makes it difficult to use them as effective biomarkers because handling stress, such as when collecting a blood sample, could confound any interpretation of the levels of circulating hormones (discussed in Matt et al. 1997; Benn et al. 2019). Though the rapid response of this axis means even determining reliable baseline levels is difficult, measurements over time can still be useful to indicate the relative duration of a response to different stressors (Matt et al. 1997). Furthermore, activation of both the HPA and SAM axes is evident in behavioural responses. These effects are both direct (due to actions on areas of the brain involved in specific behavioural patterns) and indirect (affecting predator-related or prey-related behaviour and reproductive activity). For example, general activity levels, particularly exploratory behaviour, are associated with stress in reptiles (Greenberg 1985). In other taxa, these effects may be attributable to elevated GCs (e.g. in birds, Moyers et al. 2018) or possibly in association with the effect of CRF on central NOREPI (e.g. in mice, Berridge and Dunn 1989), though little is known about these pathways in reptiles. Exploratory behaviour, however, is another good example of Yerkes–Dodson principle; mild stress may enhance exploration, whilst higher levels may lead to less or even suppressed exploratory activity (Leshner 1979; Greenberg 1985 in *Anolis*). For example, enhanced exploration (not

due to appetitive stressors) is often regarded as an indication of positive welfare in reptiles (Benn et al. 2019) and other species (e.g. Franks et al. 2013).

An emerging perspective on SAM regulation is provided by osteocalcin, the small protein synthesised by osteoblasts and critically involved in bone formation and remodeling. This metabolite has in recent decades received attention for a diversity of formerly unappreciated endocrine functions that include the regulation of energy and response to stressors (Patterson-Buckendahl 2011). The stress connection was encouraged by Gerard Karsenty's evolutionary view (Karsenty and Olson 2016) that escaping danger is among the adaptive advantages provided by bone, thus bone tissue is involved in an entire constellation of related adaptive metabolic functions. Indeed, osteocalcin inhibits the post-synaptic neurons of the parasympathetic system, modifying the balance between sympathetic and parasympathetic tone in a manner consistent with the stress response (Berger et al. 2019). The roster of peripheral energy-related processes (summarised by Moser and van der Eerden 2019) also includes a role in brain development and cognitive functions (Oury et al. 2013; Shan et al. 2019). These connections were demonstrated in osteocalcin-deficient mice. However, many of these effects of osteocalcin deficiency were not subsequently corroborated by mice genetically modified in a different way (Diegel et al. 2020; Moriishi et al. 2020), an apparent discrepancy seeking resolution. The relationship between bone growth and stress response, as well as possible effects of osteocalcin on angiogenesis or pathological mineralisation has clear implications for animal care and welfare. Indeed, osteocalcin must be considered a candidate stress-related neuropeptide. Further work is needed generally and specifically in reptiles.

4.2.2 Colour Change as a Stress Indicator

Colouration and colour polymorphisms play important ecological roles in the thermal ecology, mating systems, and predator avoidance in a wide variety of organisms, including reptiles. However, colour change and polymorphism are complicated by developmental and seasonal variation and sensitivity to stress-related experiences. For example, social dominant male rainbow lizards (*Agama agama*) display a striking red head that is not seen in females or juveniles and appears to be suppressed in subordinate males (Harris 1964). In the mesquite lizard (*Sceloporus grammicus*), a diversity of colour phenotypes is important in reproductive isolation of sympatric morphs (Bastiaans et al. 2014). Often the orange or red colouration of lizards is due to pigments such as carotenoids, which also serve as antioxidants and immune enhancers. The general paradigm is that external stressors can reduce the brightness or intensity of colouration in a variety of taxa, including fish and bird species where these colours serve as sexual and status signals. In this situation, stressors serve to divert carotenoids away from colouration (e.g. Milinski and Bakker 1990; Brawner et al. 2000). Such patterns have also been found in reptiles; for example, female common lizards (*Zootoca vivipara*) living in populations with artificially reduced conspecific density increased red colouration on their ventral scales (Meylan et al.

2007). Whilst increased redness associated with a reduction in a stressor may be generally true, in some cases increased redness is correlated with increases in circulating corticosterone. This could be a strategy to improve immediate reproductive success in an environment when long-term prospects are low, fitting with the terminal investment hypothesis whereby organisms invest more in current reproduction as they face uncertain survival prospects (Fitze et al. 2009; Cote et al. 2010).

In many species of lizard, colour change is directly associated with the stress response and is thus useful in captive settings as an indicator of health and welfare. This was noted for the green anole (*A. carolinensis*) in stressful circumstances over 75 years ago (Greenberg and Noble 1944). Body colour change was later linked to fluctuations of EPI and NOREPI, effectively providing a real-time *in situ* bioassay of animals interacting in nature (Summers and Greenberg 1994; Greenberg 2002). Amongst the most interesting colour changes in this species is the development of a post-orbital dark spot that apparently functions as a social signal, suppressing aggression in an adversary (See Fig. 4.3; Korzan et al. 2000). Whilst green anoles darken colour, changing from green to brown, in response to stressors (Greenberg 2003), this pattern varies even among closely related species. For example, the water anole (*Anolis aquaticus*) brightens an eye-stripe and a lateral stripe along its body in response to handling stress (Boyer and Swierk 2017). Another example that may be familiar to many caring for captive reptiles is colour change in the bearded dragon (*Pogona vitticeps*), a common lizard in the pet trade. Whilst not linked to the stress response directly, lizards are known to darken or lighten body colour rapidly in response to external temperature and thermoregulatory needs (Smith et al. 2016a). Such colour changes can serve as useful signals to caretakers of captive reptiles about the appropriateness of the thermal environment. Importantly, colour change also plays a role in social signaling (Harris 1964; Smith et al. 2016a), is dependent on camouflage needs (Smith et al. 2016b), and can vary across seasons (Cadena et al. 2017), so care must be taken in interpreting colour change as solely indicative of thermal conditions. Insight into the adaptive significance of any such behaviours requires an understanding of physiological processes in the context of an individual's developmental history and ecology. We must be able to establish valid particulars at the same time as we consider the integrative biology that is so well represented by acute and chronic stress, the study of which can enable us to see their function in a variety of contexts both wild and captive.

4.2.3 Stress and Reproduction

Reproduction is, as Moberg (1985) put it, a 'barometer of animal well-being'. This is something to which all our colleagues that maintain captive reptiles in zoos and breeding colonies for conservation pay very close attention. Successful reproduction is popularly thought of as the prized reward for 'doing everything right'. However, this view is oversimplified. The urgency of reproduction as a biological need enables some animals to reproduce in extremely adverse circumstances, prioritising reproduction at the cost of reduced individual welfare (see also Mendyk and Warwick

2023; Warwick 2023). Consider the stresses of forced reproduction as in battery cages for commercially important species. This has consequences for the animals reproducing and for their offspring, particularly in light of new understanding about long-lasting effects of developmental trauma or deprivation (see discussion of cross-generation stress effects below). Acute and chronic stress involves corticotropic releasing hormone (CRH), endogenous opiates, and glucocorticoids, all of which can affect reproduction (reviewed in Greenberg and Wingfield 1987; Sapolsky et al. 2000). This may be done directly by the effect on the reproductive activity of socially dominant individuals or indirectly, limiting the reproductive opportunities of subordinates. We currently lack a clear understanding of the central mechanisms that both evoke and are affected by an individual's experience of real or perceived threats to homeostasis and the control of resources in the context of reproduction, especially in reptiles.

Stress can suppress testosterone (Sapolsky et al. 2000; Lance et al. 2004) and in some reptile taxa directly reduces reproductive activity independent of testicular function (Tokarz and Summers 2011). As Tokarz and Summers (2011) emphasised in a detailed review, central control mechanisms of physiology and behaviour must be considered along with the direct and collateral effects of all the hormones of the SAM system and the HPA axis. This is supported by the finding that stress, corticosterone, and reproduction interact across reptile and amphibian taxa, in some cases with a positive relationship between corticosterone and reproduction (Moore and Jessop 2003). This is counter to the simple presumption that stress inhibits reproduction; on the contrary, stress may potentially instigate a terminal investment in immediate reproduction if prospects for future reproductive bouts are low. For example, red-sided garter snake (*Thamnophis sirtalis parietalis*) females will copulate even when under obvious conditions of stress in natural or captive environments (Moore 1999; Dayger et al. 2013), whilst the physiological and behavioural responses to stress are decoupled in males during the mating season (Moore et al. 2000b). Much research is still needed to characterise the relationship between stress and reproduction across ecological situations among reptilian taxa. However, the data we already have caution against assuming that reproduction is an indicator that 'all is well' and an individual is not experiencing stressful conditions. Further, reproductive output under unfavourable conditions may come at the expense of future reproduction and with long-term consequences for offspring (Wingfield et al. 1998).

4.2.4 Stress and Immunity

The stress response can affect immune function, often through endocrine-mediated pathways that control both energy allocation and immune function directly (Guillette et al. 1995; McEwen and Wingfield 2003). For example, increased corticosterone levels within the operational allostatic range can serve to enhance immune function, whereas elevated levels in response to a stressor often decrease immune function, especially under conditions of chronic stress (Sapolsky et al. 2000; Korte et al. 2005;

Dantzer et al. 2014). This is supported in a study of eastern fence lizards (*Sceloporus undulatus*), whereby low levels of exogenous corticosterone enhance hemagglutination capacity (a measure of innate immune function), whilst higher levels of corticosterone are suppressive (McCormick et al. 2015). In another example, restraint stress in the yellow-bellied gecko (*Hemidactylus flaviviridis*) resulted in reduced macrophage function (a component of the innate immune response) via the activation of the SAM pathway (Roy and Rai 2004). Different ecological, social, or emotional states may evoke not just a change in the overall investment in immune function, but a shift in immune priorities (Dhabhar 2009; Tort and Teles 2011). For example, an individual may differentially allocate between the two primary divisions of the immune system, the constitutive innate (non-specific) and adaptive (acquired) arms. Furthermore, parameters within each arm may be differentially affected by the stress response. For example, French et al. (2017) found that the level of human disturbance correlated with changes to endocrine and immune profiles in Galápagos marine iguanas (*Amblyrhynchus cristatus*), but this effect was not evident across all aspects of immune function: one measure of innate immunity (bacterial killing capacity) decreased with increased disturbance, whereas others (haemolytic complement activity and wound healing) were unaffected.

The effects of stress on immune function are often connected to increases in HPA activity. For example, increases in levels of circulating corticosterone are associated with decreased immune function in both Galápagos marine iguanas (*A. cristatus*, Berger et al. 2005) and American alligators (*A. mississippiensis*, Morici et al. 1997). On the other hand, no such effect was found in painted turtles (*Chrysemys picta*) transplanted to a novel climate (Refsnider et al. 2015). Similarly, free-living eastern box turtles (*Terrapene carolina*) with higher circulating corticosterone exhibited higher levels of haemolysis, an indicator of innate immune function (West and Klukowski 2018). Such shifts in energetic and immune priorities can have important consequences for reptiles in captive environments, especially in situations where animals are housed in close quarters and pathogens may readily spread (Ippen and Zwart 1996). However, few studies have measured the energetic costs or associated trade-offs in terms of response to infection of such a shift in immune priorities as a result of stressors.

Perhaps the most common immune parameter used as a biomarker for stress is the relative abundance of circulating leukocytes, specifically in reptiles the ratio of heterophils to lymphocytes (H:L ratio). In vertebrates generally, a stress response will increase the number of circulating phagocytic immune cells (primarily heterophils in reptiles, but not always) and redistribute lymphocytes to tissues where they may be needed, resulting in an increase in the H:L value in blood across a variety of species (Sapolsky et al. 2000; Davis et al. 2008; Goessling et al. 2015). Even as the leukocyte composition of many reptile species is widely unknown, the pattern of stress inducing an increase in H:L ratios is consistent across those taxa in which it has been measured (reviewed in Davies et al. 2008). This redistribution is in part effected by increases in circulating corticosterone. Thus H:L ratios provide an indicator of the downstream impacts of corticosterone levels, though generally at longer timescales. As such, a comparison of more rapidly responding corticosterone

and slower-responding but more stable H:L ratios can provide important data on both the immediate endocrine status and the longer-term stress response status of an individual. For example, both circulating corticosterone and H:L ratios increased in juvenile green sea turtles (*Chelonia mydas*) in response to capture. The responses were more extreme and were correlated in turtles with fibropapillomatosis (non-cancerous epithelial tumours), which the authors interpret to indicate chronic stress (Aguirre et al. 1995). In both gravid and non-gravid female White's skinks (*Egernia whitii*), increased corticosterone during time in captivity is correlated with increases in circulating heterophils, though corticosterone returns to baseline levels more quickly (Cartledge et al. 2005). At the population level, tree lizards (*Urosaurus ornatus*) from a natural site had higher levels of both baseline corticosterone and H:L ratios compared with populations in more urban areas, suggesting that urban populations suppressed the stress response after frequent exposure to stressors (French et al. 2008). American alligators (*A. mississippiensis*) with experimentally induced increase in corticosterone also increased H:L ratios (Morici et al. 1997), whilst eastern box turtles exposed to handling stress increased both circulating corticosterone and leukocyte counts (Boers et al. 2019).

Despite their established functional relationship, heterophil to lymphocyte ratios and levels of circulating glucocorticoids are not always correlated within individuals and this relationship can change depending on the duration and intensity of the stressor (reviewed in Goessling et al. 2015). For example, Gangloff et al. (2017a) found that the within-individual relationship of corticosterone, glucose, and H:L ratios changed over the duration of a captive-restraint stressor in the common garter snake (*Thamnophis sirtalis*), with corticosterone and glucose generally representing physiological changes over shorter time scales compared with H:L ratios. Baseline levels of corticosterone and H:L were correlated, but this relationship was not found at subsequent time points in the stress response (Fig. 4.4). In southeastern five-lined skinks (*Plestiodon inexpectatus*), captivity-induced stress increased both corticosterone and H:L ratios, though somewhat surprisingly the two metrics were correlated within individuals after 1 h of confinement, but not at baseline or after 2 h (Seddon and Klukowski 2012). Captivity also elevated both corticosterone and H:L profiles in wild-caught western terrestrial garter snakes (*Thamnophis elegans*), though the two biomarkers were not correlated within individuals (Sparkman et al. 2014). The differential responses of physiological systems to both the intensity and duration of stressors thus underscore the need to use multiple markers when assessing physiological status (Breuner et al. 2013; Goessling et al. 2015).

Additional studies have provided some novel measures of immune parameters in relation to stressors, but many of these have yet to be examined across taxa or in other contexts. For example, Lenihan et al. (1985) found that stressed green anoles (*A. carolinensis*) dramatically increased levels of circulating platelet activating factors (PAFs), a mediator of anaphylaxis and immune function, compared to control animals. Because of the multifaceted role of this molecule in leukocyte function, inflammation, and hypertension, the authors speculate that PAFs may be an important mediator in the physiological response to chronic stress, but to our knowledge this has not been pursued in other reptile taxa. Quantification of circulating lysozyme

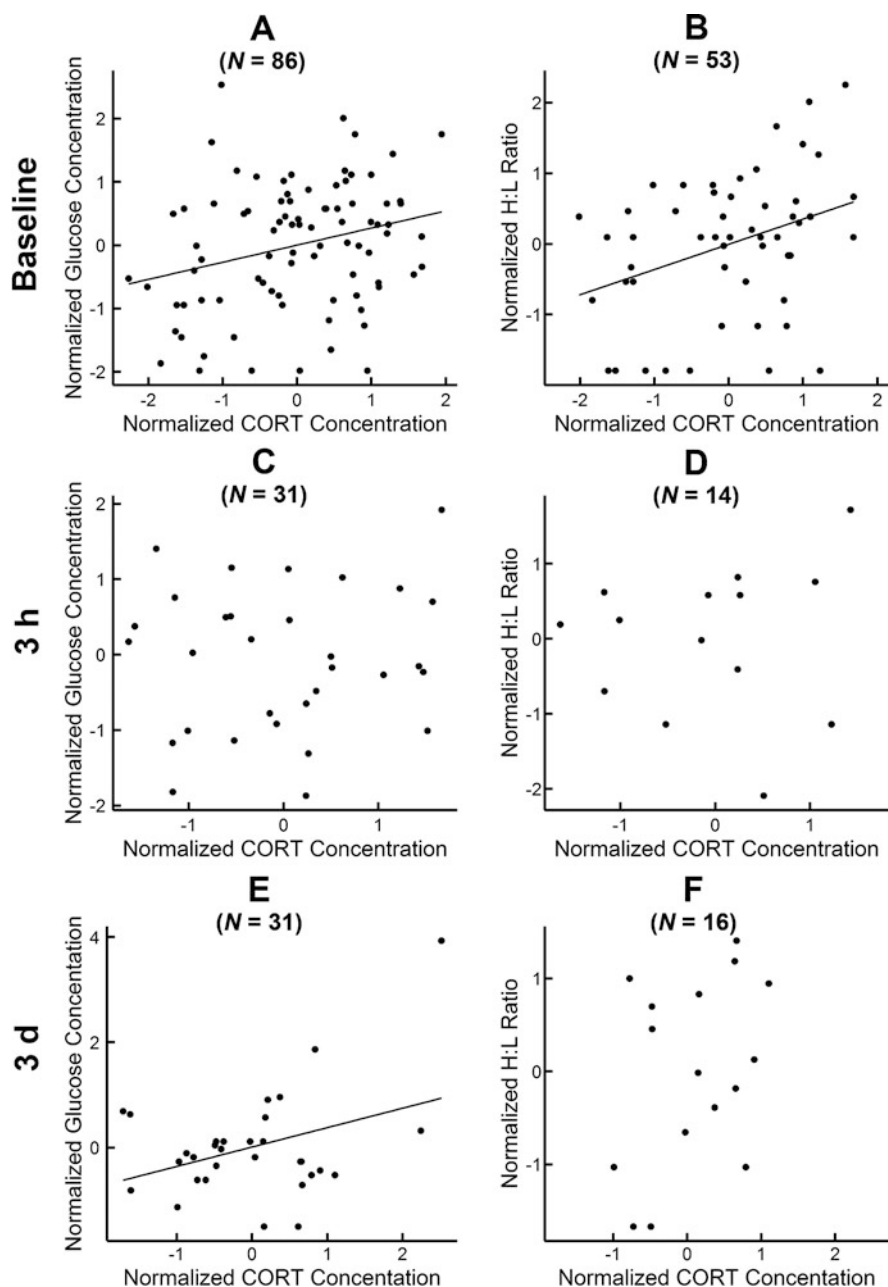


Fig. 4.4 Scatterplots of within-individual relationship between plasma corticosterone concentration and plasma glucose concentration and heterophil:lymphocyte (H:L) ratio at baseline (Panels a, b), 3 h (Panels c, d), and at 3 days (Panels e, f) for wild-caught *Thamnophis sirtalis*. Regression lines shown for significant relationships of \log_{10} -transformed and normalised variables (Reprinted from Gangloff et al. 2017a with permission from Elsevier)

activity in blood plasma, a measure of innate immune function, is another potential immunological indicator of the physiological stress response. In loggerhead sea turtles (*Caretta caretta*), this activity was elevated in response to hospitalisation at a rehabilitation facility (Caliani et al. 2019) and in response to mercury contamination (Day et al. 2007). In contrast, exposure to environmental contaminants can impair immune function, as indicated by decreased lysozyme activity with exposure to organochloride contaminants in *C. caretta* (Keller et al. 2006) and after exposure to the herbicide atrazine in the red-eared slider (*Trachemys scripta*, Soltanian 2016). Because of its versatility and ease of use, lysozyme activity in blood is a promising metric of immune function in the context of both the stress response (Caliani et al. 2019) and toxin exposure, but quantification in reptilian taxa beyond turtles is needed to assess this potential utility.

An additional immune marker that may prove useful in assessment of organismal well-being is secretory immunoglobulin A (SIgA), as proposed by Staley et al. (2018). This antibody protein is released into the mucosal system and acts in numerous defence pathways, including protection against toxins and in preventing the adhesion of pathogens to host cells (Corthésy 2010). Given its important defensive immune function and that levels of SIgA are modulated by both the HPA and SAM pathways, measurement of SIgA could prove to be a valuable biomarker in reptiles, as it has in birds and mammals (reviewed in Staley et al. 2018). Currently, the usefulness of SIgA as a biomarker in reptiles has not been evaluated, though homologous genes seem present in reptiles (Deza et al. 2007; Magadán-Mompó et al. 2013). Given especially the ease with which SIgA can be sampled (e.g. from mucus or faeces), the validation of this biomarker in reptiles could provide an extremely useful tool in evaluating animal welfare both in captivity and the wild.

4.2.5 Example Studies of Stress Response in Reptiles

All stressors associated with captivity, and indeed capture and captivity itself, are evolutionarily novel to non-domesticated animals (Warwick et al. 2013). Thus, capture and restraint have been one of the most commonly studied stressors in reptiles and elicit a nearly universal stress response. The physiological markers of captivity stress can decrease over time as animals become acclimated (Manzo et al. 1994) but are not completely eliminated even after significant time in captivity (Sparkman et al. 2014). Recent recognition of the cognitive abilities of reptiles (e.g. Wilkinson and Huber 2012; Burghardt 2013; Font et al. 2023) offers promising avenues to reduce the stress of routine husbandry and medical procedures by training animals to cooperate (reviewed in Hellmuth et al. 2012). In addition to stressors specific to captivity, a variety of other stressors have been examined across reptile taxa, including extreme temperatures, food deprivation, dehydration, and transportation (see Table 4.2). Furthermore, the effects of degraded environmental conditions, including urbanisation and pollutants, have been examined in wild-living reptiles. Table 4.2 presents some examples of studies examining the stress

Table 4.2 Selected examples of research involving stress response in reptiles. This table exemplifies the variety of stressors and biomarkers used in different reptile taxa, not a complete literature review

Stressor	Biomarker(s) Used	Taxa	Citation
Atrazine contamination	H:L ratio, lysozyme activity, leukocyte counts, other immune functions	Red-eared slider turtle (<i>Trachemys scripta</i>)	Soltanian (2016)
Captivity	Corticosterone, progesterone, leukocyte counts	White's skink (<i>Egernia whitii</i>)	Cartledge et al. (2005)
Captivity	Corticosterone, H:L ratio	Western terrestrial garter snake (<i>Thamnophis elegans</i>)	Sparkman et al. (2014)
Capture stress	Corticosterone, reproductive behaviours	Common garter snake (<i>Thamnophis sirtalis</i>)	Moore et al. (2000b)
Capture/restraint	Corticosterone, estradiol	American alligator (<i>Alligator mississippiensis</i>)	Elsey et al. (1991)
Capture/restraint	Corticosterone, EPI, NOREPI, DA, glucose, blood chemistry	American alligator (<i>Alligator mississippiensis</i>)	Lance and Elsey (1999)
Capture/restraint	Corticosterone, testosterone, estradiol	Timber rattlesnake (<i>Crotalus horridus</i>)	Lutterschmidt et al. (2009)
Capture/restraint	Corticosterone, H:L ratio, testosterone	Southeastern five-lined skink (<i>Plestiodon inexpectatus</i>)	Seddon and Klukowski (2012)
Capture/restraint	Corticosterone, H:L ratio, glucose	Common garter snake (<i>Thamnophis sirtalis</i>)	Gangloff et al. (2017b)
Capture/restraint	Corticosterone, haematocrit, leukocyte counts	Eastern box turtle (<i>Terrapene carolina</i>)	Boers et al. (2019)
Capture/restraint	Gene expression in red and white blood cells, corticosterone, testosterone, glucose, creatine kinase, aspartate aminotransferase, blood electrolytes	American alligator (<i>Alligator mississippiensis</i>)	Kohno et al. (2020)
Capture/restraint, Conspecific encounter	EPI, NOREPI, DA	Tree lizard (<i>Urosaurus ornatus</i>)	Matt et al. (1997)
Capture/restraint, tumour presence	Corticosterone, H:L ratio, glucose, leukocyte counts, plasma chemistry profiles	Green sea turtle (<i>Chelonia mydas</i>)	Aguirre et al. (1995)
Climate warming	Telomere length	Common lizard (<i>Zootoca vivipara</i>)	Dupoué et al. (2017)
Climate, habitat anthropisation	Faecal corticosterone, parasite load, body condition	Gallot's lizard or Tenerife lizard (<i>Gallotia galloti</i>)	Megía-Palma et al. (2020)
Conspecific aggression	Body colour, 'eyespot'	Green anole (<i>Anolis carolinensis</i>)	Greenberg (2002)

(continued)

Table 4.2 (continued)

Stressor	Biomarker(s) Used	Taxa	Citation
Conspecific density	Ventral colouration	Common lizard (<i>Zootoca vivipara</i>)	Meylan et al. (2007)
Contaminates, Capture/restraint	Corticosterone, testosterone, estradiol	American alligator (<i>Alligator mississippiensis</i>)	Gunderson et al. (2003)
Dehydration	Corticosterone, innate immune function, H:L ratio, leukocyte counts	Gila monster (<i>Heloderma suspectum</i>)	Moeller et al. (2017)
Dehydration, Capture/restraint	Corticosterone	Children's python (<i>Antaresia childreni</i>)	Dupoué et al. (2014)
Exhaustive exercise	Corticosterone, EPI, NOREPI	Desert iguana (<i>Dipsosaurus dorsalis</i>)	Gleeson et al. (1993)
Food restriction	Corticosterone, carotenoid-based colour, antioxidants, oxidative damage	Common lizard (<i>Zootoca vivipara</i>)	Cote et al. (2010)
Food restriction, Capture/restraint	Corticosterone	Galápagos marine iguanas (<i>Amblyrhynchus cristatus</i>)	Romero and Wikelski (2010)
Forced submergence (anoxia)	Corticosterone, EPI, NOREPI, glucose	Painted turtle (<i>Chrysemys picta</i>)	Keiver et al. (1992)
Handling	Platelet activation factor (PAF)	Green anole (<i>Anolis carolinensis</i>)	Lenihan et al. (1985)
Handling, Poor environment (lack of climbing opportunity)	Corticosterone, behaviour	Green iguana (<i>Iguana iguana</i>)	Kalliokoski et al. (2012)
High temperature	Corticosterone, gene expression (heat-shock proteins and antioxidants), reactive oxygen species production, DNA damage	Western terrestrial garter snake (<i>Thamnophis elegans</i>)	Schwartz and Bronikowski (2013)
High temperature	Corticosterone, glucose, muscle tissue metabolome	Northern alligator lizard (<i>Elgaria coerulea</i>), Southern alligator lizard (<i>E. multicarinata</i>)	Telemeco et al. (2017)
High temperature	Corticosterone, glucose, insulin, lactate	Western terrestrial garter snake (<i>Thamnophis elegans</i>)	Gangloff et al. (2016)
High temperature, Captivity, Capture/restraint	Corticosterone, triglycerides	Northern water snake (<i>Nerodia sipedon</i>)	Sykes and Klukowski (2009)
High temperature, Fire ants	Behaviour, corticosterone, glucose, innate immune function, expression of heat-shock protein genes	Eastern fence lizard (<i>Sceloporus undulatus</i>)	Telemeco et al. (2019), Telemeco and Gangloff (2020)

(continued)

Table 4.2 (continued)

Stressor	Biomarker(s) Used	Taxa	Citation
Hospitalisation	H:L ratio, various immune parameters, leukocyte counts, lysozyme activity	Loggerhead sea turtle (<i>Caretta caretta</i>)	Caliani et al. (2019)
Human activity	Corticosterone, testosterone, estradiol, wound healing, innate immune function, reproduction	Galápagos marine iguanas (<i>Amblyrhynchus cristatus</i>)	French et al. (2017)
Mercury poisoning	Haematocrit, acquired immune response (lymphocyte proliferation), other immune functions	Loggerhead sea turtle (<i>Caretta caretta</i>)	Day et al. (2007)
Noise simulating mining	Escape behaviours, head position	Eastern blue tongued lizard (<i>Tiliqua scincoides</i>)	Mancera et al. (2017)
Organochloride contaminants	Acquired immune response (lymphocyte proliferation), lysozyme activity	Loggerhead sea turtle (<i>Caretta caretta</i>)	Keller et al. (2006)
Restraint, immobilisation (via electro-shock)	Corticosterone, glucose, lactate	Estuarine crocodile (<i>Crocodylus porosus</i>)	Franklin et al. (2003)
Stocking density	Corticosterone	American alligator (<i>Alligator mississippiensis</i>)	Elsey et al. (1990)
Temperature extremes	Corticosterone	Northern alligator lizards (<i>Elgaria coerulea</i>), Southern alligator lizards (<i>E. multicarinata</i>)	Telemeco and Addis (2014)
Temperature extremes, Noise simulating transport	Escape behaviours	Eastern blue tongued lizard (<i>Tiliqua scincoides</i>)	Mancera et al. (2014)
Transportation	Corticosterone, glucose, H:L ratio, leukocyte counts	Kemp's ridley sea turtle (<i>Lepidochelys kempii</i>)	Hunt et al. (2016)
Urbanisation	Corticosterone, H:L ratio	Tree lizard (<i>Urosaurus ornatus</i>)	French et al. (2008)

response in reptiles. This table is not intended to provide a comprehensive review of relevant studies, but rather examples that span across taxa, stressors, and potential biomarkers of stress. We especially emphasise studies that include novel methodologies and those relevant to the maintenance of reptiles in captivity.

4.3 Future Directions

Studies from the past several decades have significantly enlarged our understanding of physiological stress responses and their behavioural consequences in reptiles (see Table 4.2). Here we identify several areas of research that may provide helpful basic knowledge of how reptiles view and respond to their worlds and how well-informed management and husbandry plans can mitigate risks of stressful environments. Understanding the dynamics of stress within and between the multiple levels at which it acts will surely inform veterinary medicine and procedures. Several lines of investigation in other taxa suggest innovations in experimental methods and designs, often in economically important areas, which are likely to provide new insights in reptile biology that will enable us to better steward their health and welfare.

Recent work has improved our understanding of the relationships of multiple stress biomarkers within individuals, allowing the quantification of both regulation and downstream effects of stress response pathways. A combination of biomarkers provides a more complete picture of organismal stress response than reliance on a single marker alone and is essential for describing the functional and ecological significance of variation in glucocorticoid concentrations (Breuner et al. 2013; Sparkman et al. 2014; MacDougall-Shackleton et al. 2019). For example, one of the primary actions of stress-induced concentrations of corticosterone is to modulate the level of glucose available to different tissues (Sapolsky et al. 2000; Romero and Beattie 2022). Thus, measures of both corticosterone and glucose concentrations, especially over time, provide data on both the activation of the HPA axis (corticosterone) and its downstream effect on energy mobilisation (glucose). Furthermore, glucose is regulated by overlapping regulatory systems involving multiple pathways, including catecholamines, corticosterone, insulin, and glucagon (Strack et al. 1995; Foster and McGarry 1996). Measures of these hormones can provide an additional quantification of the regulation of energy homeostasis across stressful conditions. For example, insulin, glucose, and corticosterone all responded to increasing temperatures and heat stress in the western terrestrial garter snake (*T. elegans*), though the norms of reaction differ among biomarkers (Gangloff et al. 2016).

Of course, stress ramifies more or less directly throughout all levels of organisation, multiplying potential biomarkers and providing clues about the aetiology of various dysfunctions. Amongst these is another potentially useful biomarker in DHEA (dehydroepiandrosterone). This molecule is produced by the adrenal glands, like corticosterone and adrenaline, but ordinarily regarded only as a precursor to sex hormones. However, when DHEA is produced in higher proportion to other adrenal hormones it seems to moderate the stress response and is associated with restorative effects (see Whitham et al. 2020 for a review of stress that encourages looking ‘beyond glucocorticoids’). DHEA serves as a useful example of the pleiotropic nature of so many hormones which play a role in the stress response but also any number of other physiological pathways.

The measurement of multiple biomarkers can be especially useful in describing the relationship between physiological and behavioural responses to stress. For example, Kalliokoski et al. (2012) limited perch availability to green iguanas

(*Iguana iguana*), a highly arboreal species. The study then measured faecal corticosterone levels and compared this with fine-scale behavioural observations. When deprived of climbing opportunity, lizards closed their eyes and laid down less, indicating an increase in vigilance behaviour, whilst at the same time circulating corticosterone increased (Fig. 4.5). Similarly, eastern box turtles (*Terrapene carolina*) in enriched enclosures exhibited fewer escape behaviours and reduced heterophil:lymphocyte ratios, though faecal corticosterone levels were unchanged (Case et al. 2005). These results support the well-established observation that captive reptiles exhibit greater behavioural repertoires when provided with enriching environments (e.g. Rose et al. 2014; Bashaw et al. 2016; Tetzlaff et al. 2018; Spain et al. 2020). The exhibition of behaviours matching expectations based on field observations and the natural history of an organism suggests ways to minimise

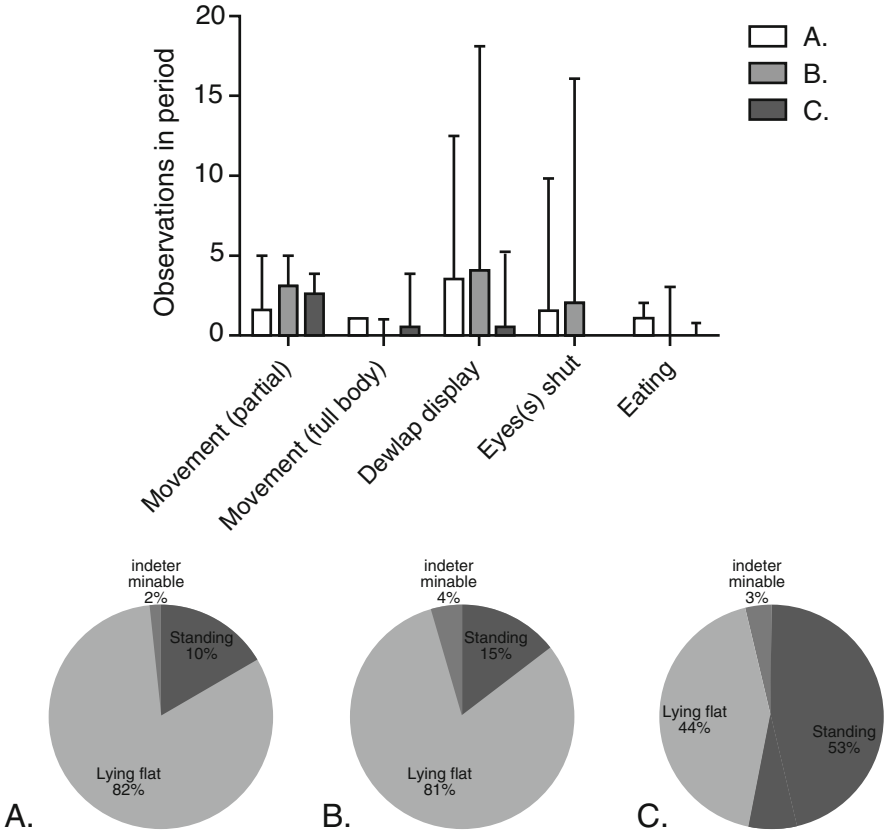


Fig. 4.5 Observed behaviour in green iguanas (*Iguana iguana*). The top graph displays the frequencies (medians with interquartile range) of the listed behaviours observed in a period (1 h, every other day, for 8 days) of: (a) rest and acclimatisation; (b) periods of handling; and (c) periods of deprived climbing. The lower graph shows the distribution between the standing and lying flat postures (Reprinted from Kalliokoski et al. 2012 with permission from Elsevier)

inadvertently caused stress in the captive environment (Greenberg 2002; Warwick et al. 2013; Martínez-Silvestre 2014). However, further work is needed to explicitly link these behaviours with indicators of physiological status. The importance of integrating physiological and behavioural stress response indicators across time has been emphasised in other contexts, for example, in the maintenance of farm animal welfare (e.g. Mormède et al. 2007).

A few recent studies have utilised gene expression, specifically in heat-shock proteins, to examine the cellular response to stressors across ecological contexts. These studies support the specificity of the stress response, a ‘many-stressors-to-many-responses’ model. For example, an exemplary study assessed multiple biomarkers across levels of organisation and examined specific nodes in the stress response networks of garter snakes (*T. elegans*) from two different life-history ecotypes (Schwartz and Bronikowski 2013). Snakes from both ecotypes increased circulating corticosterone and expression of heat-shock proteins under heat stress similarly. However, the response in levels of reactive oxygen species, DNA damage, and gene expression of antioxidant proteins to stressors differed between snakes with differing life-history strategies. The authors propose that divergence in these stress response networks may be underlying the evolutionary divergence in life-history strategies between populations, a phenomenon found in other taxa (reviewed in Schwartz and Bronikowski 2011). Another recent study examining multiple stress indicators across levels of biological organisation in the eastern fence lizard (*Sceloporus undulatus*) provides an excellent example of how stress responses can be tailored to unique stressors and how the response can vary across levels of biological organisation (Telemeco et al. 2019). Whilst the behavioural and endocrine responses were similar in lizards exposed to either heat stress or invasive fire ants, the cellular responses differed. Two metrics of innate immunity correlated with corticosterone within individuals, but in opposing directions. Furthermore, gene expression for heat-shock proteins differed between lizards exposed to heat stress or fire ants. A similar pattern linking cellular and endocrine responses to stress was found in American alligators (*A. mississippiensis*) subject to capture/restraint stress. Plasma corticosterone, uric acid, creatine kinase, and glucose all increased during a stressor. Further, gene expression for heat-shock proteins and glucocorticoid receptors were correlated with the increase in corticosterone (Kohno et al. 2020). This study is noteworthy for its use of gene expression in blood cells, thus allowing non-destructive sampling of individuals. Taken together these findings clearly demonstrate the nuances of the stress response, across levels of biological organisation and in different ecological contexts (Romero et al. 2015), as well as the urgency of appreciating the differences in modes of action at different levels of organisation. Newer statistical tools will facilitate this use of multiple biomarkers in the characterisation and comparison of stress states among individuals and in different contexts (Telemeco and Gangloff 2020). Future work directed at examining the mechanistic relationships between these organismal systems, as well as modeling interactive effects on population dynamics, is crucial to improving husbandry practices and implementing effective management strategies for wild populations.

The stress response is important not only for the individual's ability to cope with ongoing environmental conditions, but can also manifest across generations. Cross-generational effects of stress have been reported in various classes and orders, including reptiles. Understanding the mechanistic basis for the transmission of such effects and their potential adaptive significance in preparing future generations for predicted environmental conditions is of great importance in both captive and wild circumstances (reviewed in Meylan et al. 2012; Love et al. 2013). Glucocorticoid hormones may be particularly important in this respect. Increased circulating corticosterone in reproducing females affects various aspects of offspring phenotypes and can induce preparative stress axis programming (Love et al. 2013). For example, antipredator behaviour was altered by experimentally increasing maternal corticosterone in the viviparous western terrestrial garter snake (*T. elegans*, Robert et al. 2009) and supplementing corticosterone in the eggs of the painted turtle (*C. picta*) influenced offspring righting behaviours and ability (Polich et al. 2018). Such effects may be potentially adaptive, for some individuals in some contexts, though evidence to support this remains weak in reptiles. In one test of the adaptive significance of hormone-manipulated offspring phenotypes, offspring from corticosterone-treated common lizards (*Z. vivipara*) exhibited decreased size, body condition, and growth. However, corticosterone-treated males enjoyed increased survivorship, suggesting that these changes may be adaptive (Meylan and Clobert 2005). Work in this same species shows that elevated maternal corticosterone also affects offspring dispersal behaviours, depending on maternal age and condition (De Fraipont et al. 2000; Meylan et al. 2002; Meylan and Clobert 2004). These and other data illustrate that the influence of elevated maternal corticosterone on offspring phenotypes varies within and across lizard species, and thus evidence for a clear fitness benefit remains equivocal (e.g. Warner et al. 2009; Cadby et al. 2010).

Dehydration stress in reproducing females alters the exploration behaviour of offspring in *Z. vivipara* (Rozen-Rechels et al. 2018) and may bear negative consequences to offspring born in later reproductive bouts (Dupoué et al. 2018b). In aspic vipers (*Vipera aspis*), maternal dehydration stress increases circulating corticosterone but enhances offspring growth rates (Dupoué et al. 2016), which is often correlated with increased survival in snakes. For example, in western terrestrial garter snakes (*T. elegans*), maternal stress-physiology and behavioural reactivity interact to affect offspring growth rates and survival, with larger snakes exhibiting higher survivorship (Gangloff et al. 2017b). In eastern fence lizards (*Sceloporus undulatus*), early-life stressful encounters with an invasive predator did not affect adult stress response, but population history of exposure to these predators did influence corticosterone responses, body size, and survival (McCormick et al. 2017; Owen et al. 2018). Although such effects have important ecological consequences, the potential for these to represent adaptive responses *versus* the results of energetic constraints remains an important direction for future work (Sheriff and Love 2013). The potential for such maternal effects to be transmitted via epigenetics is an area especially open for discovery in reptiles, given that work in other human and non-human species demonstrates that stress hormones are known

to have epigenetic consequences for brain function (Hunter 2012), that epigenetic modification can alter stress responsivity (Weaver et al. 2004; Crews et al. 2012), and that stress hormones induce other transgenerational effects (Beydoun and Saftlas 2008; Jablonka and Raz 2009; Love et al. 2013; Kilvitis et al. 2017; Donkin and Barrès 2018).

Finally, further work is needed to assess how assumptions about the causes and consequences of stress can be applied in animal ethics standards across taxa and contexts with the aim of providing guidance in minimising stress in the captive animal. To date, there are many areas where practices and procedures are sorely in need of empirical research, and which currently draw concern and even controversy. For example, European rules place much stricter regulations on procedures that are more invasive and potentially stressful than 'that caused by the introduction of a needle in accordance with good veterinary practice' (DIRECTIVE 2010/63/EU), thus limiting the use of blood sampling in some studies. However, recent work in the dice snake (*Natrix tessellata*) suggests that collecting blood samples from animals via cardiocentesis does not induce a greater response than that of capture and handling alone (Bonnet et al. 2020).

The importance of understanding stress and how best to mitigate it in practice is also manifest in the extensive concern about the use of cold temperatures (hypothermia) for anaesthesia in reptiles. Such procedures are frequently met with scepticism or disapproval by American Institutional Animal Care and Use Committees (IACUC), animal ethics committees, and others with international remit. In light of the paucity of available evidence for the humane use of hypothermia, this caution is wholly appropriate. Often, anaesthesia is strongly indicated requiring the practitioner to determine the least stressful approach from a selection of alternatives. This situation has prompted some researchers to promote a re-evaluation of the general application of hypothermia based on its apparent efficacy and safety in specific contexts (Lillywhite et al. 2017). Yet additional research is clearly needed. Whilst recent work has demonstrated that it is unlikely that certain small ectotherms experience pain when cooling to near-freezing temperatures (Shine et al. 2015; Keifer and Zheng 2017), others have pointed out that these data are limited and should be approached with caution. These authors suggest banning the use of hypothermia until its effects on both levels of stress and potential for pain are better understood (Warwick et al. 2018). For example, work is needed to quantify the effect of body size on differential cooling rates of extremities *versus* body core and how responses may differ between tropical and temperate species. In addition, it is crucial that any laboratory-based determinations are made in the context of a species' natural history and their adaptive physiological responses to temperature extremes. Characterising these responses is complicated by the observation, as indicated above (and see Fig. 4.1), that some bioindicators of stress response represent adaptive traits in specific contexts. In captivity, many procedures necessarily involve physical as well as physiological restraint, and our pursuit of the most humane alternatives can only be based on inferences from a diversity of behavioural and physiological indicators of stress responses. We applaud open discussion and data-driven debate and hope to see more research soon that can be used to clearly define best practices in

caring for and treating captive reptiles. Until conclusive data are available, we strongly encourage a precautionary approach and discourage potentially erroneous generalisations across species and contexts.

These are topics that can only move forward with the benefit of continuing data collection and open discussion. As researchers further engage these important topics, we emphasise the need to adopt an ethological approach (Greenberg 2023; Gillingham and Clark 2023; Warwick 2023). The ethological attitude we advocate is explicit about eschewing not only obvious bias, but implicit modes of bias, which are notoriously harder to root out.

In this chapter we have indicated some methods for identifying, understanding, and avoiding or mitigating stress in reptiles. We have also encountered a fair measure of apparent paradox attributable to the use of bioindicators of welfare that represent multiple and sometimes conflicting evidence across levels of organisation. Further, interpretation is informed by differing views of animal needs and their relative priorities. This reinforces the message of Langkilde and Shine (2006), urging ‘researchers to seek objective information on the effects of their activities on research subjects, rather than relying upon subjectivity and anthropomorphism in making these evaluations’. In other words, we cannot understand how best to care for captive reptiles based on any single metric such as levels of specific endocrine agents alone. Further, and in particular for those of us directly responsible for the welfare of reptiles in our trust, we must guard against potentially flawed extrapolation from other species and even within species and individuals at different stages of development and in different contexts. This is all offered in the spirit of our shared ambition to be compassionate stewards, effective practitioners, and careful researchers.

4.4 Animal Welfare Conclusions

Throughout this chapter, we have emphasised the need for using empirical evidence to identify and characterise stress and mitigate its effects. Importantly, this means that common assumptions about stressors and the stress response within and between species should be tested and validated before being applied to reptiles in captive settings. One of the recurring themes is the importance of appreciating stressors and stress responses in different contexts (free-living or captive; across life-history stages) and at different levels of organisation. Inappropriate generalising within animals can be as misleading as generalising between animals. The past three decades have seen a burst of interest in the concept of stress: how it is defined, how it is quantified, and its consequences across scales of biological organisation. Much of this work, as summarised here, provides excellent data on which to base decisions regarding the health and welfare of captive reptiles. Yet there are many areas in which we lack data or, potentially, the data we do have are seemingly contrary to our mammalian world experience.

Those responsible for animal welfare must invest in understanding the natural histories of the organisms in their charge through a variety of means, including

primary literature, reference texts, and personal observation. They could implement what is described elsewhere as an ethologically informed research design, deploying ‘DEEP (developmental, ecological, evolutionary, and physiological) ethology’ (Greenberg 2023), and including critical anthropomorphism (Burghardt 1997; Mendyk and Augustine 2023) wherever possible.

As we describe above, bioindicators of stress can vary greatly across species, within species, and even within individuals. For example, daily and seasonal hormonal cycles are part of an individual’s healthy life and these cycles must be taken into account when assessing the well-being of individual animals. Furthermore, bioindicators may be unique to particular stressors and, therefore, multiple indicators are needed to assess the broad well-being of an individual, including both physiological and behavioural observations. For example, corticosterone levels seem not to increase in response to dehydration stress in lizard species studied to date, thus making this an unreliable indicator of this potential stressor in captive populations. Low-level stressors can evoke a healthy response, but this response begins to be detrimental when evoked too often or for too long a period of time, necessitating close monitoring and repeated measures of individuals. Given these challenges, we tried to present key concepts and studies that will provide reference points for a broader understanding of theoretical concepts of stress and the mechanisms of the stress response, which can inform the practical decisions of animal care-givers. Caring for captive reptiles, like all caregiving, is a complex and challenging task that requires our best judgements based on the best data available. As we try to emphasise now, the appreciation of new conceptual advances in understanding stress, the implementation of technological advances to simplify and reduce costs of measuring biomarkers, and a continuing open debate and discussion of practices are keys to the continuing improvement in our abilities to serve the well-being of the animals in our charge.

Appendix: Abbreviations

Abbreviation	Definition
ACM	Adaptive Calibration Model of stress
ACTH	Adrenocorticotrophic hormone
CBG	Corticosterone-binding globulin
CRF	Corticosterone-releasing factor
DA	Dopamine
DHEA	Dehydroepiandrosterone
ELFS	Emergency life-history stage
EPI	Epinephrine
ELFS	Emergency life-history stage
FKBP5	FK506 binding protein 5
GR	Glucocorticoid receptor
H:L ratio	Heterophil:lymphocyte ratio
HPA axis	Hypothalamic-pituitary-adrenal axis

(continued)

Abbreviation	Definition
MR	Mineralocorticoid receptor
MSH	Melanocyte-stimulating hormone
NOREPI	Norepinephrine
PAF	Platelet activation factor
PNMT	Phenylethanolamine N-methyltransferase
POMC	Pro-opiomelanocortin
SAM axis	Sympathetic adrenomedullary axis
SIgA	Secretory immunoglobulin A

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Normal Behaviour

5

James C. Gillingham and David L. Clark

Abstract

Animal behaviour is a phenotypic manifestation that is obvious and readily observable. However, compared to morphology and even some aspects of physiology, behaviour is not so obviously preserved in the fossil record. Nonetheless, inferences can be made from fossils and have been especially useful in shaping our understanding of modern reptilian behaviour. The goal of this chapter is to provide a broad overview of the current knowledge of normal reptilian behaviour. We begin with general definitions and a focus on basic maintenance behaviours such as feeding and thermoregulation. Subsequently, we conduct a broad survey of social behaviours, including courtship and mating, parental care, and combat and territoriality. Finally, we discuss antipredator behaviours of reptiles, including avoiding detection by a predator, escaping a predator and repelling predators. Throughout our review, we address the relevance of normal behaviour as it applies to reptiles in captivity.

Keywords

Courtship · Combat · Thermoregulation · Maintenance behaviour · Aggregation

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5.1 Introduction

Animal behaviour is defined most succinctly and accurately as ‘what animals do’ (Scott 1972). An animal’s behaviour joins structure and function as one of the three phenotypic manifestations, and like the other two is shaped in evolution through natural selection. Moreover, behaviour complements and contributes significantly to the animal’s suite of adaptive characteristics. This aspect of their phenotype is most obvious and readily observable, and therefore, of these three phenotypic manifestations, behaviour is the primary avenue and easiest access through which we might gain insight into an animal’s internal biology.

This is no less the case for the turtles, crocodilians, tuatara, lizards and snakes—today classified as the non-avian reptiles, but henceforth here termed reptiles (Pough et al. 2016). This taxonomic group exhibits a host of characteristics that can be considered pivotal in the course of vertebrate evolution. The Mesozoic vertebrate adaptive radiation produced the dinosaurs whose existence stands as a confirmation of reptilian success brought about by physiological, morphological and behavioural advances. This same radiation ultimately ushered forth lineages leading to the modern reptiles, birds and mammals, which currently exhibit numerous behavioural phylogenetic affinities.

Because an animal’s behaviour is not preserved in the fossil record, accurate information on ancestral reptilian behaviour has been slow to emerge. Nevertheless, by inference, complex social behaviours, once thought to have been only within the domain of birds (avian reptiles) and mammals, may have originated with the reptiles (Hopson 1975, 1977; Ostrom 1986; Weishampel and Horner 1994). Specifically, dinosaur fossil data provide evidence for gregarious behaviour (Lockley 2016), social behaviour (Lockley 1991; Lessem 1992; Horner 2002, 2012), parental care (Weishampel and Horner 1994), courtship (Lockley et al. 2016) and even play behaviour (Rothschild 2015) (see Doody 2023). That dinosaurs may have possessed colour vision (Sillman et al. 1991; Koschowitz et al. 2014) suggests that they may also have utilised complex body colouration to enhance signals important in social communication. These inferred ethological pictures go far to support the phylogenetic importance and pivotal status of reptiles.

The goal of our chapter is to provide a broad overview of current knowledge of normal reptilian behaviour. Because of the wealth of literature available on reptilian ethology, in no way is this meant to be an in-depth review of the topic. The information presented here should provide a basic backdrop against which behaviours observed in captive reptiles can be compared and should serve to emphasise the importance of these behaviours.

5.2 Maintenance Behaviours

Maintenance behaviours may be broadly described as those activities that, on a day-to-day basis, ensure that the basic biotic requirements of the animal’s body are met. Specifically, for the reptiles such activities include feeding, drinking, defecating,

grooming, sleeping and thermoregulatory behaviours (see also Maslanka et al. 2023). Because of the wealth of information available in the literature and their overwhelming importance to the health of captive reptiles, only reptilian feeding and thermoregulatory behaviours will be considered here. Information on sleeping, defecating and grooming (including ecdysis or shedding) in captivity is primarily anecdotal and has received very little study.

5.2.1 Maintenance: Feeding Behaviour

The important role that feeding plays in the life of any organism requires little explanation. The nutritional state of an animal is a direct measure of its health and will have a profound effect on its reproduction and hence its individual fitness (Pough et al. 2016). A broad array of feeding behaviours can be seen amongst reptiles; and, for any given species, patterns of feeding appear to be integrated with all other aspects of its life history in a complex and adaptive fashion. This diversity of feeding behaviours seen in reptiles is explained, in part, by their morphology and the sensory channels through which they mediate their foraging activities.

Most reptiles are carnivorous predators that locate and consume a prey as opposed to being a herbivore that consumes plants (Stevens 2010). Less than 2% of extant reptiles are herbivores (Espinoza et al. 2004). Regardless of which strategy is exhibited, prior to any feeding event, a reptile must locate its food, and under natural conditions, this requires a search. Historically, the search or foraging behaviours of reptiles (and other animals) has been categorised in a dichotomous fashion. Those reptiles that tend to remain in one spot and wait for prey to pass within their range have been called ‘sit-and-wait’ predators, whilst those that move about and actively search for their prey are termed ‘widely-foraging’ reptiles (Pianka 1966; Huey and Pianka 1981, 2007). This distinction is particularly clear when a sit-and-wait or ambush predator exhibits highly specialised structures and behaviours adapted to that strategy. The aggressive visual mimicry exhibited by the tongue luring in the alligator snapping turtle (*Macrochelys temminckii*) (Spindel et al. 1987) and the tail- and/or lingual-luring (Fig. 5.1) seen by a variety of snakes (Hansknecht 2008; Glaudas and Alexander 2017) leave no doubt as to the sit-and-wait strategy used by these animals. Herbivorous reptiles, on the other hand, must utilise widely foraging behaviour because obviously plants do not move around and come to their consumer (Herrel 2007).

When such specialised feeding adaptations are not apparent, care must be taken in categorising reptiles into one or the other of these strategies (McLaughlin 1989; Perry et al. 1990). For example, in the past certain reptiles have been labelled as ‘widely-foraging’ or ‘sit-and-wait’ simply on the basis of their morphology (e.g. in snakes, Ruben 1977). Intermediate search patterns may be exhibited and many reptiles may switch strategies due to variable prey density and availability (Whiting 2007). Additionally, their search patterns may be tempered by the demands of behavioural thermoregulation (Secor and Nagy 1994; Ayers and Shine 1997). However, more recent investigations have shown that several reptiles do not

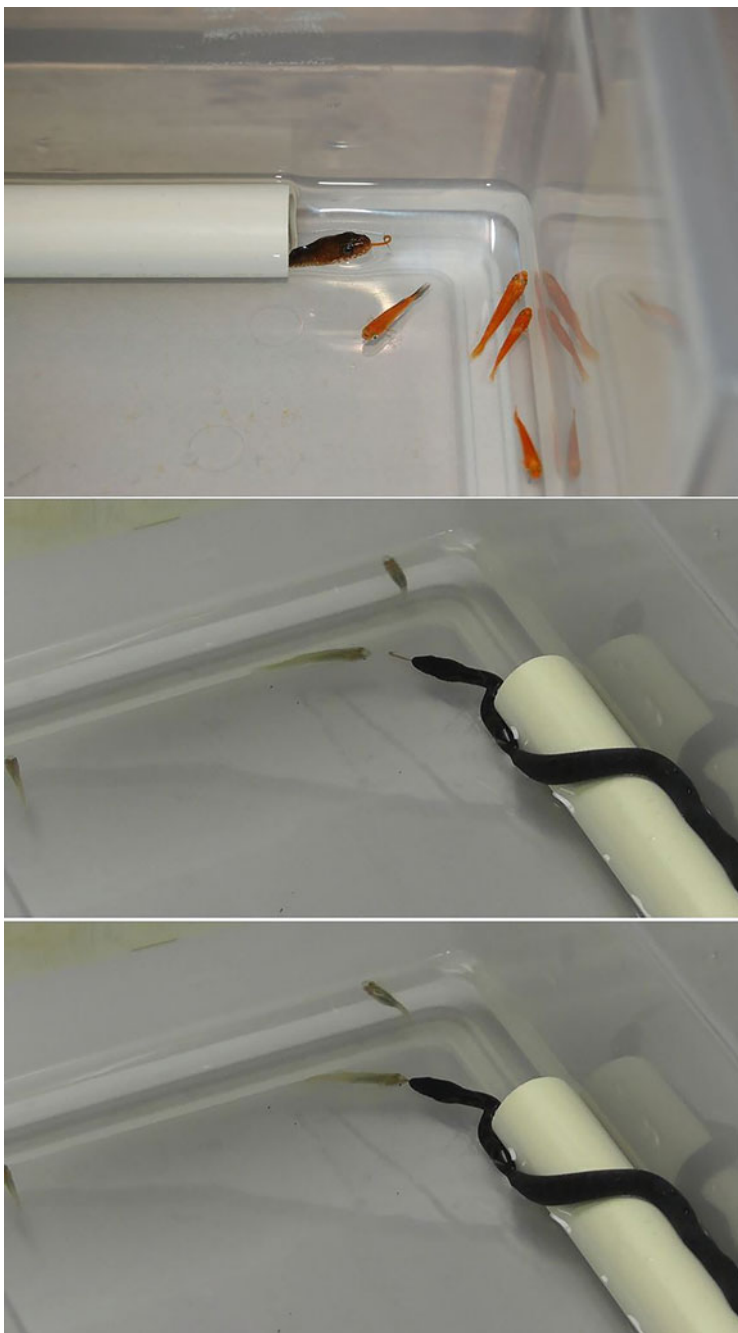


Fig. 5.1 Lingual-luring in the Mangrove saltmarsh snake, *Nerodia clarkii*. Above: tongue contortions during active luring in the vicinity of potential prey fish (*Xiphophorus*). Center and below: active luring and approach by potential prey fish (*Xiphophorus*). Photos courtesy of Kerry Hansknecht

conform to these preconceived categories and that this dichotomy should actually be a continuum (Miles et al. 2007).

Whatever the search strategy exhibited, this component of a successful predatory event is followed by the location of the food item being sought. Irrespective of whether their 'prey' is a plant or animal, reptiles have evolved sensory systems that are adapted for prey location. Photoreception via the eyes, infra-red reception through pit organs, mechanoreception via the ears and/or integument and chemoreception through the tongue, nose and/or vomeronasal organ all contribute to successful prey location in varying degrees (see Lillywhite 2023; Crowe-Riddell and Lillywhite 2023). The squamates (lizards and snakes), crocodylians, turtles and tuatara each exhibit differences in their reliance on a specific sensory system during distance-reducing social behaviours (see below, and Doody 2023) as well as in prey detection.

The tuatara (*Sphenodon punctatus*) is a carnivorous predator feeding primarily on insects and only rarely intentionally ingesting plant material (Walls 1981). Although its fleshy tongue contains taste buds (Schwenk 1986), and it possesses a tubular vomeronasal system (Halpern 1992), vision seems to be the dominant sensory modality utilised in prey location. Prey movement cues are important in bringing about a rapid prey attack and capture, followed by ingestion. Walls (1981) states, 'Tuatara will attempt to ingest almost anything that moves'. That tuatara have been known to occasionally feed on stationary food items such as carrion and fruit (Bredeweg and Nelson 2010) may indicate that chemosensory channels may also be used in their search for food. Although tuatara seem to primarily show a sit-and-wait foraging strategy, they have been shown to widely forage on occasion (Cree 2014).

With the exception of a few species, notably the alligator snapping turtle (*Macrochelys temminckii*) and the mata-mata (*Chelus fimbriata*), turtles tend to be active foragers. There is ample evidence that both chemosensory as well as visual channels are used in prey detection. Through vomerolfaction freshwater species in particular are capable of identifying prey items as well as conspecifics (Punzo and Alton 2002; Ibanez and Vogt 2015). Turtles possess colour vision (Emerling 2017), and so it is not surprising that they may use this sensory mode in their foraging as well. This is certainly the case for sea turtles and specifically the leatherback turtle (*Dermochelys coriacea*) (Wallace et al. 2015). Unfortunately, the current oceanic accumulation of anthropogenic plastic debris in all major oceans has led to its ingestion by sea turtles due to its visual misidentification as prey. This situation has led to the death of as well as sublethal effects on turtles and other wildlife (Schuyler et al. 2013; Santos et al. 2016).

Crocodylians forage using a combination of active hunting as well as sit-and-wait strategies in their location of prey (Grigg and Kirshner 2015). Generally, this strategy takes place in the water or at the land-water interface but can take place entirely on land, especially at night and for larger species (Dinets 2011). Crocodylians, like birds, lack a vomeronasal organ but do have well-developed olfactory and gustatory systems (Schwenk 2008), which have been shown to be used in food location and recognition both in the water and on land (Weldon and Ferguson 1993). Although crocodylians possess colour vision (Sillman et al. 1991),

their underwater visual acuity is apparently poor. Despite this apparent lack of acuity, they hunt very successfully in this environment (Fleishman and Rand 1989). This ability is probably due to the presence of touch receptors and integumentary sense organs (ISOs) on the surface of the crocodylian head and body (Grigg and Kirshner 2015; Schneider et al. 2016; see also Lillywhite 2023; Crowe-Riddell and Lillywhite 2023). These senses, along with chemosensation, undoubtedly contribute to the crocodylian success at foraging underwater and at night.

Of the major sensory modalities, the chemosensory system plays a central role in the feeding behaviour of the squamate reptiles (Halpern 1992; Lillywhite 2023; Crowe-Riddell and Lillywhite 2023). Using their tongues to transfer information to their well-developed vomeronasal organs, the non-airborne chemical attributes of prey are used by predatory lizards and snakes as cues to locate prey (Schwenk 1995). More volatile, airborne chemical cues are picked up by the nasal olfactory system (Pianka and Vitt 2003).

Using garter snakes (*Thamnophis*) as models, Burghardt and his team of students have contributed a great deal to our understanding of the snake predator-prey interaction. The bifurcate ophidian tongue acts as an environmental probe in frequently and regularly sampling the snake's surroundings for relevant stimuli. Tongue-flick rate, therefore, is an accurate and proportional measure of a snake's level of interest in its environment, particularly whilst searching for food (Burghardt 1980), whether earthworm, fish or amphibian. For garter snakes, this tool has been used to assess the role previous experience plays in prey preference (Burghardt 1977; Ford and Burghardt 1993), how ontogeny affects these preferences (Burghardt 1978) and how chemical cues mediate an attack response (Burghardt 1966).

Further, Chiszar et al. (1983) have described a behaviour observed in the venomous crotalid snakes termed 'strike-induced chemosensory searching' (SICS). Rattlesnakes elevate their tongue-flick rate following biting a prey item, which may facilitate the location of released or escaped prey. This search behaviour continues to be studied in rattlesnakes (Putman et al. 2016) and has also been documented in several harmless colubrid snakes (Cooper et al. 1989) and even in lizards (Cooper 1992), so this behaviour may be more widespread amongst the squamate reptiles than previously thought.

Studies focusing on vomerolfaction and the specific nature of the cues used by snakes in prey location have been slow to emerge. Earthworms form a large proportion of the diet for the eastern garter snake (*Thamnophis sirtalis*) and it has been shown that these snakes use earthworm soil castings to locate these prey (Gillingham et al. 1990) and that the specific stimuli involved may include non-volatile single polypeptide chain glycoproteins from the earthworm integument (Jiang et al. 1990). Prairie rattlesnakes (*Crotalus viridis*) forage widely for demes (i.e. local concentrations) of rodents and once located they use ambush strategies for prey capture (Duvall et al. 1985; Duvall and Chiszar 1990). The specific chemical cue(s) used by these snakes to locate the rodent deme have not yet been identified. However, recently the specific chemical cue used by rattlesnakes to locate envenomated prey following SICS has been identified as non-enzymatic disintegrins crotatroxin 1 and 2, components of the venom (Saviola et al. 2013; Lillywhite 2023; Crowe-Riddell and Lillywhite 2023).

Blindsnakes in both North America (*Leptotyphlops* and *Typhlops*; Gehlbach et al. 1971) and Australia (*Ramphotyphlops*; Webb and Shine 1992) feed on ants and termites and have been shown to follow the pheromone trail laid down by these insects. Chiszar et al. (1992) were the first to show that the internal body chemicals of a potential prey item were attractive to snakes. They demonstrated that the brown tree snake (*Boiga irregularis*) exhibited an elevated tongue-flick response to mammalian blood as compared with water and other control substances.

Scavenging behaviour (feeding on dead and putrid prey) is quite common in snakes as this behaviour has been recorded for nearly 40 species (DeVault and Krochmal 2002; Casper et al. 2015). Scavenging has been documented more frequently for piscivorous (fish-eating) species and pit vipers (Marques et al. 2017) and the latter have been shown to mediate this behaviour through chemosensory channels (Gillingham and Baker 1981). Living prey is undoubtedly the main food sought by these snake species, but it is expected that terrestrial species with rather catholic dietary preferences and that use a variety of sensory cues in the location of their prey may show occasional scavenging behaviour (Sazima and Strussman 1990; Kane et al. 2016). Although not as well-documented amongst the lizards, scavenging behaviour has been observed in the monitors (Varanidae) (Rahman et al. 2017).

Like the snakes, lizards also rely on chemical cues via tongue-flicking to identify food during their foraging episodes (Cooper 2007). Prey odour discrimination has been demonstrated for most of these carnivorous and/or insectivorous species (Cooper 1992) but, importantly, chemical cues are also used by herbivorous lizards, such as the desert iguana (*Dipsosaurus dorsalis*), to locate their food (Cooper and Alberts 1990; Herrel 2007). It has long been accepted that herbivorous or carnivorous, lizard search strategies are exhibited along phylogenetic lines (Pough et al. 2016). Lacertid, Scincid, Teiid and Varanid lizards are primarily active foragers whilst most iguanid lizards tend to be sit-and-wait predators. However, for the squamates as a whole, baseline tongue flick rate (TFR) may more accurately predict foraging strategy—ambush or sit-and-wait foragers exhibiting higher TFRs (Baeckens et al. 2016).

Vision also plays an important role in the squamate reptile's predatory behaviour. Burghardt and Denny (1983) and Teather (1991) have shown that visual cues are important in initially attracting the attention of garter snakes (*Thamnophis*) to their prey and are further enhanced by the presence of prey odour. Such cues are apparently not involved in eliciting prey attack but are important in the snake's orientation to the prey. However, in certain aquatic species of *Thamnophis* (for example, *T. couchi*) and in North American water snakes (*Nerodia* spp.) prey attack can be elicited by visual stimuli alone (Drummond 1985).

Lizards have long been known to be highly visually oriented animals (Carpenter and Ferguson 1977; Eason and Stamps 1991) and some genera (for example, *Chamaeleo*) rely on vision as their principal sensory modality (Pianka and Vitt 2003) because the tongue has evolved into a specialized feeding organ. Most lizards possess colour vision, and those with high visual acuity, such as the anoline lizards, utilise this sensory modality in both feeding as well as social situations (Fleishman et al. 2017). However, in a similar manner to the terrestrial snakes described above,

vision and vomerolfaction in lizards appear to act in synergy during feeding episodes.

5.2.2 Feeding Behaviour: Animal Welfare Conclusions

The highly diverse array of reptile feeding behaviours outlined here is due in part to the phylogenetic differences of the various species under consideration. However, considerable intraspecific variation in these behaviours may also be seen. Such differences are attributable to geographical background and, importantly, may be genetically controlled (Arnold 1981). An understanding of the heritability of behaviour and its relation to reptile feeding preferences is crucial to successful captive feeding of these animals. The geographical and genetic background of captive animals cannot be ignored (Brodie and Garland 1993). A prerequisite for successful captive maintenance is knowing what and how much to feed the species in question (Nagy 2001). For all reptiles, a normal feeding episode often contains searching behaviours, both prior to prey location and following a prey strike. A consideration of adequate captive space as well as the spatial arrangement of cage furnishings, particularly for those species that show active foraging behaviours, must be a prerequisite to the most successful captive maintenance of these animals.

5.2.3 Maintenance: Thermoregulatory Behaviour

The mosaic of interrelated biochemical reactions within living organisms is driven by heat energy (Huey 1982; Pough et al. 2016). Being ectotherms, reptiles must seek this thermal energy from their physical environment. Historically, Cowles and Bogert (1944) were the first to show that most reptiles are not thermoconformers that simply allow their body temperature to passively follow the highly variable ambient temperature. On the contrary, they demonstrated that many reptiles have a normal activity range (= activity temperature range; Pough and Gans 1982). In current terminology, reptiles strive to regulate their body temperatures between upper and lower setpoints (Aquilar and Cruz 2010; Pough et al. 2016). In other words, they are thermoregulators. Reptiles achieve this goal under natural conditions by behavioural, morphological and physiological means (Pough et al. 2016). Behavioural thermoregulation is accomplished by making postural adjustments and by shuttling movements into and out of microhabitats of varying heat availability. This involves using a combination of basking in the sun (heliothermy) and absorbing heat from objects in the environment (thigmothermy). Tropical and desert reptiles require areas in which to cool themselves, e.g. vegetative shade (Aquilar and Cruz 2010).

The tuatara (*Sphenodon punctatus*) has had relatively little study with regard to its thermoregulatory behaviour. On Stephens Island, New Zealand, it occupies two distinctive habitats: remnant forest areas and open meadows with old paddocks. In both sites, it uses burrows as retreat sites, but in the latter, its above-ground activity is

primarily nocturnal. In the forests, it is active both day and night (Gillingham and Miller 1991; Corkery et al. 2018). In both cases, during the daylight hours it is capable of maintaining a body temperature above ambient temperature and does so either by sitting at the burrow entrance with its head exposed (paddock animals) or by exposing its body to patches of sunlight (forest animals) (Saint Girons et al. 1980; Carmichael and Gillingham 2004). Although tuatara can be considered a thermoregulator, it apparently does so with a low level of precision (Saint Girons et al. 1980; Barwick 1982; Corkery et al. 2018; Gillingham unpublished).

Compared to other reptiles, tuatara tend to maintain lower preferred body temperatures. When captive tuatara are given a choice of temperature in a thermal gradient, they tend to select temperatures between 20 and 22 °C (Cree 2014). Similarly, their active temperature range is lower than for most reptiles, ranging between 5 and 30 °C. The ability of tuatara to tolerate cold temperatures is probably not an ancestral feature of Rhynchocephalians but is likely an adaptation to inhabiting a cool environment (Carmichael and Gillingham 2004; Cree 2014).

Turtle thermoregulatory behaviour has not been studied extensively, and more information is available for terrestrial species (e.g. *Terrapene* and *Testudo*) than for those that inhabit a freshwater or marine environment (Avery 1982; Rowe et al. 2017). Behaviourally, terrestrial forms may thermoregulate by shuttling between microhabitats (do Amaral et al. 2002; Parlin et al. 2017). Marine and freshwater turtles may bask by floating at the water's surface where they may be capable of absorbing solar radiation (McGinnis 1968; Moll and Legler 1971). One advantage that aquatic species may have is the ability to exploit multiple and very different environments to thermoregulate. It has been demonstrated that aquatic reptiles, like many freshwater turtles, will exploit both the relatively stable aquatic habitat of their environment and the more variable and cyclic atmospheric environment during their daily thermoregulatory activities (Crawford et al. 1983; Manning and Grigg 1997; Rowe et al. 2017). Freshwater species often bask on terrestrial sites (floating or protruding log, floating mat of vegetation, sand bar, protected shoreline and the like), and in some species, considerable aggression has been reported to occur between basking individuals. The North American painted turtle (*Chrysemys picta*), has been reported to exhibit open mouth gestures, biting and body displacement whilst basking in groups, suggesting basking site competition (Lovich 1988).

There appears to be considerable variation in the thermoregulatory precision amongst terrestrial and semiaquatic freshwater turtle species and it may vary seasonally or diurnally. For example, painted turtles *C. picta* was found to thermoregulate during the late evening and early morning hours and thermoconform during the afternoon (Rowe et al. 2017). The Argentine snake-necked turtle (*Hydromedusa tectifera*), a nocturnal freshwater species, tends to be a thermoconformer during its activity period (Molina and Leynaud 2017).

It has been suggested that, in contrast to freshwater and terrestrial turtles, sea turtles exhibit some degree of endothermy (Meek and Avery 1988). However, this remains unsubstantiated because raised body temperatures have been recorded in moving body parts rather than in the whole body (Standora et al. 1982). Smith et al. (1986) demonstrated that larger turtles have a greater ability to thermoregulate than

smaller individuals. The marine leatherback turtle (*Dermochelys coriacea*) uses a combination of large size, bodily insulation and cardiovascular changes to thermoregulate (Palodino et al. 1990). It has been suggested that such 'gigantothermy' may have allowed dinosaurs to inhabit thermally inhospitable regions of the earth during the cretaceous (Palodino et al. 1990).

Normal behaviour of crocodylians is exhibited over a wide range of temperatures with most species being active between 15 and 35 °C (Grigg and Kirshner 2015). Young American alligators (*Alligator mississippiensis*) have been shown to exhibit sustained treadmill performance between 25 and 35 °C (Emshwiller and Gleeson 1997) and some individuals have been recorded to tolerate temperatures down to 5 °C (Brisbin et al. 1982). Although most crocodylians do not thermoregulate with the same precision as the squamate reptiles (see below), they use a variety of behaviours to achieve body temperatures within the ranges above (Grigg and Kirshner 2015). However, one species, the Australian freshwater crocodile (*Crocodylus johnstoni*), appears to thermoregulate very much like terrestrial lizards by moving back and forth between land and water (Seebacher and Grigg 1997). All crocodylians, like freshwater turtles, bask by 'hauling out' onto dry land (Johnson et al. 1978). Smith (1979) points out that water is also used for, and important to, their thermoregulation. The American alligator (*Alligator mississippiensis*) uses a variety of thermoregulatory postures whilst in the water, ranging from 'high floating' to 'complete submergence' (Smith 1975). Further, this species is known to excavate wallowing holes in which to cool themselves under conditions of intense heat and will construct dens in which to retreat to avoid freezing conditions. Like leatherback turtles mentioned above, many crocodylians achieve sizes that are conducive to taking advantage of thermal inertia to maintain a relatively stable body temperature. Also, like other very large reptiles, a variety of morphological and physiological (especially cardiovascular system) mechanisms contribute to their behavioural thermoregulatory abilities.

In a departure from the tuatara, turtles and crocodylians, about 20% of squamate reptile species are viviparous (live-bearing) as opposed to oviparous (egg-laying). A generally accepted explanation for the evolution of this characteristic is known as the 'cold climate' hypothesis (Tinkle and Gibbons 1977; Shine 1985). Through the use of behavioural thermoregulation, gravid female squamate reptiles optimise the developmental temperature of their unborn offspring bringing about more rapid development. Such behaviours should be selected for colder climatic regimes. The frequency of lizard and snake species exhibiting viviparity does in fact increase with latitude (Tinkle and Gibbons 1977; Gregory 2009).

There is probably more information on the thermoregulatory behaviour of lizards than for any other group of reptiles (see Avery 1982, for review) and most of this information pertains to diurnal species. No lizard species can be considered to be entirely thermoconforming (Diele-Viegas et al. 2018) and in general, lizards achieve a high degree of thermoregulatory precision (DeWitt 1967; Bowker 1984). In fact, the subarctic viviparous lizard (*Zootoca vivipara*) is one of the most accurate thermoregulators among reptiles (Herczeg et al. 2003).

Lizards thermoregulate by shuttling between warmer and cooler microhabitats and bask where they can optimally achieve their preferred body temperature. In lizards such as the new world anoles (*Anolis*) that enjoy an arboreal or semiarboreal existence, trees and shrubs are used extensively as basking sites (Hertz 1992a). For species such as the old world *Podarcis* and *Psammodromus* that are quite terrestrial, the ground surface proper or ground structure (for example, rocky outcrops, stone walls) are used for basking purposes (Van Damme et al. 1990; Diaz 1991). Patterns of daily activity have profound effects on lizard behavioural thermoregulation. For diurnally active Galapagos lava lizards (*Microlophus* sp.) microhabitat use for thermoregulation can vary seasonally (Rowe et al. 2019). However, on a daily basis, lava lizards move in between sunny and shaded sandy areas throughout the day and bury themselves in the sand or hide in rock crevices overnight (Rowe et al. 2019).

Basking lizards tend to regulate the rate of heat energy uptake by additionally using body orientation (but see Greenberg 1976) to the sun or a warm object, or through changes in body posture. For example, heating rates through thigmothermy may be reduced by elevation of the trunk off the substrate, or, with the trunk in contact with the substrate, elevation of the four limbs (Avery 1979). The latter is commonly observed in the Lacertidae, Scincidae and Teiidae. Large size also contributes to substantial thermal inertia in the Komodo dragon (*Varanus komodoensis*) (McNab and Auffenberg 1976), allowing it to maintain an appreciable temperature differential with ambient temperature, day and night.

Although fewer data are available for these forms, nocturnal lizards also thermoregulate behaviourally. A number of gecko species have been shown to thermoregulate with as much precision at night as during the daylight hours (Sievert and Hutchison 1988; Kearney and Predavec 2000). Live-bearing pregnant female lizards have the ability to maintain by behavioural means the temperature of their embryos at their optimum for development. The montane North American lizard (*Sceloporus jarrovi*), is live-bearing, and pregnant females regulate with more precision than do males or nonpregnant females (Beuchat 1986). Gravid egg-laying velvet geckos (*Amalosia lesuerii*) thermoregulate at higher body temperatures than males or non-gravid females (Dayananda et al. 2017).

North American garter snakes (*Thamnophis*) apparently show an intragenerically stable thermal preferendum of 30 °C (Rosen 1991). Some (for example, *T. elegans*), following early morning heliothermic basking, regulate their body temperature at a stable plateau of 30 °C throughout the remainder of the daylight hours when enough ambient heat is available (Peterson 1987). Further, this species tends to choose retreat sites under rocks of intermediate thickness, which on hot days minimises their chances of overheating and during the night allows them to achieve temperatures closer to or within their activity temperature range (Huey et al. 1989). Snake basking site selection is an important aspect of their behavioural thermoregulation (Fitzgerald et al. 2003).

In the absence of suitable ambient heat energy, some pythons demonstrate shivering thermogenesis as a mechanism to elevate and hold steady the incubation temperature of the female's clutch of eggs which she surrounds and protects. This

behaviour, also known as facultative endothermy, was first demonstrated in captivity for Burmese pythons (*Python molurus bivittatus*) (Vinegar et al. 1970) and more recently in the field for *Morelia spilota* (Slip and Shine 1988; Pearson et al. 2003).

5.2.4 Thermoregulatory Behaviour: Animal Welfare Conclusions

There is no question as to the importance of thermoregulatory behaviour to the success of reptiles under natural conditions. Magnuson et al. (1979) suggest that the thermal environment is a resource and as such may be partitioned under competitive conditions, but, given variations in the thermal heterogeneity of a given environment, such partitioning may not be possible, especially for territorial species (Hertz 1992b). Nevertheless, the energy invested in behavioural thermoregulation by reptiles must be weighed against the costs of increased risks of predation whilst doing so (Huey and Slatkin 1976; Rocha and Bergallo 1990).

The captive environment may place serious constraints on the thermoregulatory behaviour of reptiles. In all cases, information on the natural thermal regime of a given species should be known, and the captive environment should be arranged to provide the animal with thermal microhabitats reflecting this range of temperatures. Further, this environment should be furnished with substrate heterogeneity that closely approximates natural basking and thermoregulatory sites for that species (Bashaw et al. 2016).

Most reptiles are probably ‘hard-wired’ to exhibit thermoregulatory behaviour in a thermally diverse environment and placing them in a thermally uniform environment will certainly repress such behaviours with inevitably undesirable consequences. That thermoregulatory behaviour is tightly coupled with such activities as foraging and reproductive behaviours means any disruption to this pattern will undoubtedly affect the latter. For most reptiles, basic thermal requirements can be met by providing infrared and ultraviolet light in addition to heat blocks/pads and basking sites. Captive breeders should be cognizant of the thermal preferences of their particular species.

Even handling of captive animals can disrupt a normal thermoregulatory pattern. It has been shown that some lizards (*Callopiastes*) respond to handling and thermistor probing by behaviourally elevating their body temperatures by as much as 6 °C for at least 30 min (Cabanac and Gosselin 1993). This ‘emotional fever’ could be a major factor in captive husbandry and means that the frequency and extent of physical manipulations of captive reptiles should be carefully considered and perhaps minimised.

5.3 Distance-Reducing Behaviour

Distance-reducing behaviours are those that function to decrease the distance between two individuals. Such interactions generally occur between two or more conspecifics, regardless of their relationship to one another, and can be classified as

social behaviours (Gillingham 1987). In reptiles, such sociality includes aggregation, courtship and mating, and parental care behaviours.

5.3.1 Distance-Reducing Behaviour: Aggregation

Animal grouping patterns where individuals are spaced closer together than would be expected by chance, and where such clumping is the result of a common attraction, is termed aggregation (Brown 1975; Gregory et al. 1987). If this aggregation is exhibited continually throughout the year or between the same individuals between years, it is known as a 'stable' aggregation. This type of sociality has been observed in 26 snake species, 67 lizard species and 1 amphisbaenian (Gardner et al. 2015). For most reptiles general aggregation most commonly occurs in order to bring about a higher probability of finding mates for reproduction and this will be considered in the next section. However, there are other reasons why reptiles form aggregations. In many temperate zone reptiles, aggregations often occur on a seasonal basis. These aggregations may be for winter dormancy (brumation, Mayhew 1965) or hibernation (*sensu* Gregory 1982; Ultsch 1989) where such clumping may confer some thermoregulatory advantages to the hibernators (Gregory 1982). Communal hibernation, or 'denning' is common in temperate zone snakes (Parker and Brown 1973). The well-studied red-sided garter snakes (*Thamnophis sirtalis parietalis*) exhibit massive denning congregations in Manitoba (Gregory 1974; Shine 2012). Communal hibernation has been documented for some turtles (Smith and Cherry 2016) and a few lizards (Ruby 1977; Elfstrom and Zucker 1999; Curtis and Baird 2007). In some snakes (e.g. *Crotalus* and *Thamnophis*) limited movements as a response to changes in thermal gradients probably occur within the dens during hibernation (Gillingham and Carpenter 1978; MacCartney et al. 1989; Nordberg and Cobb 2017). Further, snakes are apparently able to locate their dens by following conspecific scent trails (Ford 1986; Costanzo 1989; Mason and Parker 2010).

A number of reptiles show aggregative behaviour in response to a common food source. Feeding aggregations have been seen in water snakes (*Nerodia*; Gillingham and Rush 1974) and garter snakes (*Thamnophis*; Arnold and Wassersug 1978) in response to seasonal surges in the density of fish or amphibian prey, respectively. The carnivorous Komodo dragon (*Varanus komodoensis*) (Bull et al. 2010) and the herbivorous lizard (*Ctenosaura hemilopha*) (Carothers 1981) exhibit communal feeding behaviour. Both freshwater and marine turtles exhibit foraging aggregations (Thomson et al. 2015; Adler et al. 2018).

In a non-courtship/mating but reproductive context, fifteen species of snakes and four species of lizards exhibit gravid female aggregation (Graves and Duvall 1995). Female sea turtles (Carr and Ogren 1960; Hirth 1980) and tuatara (Cree and Thompson 1988; Cree 2014) aggregate at oviposition sites. Similarly, 20 species of snakes and sixty species of lizards show communal egg-laying (Graves and Duvall 1995). Although reptilian aggregation may be mediated through a variety of sensory channels, it has been shown to be pheromonal in snakes (Graves et al.

1991). The ringneck snake (*Diadophis punctatus*) is notorious for its aggregating in large numbers although the reasons for such grouping patterns are unclear (Dundee and Miller III 1968).

5.3.2 Aggregation: Animal Welfare Conclusions

That our understanding of the function of reptilian aggregation is not complete makes it no less important. Reptile species that are naturally gregarious should at least be given the opportunity to be so in captivity, commensurate with environmental conditions that facilitate avoidance of negative behaviours such as co-occupant aggression. Forcing a reptile that normally has a high level of physical contact with its conspecifics into a solitary behavioural existence may have profound effects on its well-being. For example, it is possible that some normally social reptiles kept in isolation may begin to exhibit spontaneous social behaviours.

Interspecific aggregation, typical of most reptiles can be replicated in captivity. Reptiles in their natural habitat normally encounter other species on a daily basis, many of which pose no predatory threat to them. Such syntopic interactions are certainly natural and may, in perhaps quite subtle ways, be important to the daily routine of that reptile. Although care must be taken as to the choice of these heterospecific associates, such groupings in captivity may be beneficial. For example, zoo displays containing both gopher tortoises (*Gopherus polyphemus*) and eastern diamondback rattlesnakes (*Crotalus adamanteus*) have resulted in greater longevity and better feeding by these captives (R. Pawley, pers. comm.).

5.3.3 Distance-Reducing Behaviour: Courtship and Mating Behaviour

Courtship is one of the most conspicuous behaviours observed in reptiles. This behaviour serves a variety of functions, including mate stimulation, species recognition, sexual recognition and mate evaluation, the goal of which is to successfully procreate. The diversity of courtship repertoires and mating systems documented for the reptiles parallels that seen in their feeding strategies, in that it is largely a reflection of the variation in their morphology and primary sensory modalities. For some reptiles, a strong case can be made for the coevolution of reproductive displays and a number of other life-history characters related to predatory behaviour (Losos 1990).

Courtship and mating in tuatara (*Sphenodon punctatus*) under natural conditions have been described by Gillingham and Miller (1991). This behaviour is mediated through visual channels and the male tuatara initiates courtship in the presence of a female by exhibiting crest erection and both trunk and gular inflation. The male slowly approaches the female using a stiff-legged walk called a '*Stoltzergang*' (Gans et al. 1984). Receptive females do not retreat down their burrows, rather they allow

the male to mount, effect cloacal apposition and mate. The pair remains *in copula* for about an hour (Gillingham and Miller 1991).

The mating system exhibited by tuatara is best described as seasonal monogamy but is polygynous from season to season (Moore et al. 2009a). Although male tuatara guard females within their territories, males outside these territories are capable of mating with these females, and therefore low levels of multiple paternity (polyandry) have been documented (Moore et al. 2009a). Large males achieve more matings (Moore et al. 2009b) and possess larger and brighter dorsal and nuchal spines than smaller individuals (Clark and Gillingham unpublished). The latter characteristic further attests to the importance of vision in mediating tuatara courtship and mating behaviour.

Turtle courtship is initiated and mediated through visual, acoustic, chemosensory and tactile channels. Box turtles (*Terrapene*) use vision and chemical cues in the location of potential mates (Dodd 2001) and the wood turtle (*Glyptemys insculpta*) apparently shows trailing behaviour of conspecifics (Tuttle and Carroll 2005; Whitear et al. 2017). Males of terrestrial genera such as *Gopherus* court potential female mates with a variety of biting and nipping behaviours as well as by using their shells for deliberate ramming of their partner (Auffenberg 1966, 1977; Weaver 1970). For the wood turtle (*Glyptemys insculpta*) courtship is similar to *Gopherus* consisting of open mouth displays, biting, lunging and chasing the female. In practice, these behaviours are similar to the aggressive displays of male-male encounters (Kaufmann 1992). For aquatic or semi-aquatic turtles, the titillation sequence observed in the emydines (Jackson and Davis 1972; Kramer and Fritz 1989) has obvious tactile elements (Fig. 5.2), but because it is performed in direct view of the female it may also be visually important. The head-swaying displays used by male Blanding's turtles (*Emydoidea blandingii*), coupled with the bright yellow ventral neck region, imply the use of these colours and movements as visual signals (Baker and Gillingham 1983). Although few studies document its importance in the context of courtship and mating, chemosensory channels are undoubtedly used by chelonians in a social context (Mahmoud 1967; Jackson and Davis 1972; Iverson 1975; Manton 1989; Scott 1989; Galeotti et al. 2007; Whitear et al.

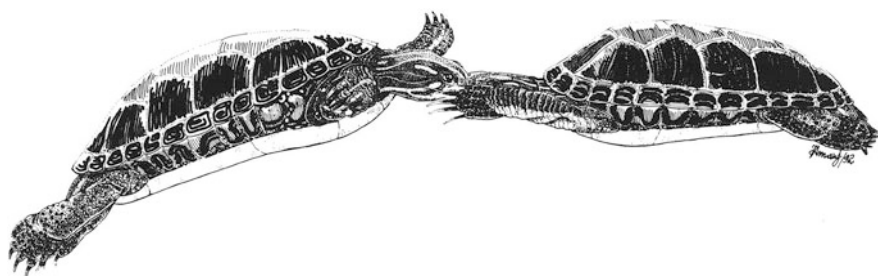


Fig. 5.2 Male (on the right) painted turtle (*Chrysemys picta*) using forelimbs and elongate toenails to titillate the head and neck of a female during aquatic courtship. (Based on photographs by the author (JCG) and illustrated by Jose Pedro do Amaral)

2017). Males of many tortoise species produce sounds that may be a factor in successful courtship and mating (Auffenberg 1977; Galeotti et al. 2005).

Female receptivity results in the male successfully bringing about cloacal apposition and penile intromission, often resulting in the male rocking back into a vertical position (Carpenter and Ferguson 1977; Baker and Gillingham 1983; Dodd 2001). The duration of coitus is variable across species but ranges from 15 minutes to over an hour. Although multiple paternity is common in many reptiles, to date it has only been shown for a little over a dozen species of turtles (Uller and Olsson 2008).

Crocodylian courtship and mating behaviour is complex and is mediated through all major sensory channels: visual, acoustic, chemosensory and tactile (Grigg and Kirshner 2015). Of the crocodylians, courtship has been particularly well-studied in the American alligator (*Alligator mississippiensis*; Garrick et al. 1978; Vliet 2001), the Nile crocodile (*Crocodylus niloticus*; Kofron 1991) and the Cuban crocodile (*Crocodylus rhombifer*; Augustine et al. 2017). These behaviours generally take place in shallow water but often occur at greater depths as pairing proceeds. Males initiate courtship using attraction or advertisement behaviours such as head slapping, bellowing, roaring and bubble blowing. This is followed by pair formation in which the two individuals make physical contact with circling, snout rubbing and more vocalisations. Final precopulatory behaviours include vocalisations, bubble blowing, snout lifting and sub-audible vibrations that create an impressive ‘water dance’ display (Fig. 5.3; Garrick et al. 1978; Vliet 1989).

A number of crocodile, caiman and alligator species have been shown to exhibit multiple paternity (Grigg and Kirshner 2015). In these cases, females are shown to have mated with multiple males (polygyny) and males have been shown to mate with more than one female (polyandry). Lewis et al. (2013) suggest that species such as

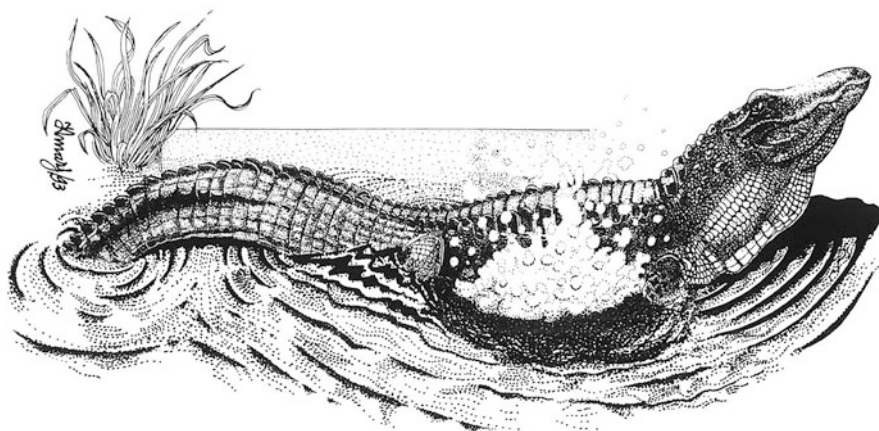


Fig. 5.3 Male American alligator (*Alligator mississippiensis*) in a typical aquatic courtship posture, creating subaudible vibrations that produce the ‘water dance’. Based on photograph by K. Vliet and illustrated by Jose Pedro do Amaral)

this exhibit a promiscuous or polygynandrous (see Rivas and Burghardt 2005) mating system.

Courtship behaviours of the lizards are reviewed in depth by Carpenter and Ferguson (1977) and Pianka and Vitt (2003). Many lizards, such as the iguanids, communicate socially using visual channels. Males, particularly in diurnally active species, are brightly coloured, and evidently possess colour vision (Pianka and Vitt 2003). Those species that tend to be visually oriented also exhibit displays that have strong visual cues, such as head-jerking with bodily colour change (*Chamaeleo jacksoni*; Van Mater 1971), push-ups and dewlap extension (*Anolis* spp.; Greenberg and Noble 1944; Jenssen 1977), head-bobbing (*Agama*; Harris 1964; *Sceloporus*; Martins 1991; Kelso and Martins 2008; *Crotaphytus*; Baird 2013) and broadside posturing (*Lygodactylus picturatus*; Greer 1967). Other lizards, like the snakes (see below), possess more highly developed systems for chemical detection (gustation, vomerolfaction; Schwenk 1995) and therefore appear to rely more on chemosensation than on visual orientation. Many of these lizards (e.g. *Crotaphytus*, *Amblyrhynchus*, *Liolaemus*) produce pheromonal secretions in their femoral glands (Martin et al. 2013; Martin and Lopez 2014; Vicente and Halloy 2016; Ibáñez et al. 2017). These species tend to exhibit much more tongue-flicking, biting and other more tactile stimulation. The six-lined racerunner (*Aspidoscelis sexlineatus*), typifies this pattern. Unisexual species (parthenogenetic) have been reported for this family where female-female courtship is remarkably similar to that of sexual species (Crews and Fitzgerald 1980). Courtship in the monitor lizards is often more complex and involves several channels of communication (Auffenberg 1981, 1988, 1994; King and Green 1999). For example, in lace monitors (*Varanus varius*), apparently all three communication channels are used in courtship and mating. Here the male exhibits distinctive body postures, with much tongue-flicking as well as tactile clawing (Carter 1990).

Mating in lizards is achieved by the male following mounting, grasping the female with all limbs and twisting the base of his tail beneath hers to achieve cloacal apposition and to effect hemipenial insertion (Carpenter and Ferguson 1977). In a number of species, the male simultaneously bites the female in the neck region. Copulation duration is variable from a few minutes to an hour and a half (Carpenter and Ferguson 1977). Forced copulations by males of nonreceptive females have been documented in common iguanas (*Iguana iguana*; Rodda 1992).

Although multiple paternity is common in lizards (Uller and Olsson 2008), historically, most lizards exhibiting territoriality were categorised as showing female defense polygyny. Females were long regarded as a defended resource within the male lizard's territory, thus limiting her mating to that male (Dugan 1982; Pianka and Vitt 2003). However, more recent data indicate that females more commonly achieve matings with additional males, and a polygynandrous mating system is a more accurate representation (Kamath and Losos 2017; Bush and Simberloff 2018; Stamps 2018). To date, only one reptile, the Australian sleepy lizard (*Tiliqua rugosa*), has been shown to exhibit long term monogamy (Bull 2000; Bull et al. 2017).

Successful location of a conspecific female by males is the critical first step in snake reproductive behaviour. In some species (e.g. rattlesnakes, *Crotalus* sp.) males travel substantial distances in search of females (Greene 1997), and this is usually accomplished by the male ‘trailing’ the female using chemical cues (Mason and Parker 2010), although the initial location may also occur visually (Carpenter and Ferguson 1977; Greene 1997). In other species (e.g. garter snakes, *Thamnophis* sp.) males and females emerge together from communal winter dormancy and no long searches are necessary (Gregory 1974; Friesen et al. 2017). The male’s sex recognition and evaluation of a located female are mediated through the use of pheromones (Mason and Parker 2010). For the red-sided garter snake (*Thamnophis sirtalis parietalis*) these pheromones have been identified as methyl ketones secreted through the female’s skin and detected via the male’s vomeronasal system. Some males of this species (known as ‘she males’) are capable of producing this female pheromone as well, confusing other males (Mason and Crews 1985).

Once contact is made, the resulting behaviours can be divided into three phases and the behaviours observed in these phases reflect the constraints imposed by one tubular animal courting another (Gillingham 1987). Phase I, or ‘tactile and chase’, consists of a male’s initial approach to the female, following or chasing her until physical contact is made and, once that occurs, mounting and using one or a combination of tactile movements (Fig. 5.4) (chin-rubbing, writhing, caudocephalic waves and so on). Phase II, or ‘tactile and alignment’, is characterised by the

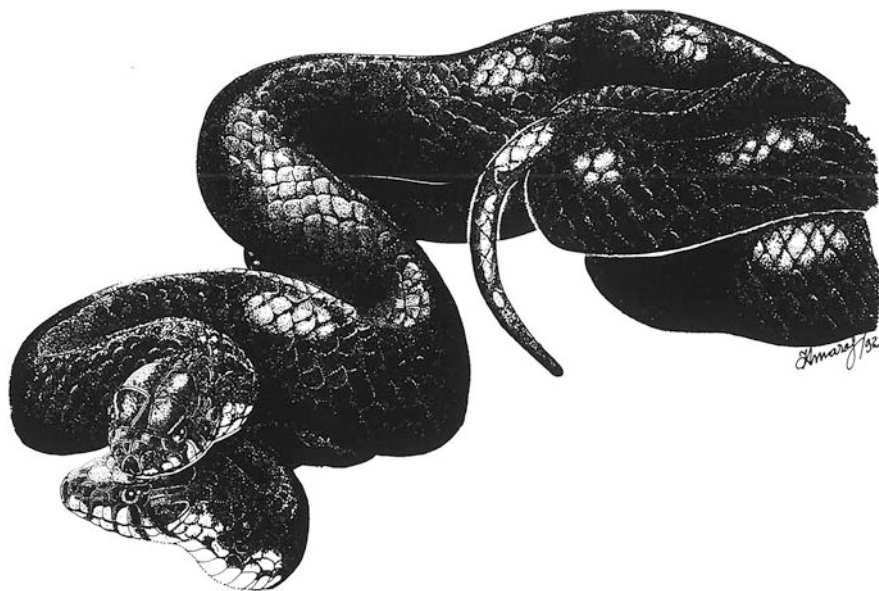


Fig. 5.4 Male indigo snake (*Drymarchon corais*) mounted on top of a female of the same species during phase I of their courtship behaviour. (Based on photographs by the author (JCG) and illustrated by Jose Pedro do Amaral)

initiation of 'tail-search copulatory attempts' (TSCAs) whilst tactile movements continue. Finally, Phase III, or 'intromission and coitus', occurs when one hemipenis penetrates the female following her cloacal-gaping (Gillingham et al. 1977; Gillingham 1979). In at least the red-sided garter snake (*Thamnophis sirtalis parietalis*) cloacal-gaping may be coercive when caudocephalic wave physical pressure results in 'hypoxic stress' leading to cloacal-gaping (Shine et al. 2003).

Courtship biting behaviour, usually behind the head, appears to be limited to the non-natricine colubrid snakes (Secor 1987). Male boids and pythons use their vestigial pelvic spurs in tactile stimulation of the female during courtship (Murphy et al. 1978; Gillingham and Chambers 1982) and the turtle-headed sea snake (*Emydocephalus annulatus*), using modified cephalic scales, prods the female during mating behaviour (Guinea 1996). The formation of a copulatory plug in the female cloaca following male ejaculation has been documented for several natricine snakes (*Thamnophis*, *Nerodia*) (Devine 1975). The period of time snake pairs remain *in copula* is extremely variable across snake families and species (Gillingham 1987).

Until more recently, the mating system most common in snakes was deemed to be polygyny, where one male mates with multiple females each reproductive season (Duvall et al. 1992). However, more current data analyses support snakes as being polygynandrous with multiple males mating with multiple females, and with some species being polyandrous (one female mating with multiple males) (Rivas and Burghardt 2005). Support for these classifications comes from phylogenetic studies (Wusterbarth et al. 2010) as well as the evidence for widespread multiple paternity in snakes (Uller and Olsson 2008).

5.3.4 Courtship and Mating Behaviour: Animal Welfare Conclusions

Because the reproductive behaviours integral to reptilian courtship and mating will only take place when the pair makes physical contact, in many cases such behaviours occur only on a seasonal basis; at other times the individuals of each sex may lead a rather solitary existence. Many temperate zone reptiles require seasonal photoperiodic and temperature shifts that prepare them physiologically for courtship, mating and reproduction (Pough et al. 2016). Attempts at captive reproduction should be mindful of these natural lifestyles. Constant interaction and interindividual stimulation may prevent any reproduction at all and possibly be detrimental to the general health and well-being of the captives.

5.3.5 Distance-Reducing Behaviour: Parental Care

Parental care in reptiles is any nongenetic contribution of an adult that increases the fitness of its offspring (Shine 1988; Stahlschmidt et al. 2012). In line with this definition, tuatara (*Sphenodon punctatus*) have been shown to exhibit parental care in the form of tending their egg clutch. Female tuatara lay their eggs in rookeries and

will show nest-site guarding for up to 4 days after oviposition in an effort to prevent other females from excavating and destroying their nest (Cree and Thompson 1988; Refsnider et al. 2009; Cree 2014). During this nest attendance, tuatara females aggressively deter the approach of other females using body inflation, lunges and biting attempts (Gillingham pers. obs.).

Parental care in turtles is rare. The desert tortoise (*Gopherus agassizii*), has been shown to aggressively defend its egg clutch against the Gila monster (*Heloderma suspectum*) (Barrett and Humphrey 1986). Iverson (1990) documented yellow mud turtle (*Kinosternon flavescens*) females remaining underground with their eggs possibly in an effort to avoid predation by the western hognose snake (*Heterodon nasicus*). More recently, vocalisations have been recorded by hatchling giant South American river turtles (*Podocnemis expansa*). These sounds may function in part to attract adults so that hatchlings may migrate with them to safer aquatic foraging areas in flooded forests (Ferrara et al. 2012). In captivity, a female Asian forest tortoise (*Manouria emys*) responded to the presence of stuffed animals (monitor lizard and armadillo) by defending her nest mound with lunges, butting and biting (McKeown 2013).

Parental care in crocodylians is better developed than in any other reptilian group, and should not come as a surprise considering their phylogenetic affinity to the birds (Grigg and Kirshner 2015). Regardless of whether the female nests in an excavated hole or builds a nesting mound, all crocodylians show nest attendance following oviposition, and the physical nest defense by the female (or the male) is probably ubiquitous (Grigg and Kirshner 2015). Following incubation, and timed with off-spring hatching, the females of most crocodylians, using their hind limbs, open the nest to free the young (Pooley 1977; Somaweera and Shine 2012). Further, many species manipulate the eggs in their mouths to facilitate the hatching (Pooley 1977). Adults are attracted to the eggs by vocalising hatchlings still in the egg (Vitt and Caldwell 2009). Once out of the egg, hatchlings are carried to the water by the female and tend to form groups called a creche or pod, which may be closely attended by the female (and sometimes the male) parent for a variable period of time (Grigg and Kirshner 2015).

Post-ovipositional nest attendance has been recorded for a number of lizard species in the Anguidae, Iguanidae, Scincidae, Teiidae and Varanidae (Shine 1988). Nest attendance accompanied by brooding behaviour, such as egg-licking, egg rearrangement and removal of spoiled eggs, is seen in some skinks (*Plestiodon*) and geckos (*Ptyodactylus*) (Pough et al. 2016). Physical nest-site defense by the female is not as common but has been observed in horned lizards (*Phrynosoma*; Sherbrooke 2017) and alligator lizards (*Gerrhonotus*; Greene et al. 2006). The long-tailed sun skink (*Eutropis longicaudata*) shows no form of parental care throughout most of its Southeast Asian range. However, on Orchid Island (Taiwan), in the presence of abundant egg-eating snakes (*Oligodon formosanus*), this species exhibits nest site defense (Pike et al. 2016). A number of Australian skinks in the *Egernia* group show parental care and kin recognition following hatching, where the parents remain with and defend their offspring in family groups for an extended period of time (Bull et al. 2001; While et al. 2015). Communal nesting has been

described for some anoles and skinks, possibly providing the clutch with a hydric advantage (Radder and Shine 2007) or a predator-swamping function (Hicks and Trivers 1983).

Snake parental care takes the form of nest and egg attendance, egg brooding and neonate guarding and defense. Nest and egg attendance has been described for a variety of snake species in most snake families, including the Boidae, Colubridae, Elapidae and Viperidae (Shine 1988; Greene et al. 2002). Of these species, the king cobra (*Ophiophagus hannah*) is the only snake to actively build a nest (Whitaker et al. 2013). The nest mound has chambers; the lower contains the eggs and the upper is used by the female (Hrima et al. 2014). As with some lizards, there is evidence that this cobra exhibits nest cleaning behaviour by removing unviable eggs (Dolia 2018).

Brooding behaviour is well-documented for the pythons where in all species the female coils about the egg mass providing physiological benefits to the developing embryos. The Burmese python (*Python molurus bivittatus*) and the diamond python (*Morelia spilota*) use facultative (shivering) thermogenesis to elevate egg clutch temperatures above ambient temperature (Vinegar et al. 1970; Slip and Shine 1988). Although all remaining python species are apparently not thermogenic, they do demonstrate other maternal behaviours beneficial to the developing eggs. By adjusting the tightness and/or conformation of the coil and movements on and off the egg clutch, females are able to affect the thermoregulation, hydoregulation and respiration of the clutch (Stahlschmidt and DeNardo 2011; Stahlschmidt et al. 2012; see also Lillywhite 2023).

Maternal neonate attendance has been well-documented for the Viperidae and is probably ubiquitous in the pit vipers. This behaviour often occurs in aggregations of neonates and post-parturient females at the birthing sites (Graves and Duvall 1995). Mother-offspring congregations, in addition to having possible thermoregulatory and hydoregulatory functions, may also lead to active defense of potential predators as has been documented for the pygmy rattlesnake (*Sistrurus miliarius*) (Greene et al. 2002), and the prairie rattlesnake (*Crotalus viridis*) (Graves 1989). However, postparturient female cottonmouth (*piscivorous*) show lower levels of aggression in the presence of neonates (Hoss and Clark 2014). Maternal attendance in this species also ceases after the offspring shed their skin for the first time (Hoss et al. 2014). Neonates in numerous snake species show the ability to recognise kin, which undoubtedly functions in group cohesion as well as in trailing conspecifics to denning sites (Clark 2004; Pernetta et al. 2009; Hileman et al. 2015; Muellman et al. 2018).

5.3.6 Parental Care: Animal Welfare Conclusions

Parental care in reptiles, although not widespread, may occupy a substantial proportion of the time allocated toward reproduction. In captive reptiles that normally exhibit parental care, a disruption of these behaviours would occur if egg clutches or young were prematurely removed from the parent. Like other reproductive behaviours, parental care is undoubtedly driven by hormonal mechanisms, and the removal of offspring leaves the reptile with no outlet for these behaviours.. Further,

the period during which parental care behaviours may be manifest may also be used by the female parent to recoup energy for future reproductive effort. If young are removed from captive reptiles for the purpose of reducing the time until subsequent reproduction, this may result in lowered fecundity due to a depletion of internal resources.

5.4 Agonistic Behaviour

Behaviours that function to increase the distance between two animals, often through the use of aggression, are termed 'agonistic'. Reptilian intraspecific agonistic behaviours are generally observed within a social context, such as in the defense of a territory, competition for hierarchical status or competitive combat for mates or mating opportunities. Antipredator reactions are observed in reptiles as they attempt to defend themselves against potential predators, and these may be classified as interspecific agonistic behaviours.

5.4.1 Agonistic Behaviour: Territoriality and Combat

An animal's territory has classically been defined as 'any defended area' (Noble 1939), but has since been viewed as an exclusive area within which an animal is dominant and therefore has priority of access to resources (Davies and Houston 1984). When a territorial animal moves out of its territory, it no longer enjoys this dominant status, and such a social system has been termed that of relative dominance (Kaufmann 1983). Distinctive from territoriality, and at the other end of this social spectrum, is a system where individuals may achieve a particular level of dominance (i.e. status position within a dominance hierarchy) and hold this status no matter where they move within their home range. This system may be termed 'absolute dominance' (Kaufmann 1983).

The evolution of traits that allow some males to achieve more matings than others has been called sexual selection (Darwin 1871). This occurs through either mate choice (intersexual selection) or male-male competition (intrasexual selection). The latter, in reptiles, often manifests itself as combat behaviour. Although such behaviour is not universal among the reptiles, in those forms where male-male fighting has been observed, sexual size dimorphism (males larger than females) is often the result. Male-male fighting is often exhibited by reptiles as they actively defend their territories.

Male tuatara are highly territorial; they defend territories the size of which varies inversely with the quality of the habitat and varies directly with the size of the defending male (Gillingham and Miller 1991). The initial response of a male tuatara to an intruding male is to stand with the body held above the substrate and the head positioned such that the bluish-grey coloured throat is exposed. The continued approach of another male typically elicits crest erection where the neck and dorsal spines become fully erect. Males often position themselves laterally to maximise

body surface area directed at the opponent. If the opponent does not retreat, the male will gape his mouth slowly and widely. Finally, the interaction may escalate into a full attack where the male lunges and attempts to bite the opponent (Gillingham and Clark pers. obs.; Gillingham and Miller 1991). Descriptions of combat behaviour between captive and free-ranging tuatara are virtually the same although the outcomes may differ. The space constraints of the captive situation prevent 'losers' from escape, as would not be the case under natural conditions (Gans et al. 1984; Gillingham and Miller 1991). As expected, tuatara exhibit pronounced sexual dimorphism with males being significantly larger than females (Cree 2014).

Remarkably, the territorial defense responses of male tuatara are so strong that they will respond to computer-animated versions of a perceived intruder. Male tuatara were tested on Stephens Island, New Zealand, using a digitised video sequence played on portable laptop computers. The computer-animated sequence depicted an adult male tuatara exhibiting the species-typical courtship walk, or *Stolzergang*, followed by two animated mouth gapes. Importantly, 14 of 15 males tested responded with escalating aggressive behaviours and five of these positive responses terminated in a physical biting attack of the laptop screen (Fig. 5.5; Clark and Gillingham pers. obs.).



Fig. 5.5 Territorial male tuatara (*Sphenodon punctatus*) responding to video of another male. This interaction resulted in the male being tested biting the screen (Video photograph by the author, DC)

A few studies imply that certain turtle species may show territoriality (e.g. softshell, *Apalone spiniferus*; Lardie 1964; yellow mud turtle, *Kinosternon flavescens*; Lardie 1983), but this behaviour has not been substantiated (Kramer 1986; Galbraith et al. 1987) and is probably rare (Freeman et al. 2018). In spite of this, aggressive interactions and combat are common within fully terrestrial and semi-aquatic species (Berry and Shine 1980). Male tortoises exhibit combat behaviour using a variety of tactile behaviours including, biting, ramming, pushing and back-flipping (Auffenberg 1977). Snapping turtle (*Chelydra serpentina*) males fight using biting and chasing behaviours (Janzen and O'Steen 1990; Keevil et al. 2017). Wood turtles (*Glyptemys insculpta*) have been shown to use aggression to set up male linear dominance hierarchies (absolute dominance), which contributes to male reproductive success (Kaufmann 1992). This aggression includes open-mouth snapping gestures that may result in physical contact (Barzilay 1980).

Territoriality in the crocodylians is apparently ubiquitous (Grigg and Kirshner 2015). Garrick and Lang (1977) describe the behavioural repertoire involved in the set-up and use of mating territories for the American alligator (*Alligator mississippiensis*), American crocodile (*Crocodylus acutus*) and Nile crocodile (*Crocodylus niloticus*). They further reported that female American alligators will set up dominance hierarchies and will defend their nesting areas against other females. Recent studies on the Nile crocodile indicate that its territorial behaviour may be suspended during the non-breeding season (Calverley and Downs 2015). Although actual boundary defense has not been observed, the distributions of male dwarf caimans (*Paleosuchus trigonatus*) suggest that they are also territorial (Magnusson and Lima 1991). Territorial defense often involves visual and acoustic open mouth displays, bodily contact, 'snout fencing behaviour' and head oblique, tail arched (HOTA) postures (Grigg and Kirshner 2015). Crocodylians tend to show significant size dimorphism with males being larger than females (Warner et al. 2016).

Many lizard species within the Agamidae, Chamaeleonidae and Iguanidae show well-defined territoriality and use aggression in the defense of their home ranges (Pianka and Vitt 2003). These species tend to be diurnal, visually oriented and sit-and-wait foragers (Stamps 1977; Stuart-Fox et al. 2007). Some of the best-studied territorial forms are the anoline lizards. *Anolis* males patrol territorial boundaries and advertise their presence using conspicuous visual displays that involve gular dewlap extension (Fig. 5.6) as well as head-bobbing patterns (Jenssen 1977, 1979). Body and dewlap colour are also components of these displays, and recently their importance has been measured using lizard robots (Macedonia et al. 2013, 2015). Here, as in other Iguaninene lizards, in the presence of a potential intruder the male makes a lateral presentation and will circle the intruder until within a distance of a few body lengths. This confrontation may escalate to outright combat: biting intention movements, actual biting with jaw-locking, and attempts to dislodge the intruder from his perch (Carpenter and Ferguson 1977). Anoline lizards as well as most other lizards show sexual size dimorphism where males possess a larger body (and often head) size than females. However, there are numerous exceptions where females are larger than males (Pianka and Vitt 2003).



Fig. 5.6 Male tree anole (*Anolis livitis*) exhibiting dewlap extension in conjunction with defence of its territory. Photo courtesy of Jonathan Losos

Most lizards in the Scleroglossa (e.g. Anguidae, Gekkonidae, Scincidae, Teiidae, Lacertidae, Varanidae) are non-territorial, rely on chemosensation more than the iguanines and tend to be active foragers. In spite of their not defending a territory these lizards tend to show dominance hierarchies, (absolute dominance) and male-male encounters often result in combat (e.g. *Aspidoscelis* (*Cnemidophorus*) *tigris* and *Ameiva ameiva*: Anderson and Vitt 1990; *Heloderma horridum*: Beck and Ramirez-Bautista 1991). In the Komodo dragon (*Varanus komodiensis*), combat bouts often with wrestling and biting occur in competition for a food resource (Auffenberg 1981). Males of the much smaller pygmy mulga monitors vigorously ‘wrestle’ forming an arch with their bodies supported by their snouts and tails (Fig. 5.7; Carpenter et al. 1976). Interestingly, combat in the legless ‘snake-like’ anguid lizard (*Pseudopus apodus*), involves biting, as well as body entwining and twisting, similar to snake combat described below (Jablonski 2018). As with territorial lizards, most of these non-territorial species exhibit male size dimorphism.

Until recently, territoriality had not been documented in snakes. Huang et al. (2011) recorded this behaviour for the first time in the Taiwanese egg-eating snake (*Oligodon formosanus*). Females of this colubrid snake actively defend sea turtle nests, feeding upon the eggs for weeks, and exhibit biting and combat behaviour as a part of this defense against conspecific intruders. Male Australian small-eyed snakes (*Cryptophis nigrescens*, elapidae) defend rocks that are ideal for thermoregulation



Fig. 5.7 The combat ritual of a pair of male pygmy mulga monitors (*Varanus gilleni*) at the Dallas Zoo. (Photograph by the author, JCG)

(‘hot rocks’) from rival males (Webb et al. 2015). Because reproductive females also use these rocks at times, defense of these sites can lead to a fitness advantage for the defending males. Similarly, male timber rattlesnakes (*Crotalus horridus*) have recently been shown to defend females using thermally optimal sites (Howey and Maisch 2017). However, in this case, it is not clear whether the male rattlesnakes are defending the females or the site, so this is possibly not territoriality, but mate-guarding. Combat behaviour, or male-male fighting, has been associated with all of the above examples.

Male snake combat behaviour is exhibited by some members of the Colubridae (*Pantherophis*; Gillingham 1980) and is widespread among the Viperids, Elapids, Boids and Pythonids (Carpenter 1977). There is an apparent correlation between male-male fighting and the mode of prey subjugation: constriction and/or envenomation (Schuett et al. 2001). This male-male fighting, like courtship, is tempered by the constraints of a tubular morphology (Gillingham 1987; Schuett and Gillingham 1989). Generally, two interacting males make repeated attempts to position their heads and/or trunks above that of the other, and in so doing the two animals often entwine their bodies. In most snakes that exhibit combat these ‘wrestling bouts’ occur on a horizontal plane with the heads of the males elevated to some degree. In many of the viperids the two males ascend to impressive vertical positions with more than half their bodies elevated (Carpenter 1977). Regardless of the positioning, the match continues with repeated ‘topping’ attempts until one individual achieves dominance over the other (Fig. 5.8). In some species (e.g. western diamondback

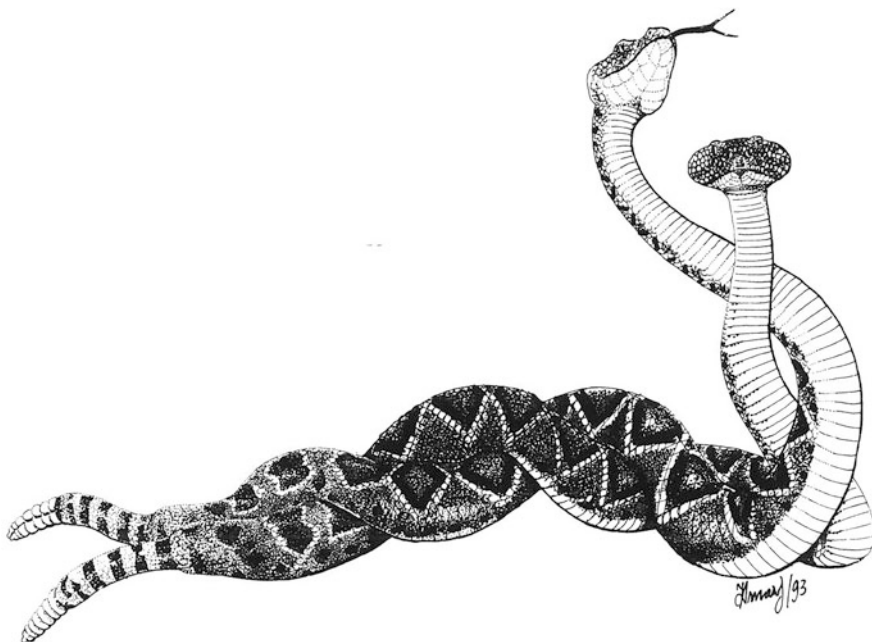


Fig. 5.8 Two male western diamondback rattlesnakes (*Crotalus atrox*) fully ascended in typical combat postures. (Based on videotape by the author (JCG) and illustrated by Jose Pedro do Amaral)

rattlesnakes, *Crotalus atrox*), this fighting results in one individual achieving dominance that is recognised for some time by subordinated animals (Gillingham et al. 1983). The combat behaviours observed in snakes under captive conditions are virtually the same as those seen in the wild (e.g. *Pantherophis*: Gillingham 1979; Barten 1992).

5.4.2 Territoriality and Combat: Animal Welfare Conclusions

Space constraints may represent one of the most serious problems to especially territorial and naturally migratory ‘transient’ reptiles held in captivity. Territorial defense is costly in terms of the investment of time and energy but should pay off through the sequestered resources (food, mates and so on). Captive animals in too small a space will be unable to achieve the defense of ‘normal-sized’ areas but may continue to try to do so, thus expending more energy than is required for the task under natural conditions. This energy is used at the expense of energy allocated for other activities (feeding, mating and so on) and may ultimately affect the reptile’s quality of life. Reptile care providers should create environmental heterogeneity through the use of ground cover, stratification of perching/basking sites etc., of the captive environment.

If the primary resource being defended by a given species of reptile is food, it is possible that in captivity the effects of spatial constraints may be lessened by providing an adequate supply of food. On the other hand, territory size may be determined by habitat visibility (for the purpose of social communication). For some species (for example, anoles, *Anolis aeneus*) an increase in structural heterogeneity under captive conditions led to decreased territory size (Eason and Stamps 1991). Thus, cage provisioning represents another way in which the pressure of spatial constraints might be at least partially alleviated.

Combat behaviours in reptiles operate in the context of sexual selection and are often spectacular when observed in the wild or in captivity. In spite of initial impressions, they are seldom fights to the death, and most are highly ritualised tests of strength and endurance. The 'winner' of these contests gains a dominant status whilst the 'loser' is subordinated and retreats. However, once again the spatial constraints of captivity may severely alter these behaviour patterns. Here, combat sequences limit the avenues of retreat for subordinate reptiles. This may lead to unnaturally prolonged interactions between competing individuals and possibly result in physical injury.

5.4.3 Agonistic Behaviour: Antipredator Behaviour

Reptiles are prey to a variety of invertebrate and vertebrate predators and have evolved a diversity of antipredator behaviours as a response to predation (see Greene 1988, for a thorough review). The apparent objectives of these reptilian behaviours may be categorised as follows:

1. **Avoiding Detection by Predator.** Many reptiles attempt to avoid detection by predators through the use of crypsis, or blending into their microhabitat (Nunes et al. 2012). Garter snakes (*Thamnophis*) have been shown to choose basking sites that make them more cryptic than random sites (Isaac and Gregory 2013). This mimicry or camouflage is enhanced by immobility (Greene 1988) and through the use of cryptic colouration, disruptive colour patterns and predator-specific camouflage (Pough 1988; Stuart-Fox et al. 2008). Sleep site selection has been demonstrated to be an important predator avoidance mechanism in certain lizard species (Clark and Gillingham 1990). Interestingly, the puff adder (*Bitis arietans*) shows chemical crypsis that prevents location by dogs and meerkats (Miller et al. 2015).
2. **Escaping Predators.** If a reptile is detected by a predator it may avoid contact by direct evasion, by simply running, swimming, climbing or slithering away to other locations (locomotor escape; Greene 1988) or retreat sites (inaccessibility; Greene 1988). The effectiveness of this strategy is very much dependent on the locomotor abilities of the potential prey as well as its reproductive condition: female common wall lizards (*Podarcis muralis*) switch their predator avoidance tactic from escape to crypsis when pregnant (Brana 1993), and pregnant female

Australian keelback snakes (*Tropidonophis mairii*) show escape behaviour at a greater predator approach distance than males (Brown and Shine 2004).

3. Repelling Predators. Many reptiles, on detection of predator approach or contact, may resort to the use of behaviours that somehow serve to fend off the intruder. This repulsion effort may take many forms. Most snakes use aggressive biting and/or striking when confronted, threatened or captured by a potential predator (Greene 1997). Emission of noxious chemicals such as musk, faeces, urine and skin secretions occurs as a predator repellent in many snakes (Greene 1997), some turtles (Ernst et al. 1994) and some lizards (Pianka and Vitt 2003). Monacled or spectacled cobras (*Naja*) in Africa and Asia accurately spit venom at potential enemies (Greene 1997). A number of snakes resort to death-feigning (e.g. *Heterodon*, *Natrix*) when contacted by a predator (Fig. 5.9; Edgren 1955; Platt 1969; Gregory et al. 2007; Gillingham pers. obs). Horned lizards (*Phrynosoma*) resort to the rather drastic defense mechanism of squirting streams of blood from sinuses surrounding their eyes (Hodges 2004).

Startle or deimatic displays function to frighten away the predator, and are seen in cobras hooding to expose an ‘eye’ pattern (Greene 1997), in the rapid erection of the neck frill in frilled lizard *Chlamydosaurus kingii* (Shine 1990), and in the protraction of the bright blue tongue of a mouth-gaping blue-tongued skinks (*Tiliqua scincoides*) (Fig. 5.10; Badiane et al. 2018). If such display signals indicate that the sender is noxious or possesses the ability to do serious harm to the would-be assailant, it is classified as aposematic. The cobra ‘eye’ pattern, black and white rings



Fig. 5.9 Death-feigning in the European grass snake (*Natrix natrix*) as an antipredator response. (Photograph by the author (JCG))



Fig. 5.10 Blue-tongued skink (*Tiliqua scincoides*) gaping and protracting its blue tongue as an antipredator response. Photograph by Peter Street, courtesy of Martin Whiting

on tails of a number of rattlesnakes and the red-yellow-black banding on many coral snakes are apparently aposematic (Pough et al. 2016).

Crotaline vipers exhibit an ophiophage defensive response in which they form a pronounced body bridge in the presence of a snake-eating predator (Carpenter and Gillingham 1975; Weldon and Burghardt 1979). This body bridge sways back and forth toward the potential predator, such as a kingsnake (*Lampropeltis getula*), in an effort to deter its advance. Tail autotomy, where a portion of the tail is shed following a predatory attack on the tail, is an antipredatory behaviour recorded for tuatara (*Sphenodon punctatus*; Gillingham pers. obs.; Cree 2014) and is widespread in lizards (Arnold 1988; Pianka and Vitt 2003).

5.4.4 Antipredator Behaviour: Animal Welfare Conclusions

Although a captive reptile is unlikely to encounter natural predators and therefore would seem to have little need to elicit these antipredator behaviours, its keeper may provide a suitable stimulus to such behaviours. In the case of species or individuals that remain 'nervous' and respond in this fashion to human presence, it is possible that overstimulation may lead to an 'unnatural' habituation to the stimuli which may alter other behaviours in subtle or perhaps imperceptible ways. Such species should be given the opportunity to escape from such stimulation. In addition, animals arbitrarily removed from established dominant positions for incidental relocation to novel environments may potentially lose their former established status and

become exposed to imposed stress associated with their newly derogated order in an unfamiliar environment.

5.5 Animal Welfare Conclusions

Reptile behavioural diversity approaches, parallels and often surpasses that seen within the birds and mammals. Social structure in the form of aggregation, territoriality, formation of dominance hierarchies and mating systems shows clear parallels to these other vertebrates. An elevated level of behavioural diversity amongst the extant reptiles is due in part to the broad spectrum of niches into which they radiated and now occupy, and the equally varied array of body forms seen within this class. Because morphology and behaviour are interrelated, the loss of legs or the possession of a protective exoskeletal shell profoundly modifies the same behaviours seen in reptiles lacking these characteristics.

A reptile's behaviour is often a reflection of its physiological internal state. The coactive interaction of hormones and behaviour in reptilian sexual and social systems is well substantiated (see Crews and Gans 1992, for review; Lind and Beaupre 2015; Lillywhite 2016). Similarly, the energetic capacities and metabolism of reptiles may have not only ecological consequences but also profound effects on their behaviour (Avery 1982; Garland et al. 1990; Stuginski et al. 2018). The demands imposed by reptilian ectothermy add a further behavioural dimension not seen in the endothermic vertebrates.

The body of literature describing reptilian behaviour is indeed enormous with much of it based largely on captive studies. Although such studies have provided useful first descriptions of unique behaviours and experimentally allowed for closer controls, natural studies are ultimately preferable. Observations on reptiles in their natural environment lend context to their behaviours and therefore allow a more accurate and adaptive interpretation of them (Greene 2005). Captive studies often risk observer effects on the data (Sugerman and Hacker 1980) and, perhaps more profoundly, the reptile's behaviour may be altered by captive conditions (Warwick 1990a, b). In reality, it is probably impossible to duplicate a reptile's natural environment in captivity. Short of this, every effort should be made to provide the captive reptiles with environmental conditions that allow them to manifest normal behaviour patterns. An understanding of normal reptilian behaviour is important and essential because any physiological or morphological problems that may arise in captive animals will first be reflected and most easily detected through their behaviour (Warwick 1990a, b; Hernandez-Divers 2001). Behaviour is therefore an important window through which to view the well-being of reptiles in captivity.

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Social Behaviour as a Challenge for Welfare

6

J. Sean Doody

Abstract

In recent decades, husbandry techniques have generally improved to better facilitate the general health and welfare of captive reptiles, although many harmful practices remain. In the meantime, our understanding of the natural history, and thus requirements, of reptiles in nature has burgeoned. Compared to birds and mammals, reptiles have generally been dismissed as ‘non-social’ or ‘asocial’, lacking complex social behaviour, cognition, deception, emotions, and other behaviours and states. However, a recent review of social behaviour revealed that reptiles have the widest range of sociality of the vertebrates; reptiles are capable of complex social interactions including long-term monogamy, group living, delicate parental care, elaborate courtship, complex communication among sibling embryos and hatchlings to synchronise hatching and emergence, and grouping together to find food and shelter or avoid predators. Research into the captive welfare of reptiles has also lagged behind that for birds, and particularly for mammals. Although detrimental effects of some social interactions on captive reptiles are well known, beneficial effects are less obvious. Herein I review evidence for the effects of social behaviour on the welfare of captive reptiles, and suggest ways forward based on our current knowledge of social behaviour in reptiles in nature and in captivity.

Keywords

Captive welfare · Social behaviour · Social context · Group living · Captive-related stress

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6.1 Introduction

In recent decades, reptile-keeping appears to have increased in popularity (e.g. Whitehead and Forbes 2013), although in scale the practice may fluctuate as the number of new acquirers of animals may be offset by those who renounce their interest, often due to husbandry challenges (Whitehead and Forbes 2014; Tedds et al. 2020). In some respects, husbandry techniques have improved to better facilitate the general health and welfare of captive reptiles, although many unscientific and harmful practices remain common and ingrained (see Mendyk and Warwick 2023). Concurrently, our understanding of the natural history and thus, requirements, of reptiles in nature has burgeoned. However, this understanding is replete with knowledge gaps, and tends to lag behind that of other vertebrates such as birds and mammals (Doody et al. 2013). In particular, we have a relatively poor understanding of the social behaviour of reptiles in nature (Doody et al. 2013, Doody et al. 2021).

Social behaviour is important in the successful husbandry of many reptile species, and although detrimental effects of some social interactions on captive animals are already well known (e.g. housing aggressive male lizards together during the breeding season), beneficial effects are less well known. After discussing potential play behaviour between juvenile turtles, Burghardt (2013) concluded that social partners may be useful components of ‘enrichment’ for some reptiles. The goal here is to extend the successful keeper’s repertoire to include social aspects of reptile biology and to stimulate further research into the effects of social context on health and welfare.

This chapter summarises the current understanding (and the unknown frontiers) of the social behaviour of reptiles in nature (reviewed in Doody et al. 2021), as well as briefly reviews the literature for evidence of social factors influencing health and welfare. The chapter also provides various hypotheses on how social context might contribute to the welfare of captive species, and how research might proceed to test these hypotheses. Finally, methodologies for measuring welfare are considered and recommendations offered regarding future research directions for successful husbandry of captive reptiles.

In 1976, at the annual meeting of the *American Society of Zoologists* in New Orleans, Louisiana (USA), animal behaviour researchers converged in a special symposium to recognise and celebrate, for the first time, the revelation of social behaviour in reptiles. One by one, the speakers, including Professor Gordon Burghardt of the University of Tennessee, revealed examples of reptilian social behaviour ranging from communication in neonate iguanas to vocal and territorial displays in crocodylians (Burghardt 1977; Garrick and Lang 1977). In a remarkable example of déjà vu, exactly 40 years later, again featuring Gordon Burghardt and again in New Orleans, ecologists held a second symposium on the social behaviour of reptiles, for which four decades of research and observations had produced a bewildering array of examples demonstrating sociality. The second symposium earmarked a gradual paradigm shift that saw reptiles emerge as being capable of sophisticated and complex social interactions—a far cry from the previous conventional wisdom that reptiles were essentially ‘asocial’ (Doody et al. 2013, Doody et al.

2021). Much of this misunderstanding was due to the preceding lack of social behaviour research on reptiles and its perpetuating effect—historical students of social behaviour were drawn to fishes, birds, and mammals, whose complex social behaviour was well known (Gaston and May 1992; Bonnet et al. 2002; Pawar 2003).

At least part of the ‘understudied’ problem was the difficulty in obtaining research funding for reptiles compared to birds and mammals (Czech et al. 1998). In turn, the bias against research on reptiles compared to birds and mammals can be attributed, at least in part, to both the generally more secretive nature of the former and the higher human affinity for the latter (Doody et al. 2013, and references therein).

6.2 Brief Taxonomic Breakdown of Social Behaviour in Reptiles

A recent review (Doody et al. 2021) sets out numerous examples of sociality in reptiles, which are briefly summarised below with some notable examples for each higher taxon. To date, lizards have been demonstrated to be the most socially diverse and complex reptiles (although there could be bias in effort here that has not been quantified). Whilst these animals have long been known to engage in social behaviours associated with dominance hierarchies, territoriality, and communal nesting, more recent research has revealed stable aggregations (family groups with overlapping home ranges and long-term membership), social monogamy (Fig. 6.1),



Fig. 6.1 A pair of sleepy lizards, *Tiliqua rugosa*. This species exhibits seasonal monogamy, whereby the same pair unite annually and spend 6–8 weeks together prior to mating; then they disperse (Bull 1988; Bull et al. 1998). One pair has remained monogamous for 27 years and counting (Leu et al. 2015)

and complex signalling associated with mate choice and courtship. Indeed, perhaps the most complex suite of social behaviours in lizards is associated with ‘group living’. Several species of Australian skinks (most notably, members of the genera *Egernia* and *Tiliqua*) form stable aggregations that include adult pair bonds, parent-offspring associations, and four or more overlapping generations (reviewed in Gardner et al. 2016; Whiting and While 2017; While et al. 2019). These skinks tend to be crevice-dwellers, but groups can occupy other microhabitats, and in some cases, in many *Egernia* spp.—the lizards pile their scats around their homes to signal resident status to a family group (Bull et al. 1999, 2001; Bull 2000; Chapple 2003; Wilgers and Horne 2009). In an extraordinary example of sociality and cooperation among reptiles, the great desert skink (*Liopholis kintorei*) constructs an elaborate burrow system as a home for family members; multiple generations contribute to burrow construction and maintenance, and burrows can be occupied for at least 7 years (McAlpin et al. 2011).

Perhaps second to the lizards in terms of social diversity, are turtles. Historically, turtles are recognised for nesting, hatching, and emerging in large groups (e.g. sea turtles) and basking in groups (e.g. freshwater turtles). Indeed, communal nesting is much more common than previously realised (Doody et al. 2009), but few could imagine that freshwater turtles and sea turtles were communicating via underwater vocalisations; Giant Amazon river turtles (*Podocnemis* sp.) are known to emit at least 6 types of sounds, whilst long-necked turtles from Australia (*Chelodina* sp.) have been recorded to emit 17 types of sounds (Giles et al. 2009; Ferrara et al. 2014a). Vocalisations of some type have now been revealed for ~50 species of turtles (reviewed by Ferrara et al. 2014b), although their function and context remain unclear. Moreover, sibling embryos and hatchlings also vocalise to one another or detect one another’s vibrations, perhaps to facilitate synchronous and/or rapid hatching (Doody et al. 2012; Ferrara et al. 2014a, b; but see McKenna et al. 2019). Perhaps less surprisingly, turtles have recently displayed social learning in the laboratory, whereby individuals learned to perform a task solely from watching conspecifics (Wilkinson et al. 2010; Davis and Burghardt 2011; see also Gillingham and Clark 2023).

Maternal behaviour in crocodylians may seem like old news, but recent research has demonstrated new extensions of these behaviours. Numerous wildlife documentaries have featured mother crocodylians responding to the calls of their near-term embryos, excavating and carrying their young to the water, and even assisting in the hatching process. We now know that some species exhibit biparental care, some feed their young, and in others, females take turns defending multi-brood creches (Pinheiro 1996; Brueggen 2001; Whitaker 2007). Remarkably, male Indian gharials guard extensive communal crèches that can comprise more than a thousand juveniles from many broods (Lang and Kumar 2016; Vashistha et al. 2021).

Snakes currently appear less socially diverse than other reptiles, but this is tainted by appreciable bias—they are the most secretive members of the group, and they are less studied. Nearly everything they do is undercover or in private, including courtship, mating, fighting, egg-laying, or giving birth; indeed, without techniques such as radio-telemetry, researchers have great difficulty observing behaviours of

individuals over time. In fact, snakes can be surprisingly social: anyone who has housed multiple individual snakes together has likely noticed that the snakes aggregate within the enclosure, irrespective of a common resource (basking light, hide box, space). Snakes are, unfortunately, disliked and feared by many, which may ultimately contribute to their receiving less research attention. Regardless, snakes can exhibit relatively complex social behaviours, including communal nesting and birthing, ritualised male combat, and parental care, and can form groups associated with food and other resources (reviewed in Doody et al. 2021). Noteworthy are the relatively recent discoveries of kin-based groups in rattlesnakes. For example, Clark et al. (2012) revealed that pregnant timber rattlesnakes not only aggregate together in spring, but also preferentially aggregate with their (juvenile) kin for weeks after birth. Rattlesnakes and other pit vipers exhibit other advanced social behaviours, including group defence, conspecific alarm signals, and maternal defence of young (Graves and Duvall 1987, 1988; Graves 1989; Greene et al. 2002; Schuett et al. 2016).

Each reptile group is thus known for particular forms of social behaviour. However, importantly, there is marked variation within each group. Not all lizards live in family groups, not all turtles nest communally, not all crocodylians excavate their young from the nest, and not all snakes exhibit group defence. Knowledge of the natural history, life history, or fundamental ecology and behaviour is therefore required on a species-by-species basis prior to determining optimal conditions for the health and welfare of captive reptiles. However, a big challenge is not only revealing social behaviour in nature, but conducting experiments to determine the role of social factors on the welfare of captive reptiles.

6.3 The Welfare of Captive Reptiles and Its Assessment

As with the overall taxonomic bias in research and funding, there is a similar taxonomic bias towards mammals in efforts to improve animal welfare. A review of zoo research (Melfi 2009), undertaken in British and Irish Association of Zoos and Aquariums member zoos since 1998, demonstrated that the majority of animal welfare studies undertaken were on just a few species. Of 774 projects, 690 were undertaken on mammals and of these 490 focused on primates (see Stoinski et al. 1998 for a similar finding from a review of zoo research undertaken in Association of Zoos and Aquariums). Relatedly, a review of 744 environmental enrichment studies published during 1985–2004 noted a clear and dramatic taxonomic bias; most studies were undertaken on mammals (92.2%); reptiles comprised a mere 0.6% of studies (de Azevedo et al. 2007). This trend shows little signs of changing: 7% of peer-reviewed articles evaluating zoo enrichment published between 2002 and 2014 involved reptiles (and amphibians), compared to 74% on mammals (Alligood and Leighty 2015).

The above taxonomic bias does not reflect the number of reptiles available for study or the number of zoos that house them. For example, the number of individual reptiles and the number of zoos with reptiles are comparable to those respective

categories for mammals (Melfi 2009). Clearly, projects or studies on the welfare of captive reptiles lag behind that of mammals, perhaps for the same reasons as the taxonomic bias in studies of vertebrates in general. This taxonomic lag clearly hinders our understanding and assessment of the welfare and husbandry needs of reptiles.

Meanwhile, based on unacceptably high mortality rates (Toland et al. 2012; Robinson et al. 2015), there is an urgent need for guidelines for the welfare of captive reptiles (Altherr and Fryer 2001; Moszuti et al. 2017). Furthermore, these losses result in considerable costs to the consumer, whether a private keeper, pet store retailer, pet trade wholesaler, zoo, or researcher. However, researchers and keepers alike need to know more about how captive environments affect reptile welfare, and thus how both health assessments and husbandry practices can be improved (Warwick et al. 1995, 2013; Burghardt 2013; Moszuti et al. 2017). Numerous studies have directly addressed captive reptile welfare and the need thereof (reviewed in Burghardt 2013; Moszuti et al. 2017). Most of these studies addressed the effect of housing or handling on the behaviour and/or physiology of captive reptiles (e.g. Kreger and Mench 1993; Lance and Elsey 1999; Schuett et al. 2004; Case et al. 2005; Kalliokoski et al. 2012). On the other hand, relatively few studies have explicitly examined the effects of social context on the welfare of captive reptiles (but see pioneering experimental work on anole social behaviour by Neil Greenberg (e.g. Greenberg et al. 1984; Greenberg 2003).

The welfare of captive reptiles can vary markedly not only based on care, but also among taxa (Warwick et al. 2013). For example, in some respects, certain species (e.g. bearded dragons [*Pogona* sp.]) appear to be managed more easily than others [e.g. chameleons [*Chamaeleonidae*]], which are notoriously problematic. However, even for *Pogona* many behavioural and physical problems are commonly reported. More specifically, the addition of a conspecific (or lack thereof) can be considered a potential stressor, and many animals respond to stressors by exhibiting ‘opposing’ behaviours (Morgan and Tromborg 2007). For example, stressors can cause individuals to freeze or flee, hide or investigate, or become silent or vocal. Thus, we cannot over-generalise on a suite of symptoms for the potentially stressful situation induced by a conspecific, or lack thereof. We thus require species-specific experiments with some objective evaluation criteria, and a better understanding of a species’ natural history including social aspects.

A formidable challenge is how to measure welfare in animals that differ from humans and other mammals in their communication modalities, facial expressions, and demeanour. A major index of welfare is ‘captivity stress’ or ‘captivity-related stress’. Although certain assessments of stress can be made using hormone assays (e.g. Greenberg and Wingfield 1987; Elsey et al. 1990; Lance 1990, 1992; Lance and Elsey 1999; Martinez-Silvestre 2014; Van Waeyenberge et al. 2018; Gangloff and Greenberg 2023), this commonly requires taking blood from individuals for analysis—a practice that is not commonplace for most reptile keepers, and although other methods such as faecal or ecdysis sampling are available, their reliability (as with other physiological means) is uncertain (Warwick et al. 2013; Martinez-Silvestre 2014; Gangloff and Greenberg 2023). Furthermore, baseline levels of stress

hormones are often not available. Another option is measuring growth rates (Elsey et al. 1990; McKnight and Gutske 1993). For example, social factors can result in some individuals exhibiting poor growth rate (Broom 1986). However, measuring growth rates is somewhat labour intensive and, again, requires a benchmark for comparison. Moreover, ‘good’ growth rates cannot be taken to mean that there is no welfare problem (Broom 1986, 1988). This leaves us with assessing captivity stress by carefully observing and monitoring behaviours and comparing these to known signs of stress. A plethora of ‘behavioural signs of captivity stress’ have been identified in reptiles, including hyperactivity, anorexia, head-hiding, aggression, death feigning, freezing, panting, regurgitation, and colour change (for a complete list, see Table 1 in Warwick et al. 2013; Warwick 2023). Warwick et al. (2013) also identified nine contrasting ‘behavioural signs of quiescence and comfort’: relaxed alertness, calm smelling or tasting, subtle body posture/orientation, unhurried body movements and locomotion, moderate to relaxed grip on handler or object, relaxed drinking, relaxed feeding, relaxed breathing, and physical quiescence. Whilst these behaviours can vary across species, they would also be expected to vary between individuals within species, based on the degree of captivity stress (Warwick et al. 2013), and perhaps based on individual personalities (Davis 2009; Burghardt and Layne-Colon 2023). Accordingly, assessing reptile behaviours requires intimate and progressive familiarity with species and individuals, but also experimental research (Warwick et al. 2013; Warwick 2023).

Another potential index of captive welfare is ‘depression’. There has been an abundance of published papers on animal depression in the last few decades (e.g. Stanner 1999; Greenberg et al. 2002; Korte et al. 2005; Del Guidice et al. 2011). Although some of these studies explore animals as models for human depression, others include psychological and behavioural aspects that can be insightful to those interested in animal welfare (e.g. Willner 1984, 1990; Greenberg et al. 2002; Korte et al. 2005; Del Guidice et al. 2011). Unsurprisingly, virtually all of this research has focused on birds and mammals (Lorenz 1952; Dilger 1960; McKinney and Bunney 1969). According to McKinney and Bunney (1969), ‘social’ animals are more likely to become depressed, especially if forced into isolation. Stanner (1999) pointed out that the reverse could also hold: ‘solitary’ animals can become depressed when forced into socialisation. Stanner noted that overcrowding induced depression in rats (Naitoh et al. 1992), which are considered ‘social’ animals, and the author presented evidence for depression in monitor lizards (see later section for more details of the captive situation). Stanner (1999) concluded by noting that depression in reptiles may not be uncommon; for example, it is well known among snake breeders that individual snakes ‘go on hunger strikes’ for no obvious reason, resulting in emaciation and the need to be force fed. Of course, cessation of feeding may not, in every case, be due to depression, but may reflect years of repeated practices in poor husbandry. More research is needed.

6.3.1 Social Factors and Welfare

What is the evidence, for animals in general, and for reptiles in particular, that social factors influence welfare in a captive setting? Although perhaps an oversimplification, individual reptiles could either thrive or struggle in a group or in isolation, and there are likely factors that can modulate those outcomes (e.g., spatial, habitat, and dietary provisions). Let us first examine the potential advantages and disadvantages of housing reptiles together. Increasing densities by housing individuals together can create problems, for example, where the species is territorial or the individuals are of different size or age classes (Hayes et al. 1998). Probably, every zookeeper tending to reptiles has observed some aggression between certain individuals within an enclosure; for example, two male lizards (Fig. 6.2). Therefore, for some species conspecific males often are not kept together, and males can even harm females that are co-housed for extended periods (Herrmann 1999). In one study, young monitor lizards (*Varanus salvator*) housed together lost weight and died (Herrmann 1999). It is widely acknowledged that growth and survival rates of juvenile crocodylians increase with the removal of larger conspecifics, the inclusion of hiding shelters, and the use of visual barriers (Riese 1991; Mayer 1998; Huchzermeyer 2003; Brien et al. 2014).

However, reptile social tendencies vary among species and groups, and this theoretically can be manifested in their captive welfare. For example, some lizard species are highly territorial and others establish dominance hierarchies (see Stamps 1977), whilst snakes rarely defend territories (Alberts 1994; Duvall et al. 1993; but see Huang et al. 2011; Webb et al. 2015). Territoriality can even vary among



Fig. 6.2 Two male sand lizards (*Lacerta agilis*) fighting. Photograph by Reinhold Moller

populations of the same species or with context; for instance, collared lizard (*Crotaphytus collaris*) males were more aggressive towards conspecific strangers than conspecific neighbours (Fox and Baird 1992). Conspecific interactions in nature, reflected by differences in social system, could strongly influence similar interactions within an enclosure in captivity. The main difference is that captive animals have little or no control over their surroundings, including conspecifics; they have no control over what individuals serve as their social partners or their mate(s), or how much space they are able to put between themselves and other conspecifics (Sambrook and Buchanan-Smith 1997). Thus, housing territorial conspecifics together could result in aggressive encounters that create stress, poor health, and even mortality, because, unlike in nature, captive individuals cannot retreat from conspecifics or from agonistic interactions, unless they are given large, complex structures (McKeown 1985; Hayes et al. 1998; Morgan and Tromborg 2007).

Housing individuals of different size classes in the same enclosure can also result in extreme responses such as cannibalism or larger individuals killing smaller ones. Cannibalism is common and widespread in reptiles in nature (Polis and Myers 1985; Mitchell 1986). However, less extreme responses also occur, such as subordinates having less access to food, space, or mates, or involve sub-lethal aggressive encounters that cause short- or longer-term health issues (Hayes et al. 1998). For example, in the laboratory subordinate male geckos (*Oedura lesueurii*) were forced to use cooler and predator-scented retreat sites in the presence of dominant males, and experiments with monitor lizards (*Varanus exanthematicus*) showed that males housed with females repeatedly attempted to mate with them, causing stress-induced infertility in eggs (Bayless 1994 in: Wicker et al. 1999; Downes and Shine 1998). Presumably, other welfare issues such as body condition and injury rates can be added to the list of sub-lethal effects of housing individuals from different size classes. It is noteworthy that there is both an environmental (e.g. enclosure size) and temporal component to social behaviour that would be expected to contribute to captive welfare. For example, larger enclosures or more structures such as hide boxes could reduce negative interactions (Reid 1981; Mason 1991; Rommers et al. 2014), and aggression that might negatively affect captive welfare may be limited to the breeding season (e.g. Moore 1988). Thus, the challenge of achieving optimal well-being in captivity would require understanding the spatial arrangement and social system and interactions that occur in nature for the species in question.

Whilst the welfare costs of housing territorial species together may be obvious, the welfare costs of housing gregarious species in isolation may be less evident (Hayes et al. 1998). It has long been known that deprivation of social bonding can induce depression in social animals (McKinney and Bunney 1969). In 'highly social' domesticated mammal species that routinely reside in groups, isolation can be stressful (Morgan and Tromborg 2007). For example, isolation causes an increase in abnormal behaviours in dogs, an increase in escape behaviour and a decrease in play behaviour in piglets, and increased breathing rate, serum cortisol, vocalisations, and locomotion in ewes (Hetts et al. 1992; Hubrecht et al. 1992; Herskin and Jensen 2000; Carbajal and Orihuela 2001). Similar isolation effects have been found in rats, cattle, and especially in primates (Harlow and Harlow 1971; Mason 1991; Boissy

and Le Neindre 1997; Weiss et al. 2007). Such experiments are lacking for reptiles, and it is possible that some species will display captivity-related stress when isolated compared to those maintained in groups.

Does the lack of social contact with conspecifics in reptiles housed in isolation adversely affect their welfare? There is very little documented evidence for this phenomenon, although this deficiency may simply reflect a dearth of research. Little doubt exists that when the goal is reproduction, social context can be critical. First, successful breeding in captivity requires pairing, but long-term habituation can lead to 'reproductive lethargy' (Gillingham 1987; Hayes et al. 1998). Breaking reproductive lethargy requires manipulations such as removal and replacement of one individual (Radcliffe and Murphy 1984); or according to Hayes et al. (1998), the addition of one or more conspecifics; moving both individuals to a novel enclosure; or changing environmental conditions. Second, conservation-related repatriation or head-starting programmes can require adequate socialisation (Hayes et al. 1998; Tetzlaff et al. 2019). Beyond breeding and release programmes, some species may exhibit less captivity-related stress when alone, and this will likely vary with species, group, or individual. For example, housing individuals in isolation that do not defend territories, but which prefer to roost in groups in nature could cause stress and result in poor health or reduced well-being in captivity. Aggregations in nature have been recorded for lizards (e.g. Cooper et al. 1985; Cooper and Garstka 1987; Lemos-Espinal et al. 1997; Mouton et al. 1999; Kearney et al. 2001, Hare and Hoare 2005), snakes (Amr et al. 1997; Ashton 1999; Gregory 1982), turtles (Carr 1967; Pritchard and Trebbeau 1984; Doody et al. 2001), crocodylians (Cott 1961; Platt and Thorbjarnarson 2000), and the tuatara (Thompson et al. 1992). Although many reptile species aggregate to mate, hibernate, lay eggs, or give birth (Gregory 1982; Graves and Duvall 1995; Doody et al. 2009), many of the above references reflect instances of aggregation for reasons other than reproduction or hibernation (Doody et al. 2021). Finally, neonate reptiles may stay with their mothers or even fathers, albeit for only a few days or weeks in a few species (Alexander 2018; Doody et al. 2021); separating neonates from their parent(s) could have negative consequences for their captive welfare.

Relatedly, inappropriate social contexts can also cause captive-related stress (Morgan and Tromborg 2007). For example, some mammals form same-sex groupings in nature, and can exhibit stress when forced into other social groupings, or vice versa (e.g. Stoinski et al. 2001). Same-sex social groupings in reptiles do occur; for example, the gathering of gravid or pregnant females prior to nesting or birthing (Graves and Duvall 1995; Doody et al. 2009), but we have little or no understanding of how this might translate into welfare in captivity.

Another consideration is 'social instability', which includes temporary overcrowding and/or the mixing of unfamiliar individuals, which is a common practice during the cleaning of enclosures or other husbandry tasks (reviewed in Morgan and Tromborg 2007). In nature, individuals can retreat from agonistic behaviours or dominant conspecifics, but this is often not possible in enclosures. There is evidence for crowding and re-mixing causing stress responses in mammals, including fighting, aggression, weight loss, or an increase in corticosterone in

monkeys, deer, dolphins, pigs, and rats (Francis et al. 1996; Blanc and Theriez 1998; Boyce et al. 1998; Haller et al. 1999; Waples and Gales 2002). Reptiles that are used in outreach programmes are often transported away from their normal enclosure (e.g. Tetzlaff et al. 2016); how this affects various aspects of welfare is not well known, particularly when such animals are housed in groups. For example, can removing a cage mate, even temporarily, be ‘detrimental’ to welfare of the animal that is removed or the one(s) that is/are left behind? Similarly, could social structure be affected for a group of conspecifics used in outreach programmes?

Perhaps the most illuminating and well-supported example of the effect of conspecific overcrowding on reptile welfare was presented by Stanner (1999). The desert monitor (*Varanus griseus*) is said to be ‘solitary’ in many of its habits, and changed housing conditions provided experimental evidence of the effects of conspecifics on the welfare of the lizards: group-rearing in outdoor enclosures had negative effects on nine individual adults, including eight diagnosed with psychotic depression. Depressed lizards spent most or all of their time in shelters (wooden boxes), did not feed, became emaciated with reduced muscle tonus, and did not moult. Lizards subsequently moved to their own enclosures were more active, fed, gained weight, and moulted, but when moved back to the original enclosures with conspecifics they once more became depressed, did not emerge much, and stopped feeding and shedding. Half of the lizards died within 18 months. Stanner (1999) concluded that solitary lizards might well be induced to become depressed by forced socialisation, or deprivation of a solitary lifestyle. Although the prognosis of depression in these lizards may be debatable, their social situation nevertheless caused their condition to decline.

6.4 Problems and Future Directions

At least three key factors are relevant to consider when asking how the social behaviour of a reptile species might affect its welfare in a captive setting. First, in reptiles the degree of sociality is difficult to quantify. For example, some lizards attend and protect nests whilst others form stable aggregations, which are more social? No framework has been successfully advanced that would allow such comparisons (Doody et al. 2021). A framework would provide a foundation on which the social behaviour of each species could be characterised. Second, different types of social behaviours might warrant differing requirements for successful husbandry. Third and relatedly, a mismatch between the social repertoire of a species in nature and that in captivity could have consequences that are negative, neutral, or positive, and the following attempts to elaborate on these three considerations.

Classifying a particular reptile species or a group of individual reptiles as ‘social’ versus asocial or ‘solitary’ is problematic. Reptiles as a class are socially diverse, comprising species that have limited interactions and those that live in family groups for much of their lives. Moreover, high population densities can cause individuals to become more social (Doody et al. 2009). Thus, dichotomising reptiles as social or asocial is overly simplistic, neglects the diversity of vertebrate social systems,

impedes our understanding of the evolution of social behaviour, and perpetuates the erroneous belief that one class—the reptiles—is primarily ‘non-social’ (Doody et al. 2013; Doody et al. 2021).

In some cases, a particular behaviour may be irrelevant to the species’ successful husbandry. For example, if reproduction is not a priority, then providing cues for successful reproduction (which might involve not only the production of sex hormones associated with temperature changes, but also the presence of the opposite sex at the right time) may not be ‘needed’. In another general example, a gregarious species may ingest food or grow at a faster rate in the presence of conspecifics than if housed alone. In this way, some social contexts (i.e. housing with conspecifics) could be beneficial to the health and welfare of captive individuals. Conversely, it is well known that some social contexts are detrimental to the health and welfare of individuals, such as keeping two male lizards of an aggressive species in the same small habitat during the breeding season when testosterone levels are high, or housing too many individuals within an enclosure (Warwick et al. 2013). Trial and error over many years of captive husbandry have revealed such patterns in detrimental aggressive behaviours (e.g. Herrmann 1999), whilst beneficial contexts are less well known.

Accordingly, the question arises, as to which species’ welfare would benefit from the inclusion of a conspecific(s)? Or, more pragmatically, how can we assess whether the welfare of a given species will be improved in the presence of conspecifics? Experiments are lacking, but one option would be to assess anxiety levels in the presence of conspecifics. Researchers have used a method of assessing welfare in animals by scoring an anxiety-like behaviour in response to a ‘novel environment’ (one that differs in size, shape, colour, or illumination). Commonly recorded welfare measures include the latency to move, total time spent moving around the environment, frequency of defecation or urination, immobility, escape behaviour, self-grooming behaviour, feeding behaviour, and heart rate (Moszuti et al. 2017). For example, Moszuti et al. (2017) determined that red-footed tortoises (*Chelonoidis carbonaria*), but not bearded dragons (*Pogona vitticeps*), exhibited a higher latency to move in a novel environment compared to a familiar environment (see also Siviter et al. 2017). The tortoises also extended their necks further in the familiar environment; this result combined with further neck extension with time in both novel and familiar environments suggested that neck retraction can be an anxiety response (see also Pike et al. 2005), whilst full neck extension can reflect a relaxed state (Moszuti et al. 2017).

Experiments manipulating the social context (e.g. isolated male, isolated female, pair of males, pair of females, groups) and assessing subsequent individual welfare could extend the above research into the social arena. Although any species could be tested, the best results would likely stem from choosing species for which there is evidence of some form of aggregations. Although many species may engage in complex social behaviours without our knowledge (see opening sections), some species, such as certain geckos and skinks, are becoming noted for living in groups. For example, common geckos (*Woodworthia maculata*) form diurnal aggregations of up to ~100 at denning sites; these aggregations are not caused by lack of suitable

sites (Hare and Hoare 2005). Similarly, some snake species often overwinter in groups comprising conspecifics (e.g. Schuett et al. 2016) and may thus fare better when housed in groups. Future research is required to determine if individuals of these species fare better in groups (*versus* in solitude). Recent novel research manipulating social groupings revealed that garter snakes (*Thamnophis sirtalis*) actively sought social interactions, preferred to remain in larger aggregates, and associated non-randomly with certain individuals or groups (Skinner and Miller 2020). Studies by Aragón et al. (2000, 2001) showed that the rock lizard (*Lacerta monticola*) expressed differential rates of tongue-flicking when discriminating odours of familiar and unfamiliar conspecifics. Individual recognition is likely to be ubiquitous among reptiles, providing scope for forming preferred social aggregations in captive environments, and such ‘cliques’ could provide enrichment in certain species. Finally, play behaviour has been revealed in some reptiles and may occur in many more (Burghardt 1998; Doody et al. 2021). For example, titillation displays with the long foreclaws of some aquatic turtles, typically only found in adult males during courtship, are seen in hatchlings and juveniles of both sexes prior to sexual maturity, and are considered social play behaviour (Kramer and Burghardt 1998). The secretive nature of reptiles and the difficulty in observing many of them in nature likely obscures the prevalence of play behaviour in the group. Perhaps more careful behavioural observations of captive reptiles, through improved captive welfare, will contribute to the revelation of play behaviour in more species of these remarkable animals.

6.5 Animal Welfare Conclusions

In summary, for some individuals of some reptile species the addition of conspecifics within a captive context could be seen as a form of enrichment (Burghardt 2013; Kuppert 2013), whilst in others the same forced social groupings could have negative effects. Social behaviours will vary with species, size, age, sex, season, environment, population, and perhaps experience and cognitive processes, and the outcomes can be context dependent (e.g. behavioural diversity or reproduction). The varied human ‘uses’ of the major groups of reptiles may also influence the role of social experience in captive welfare. For example, turtles and crocodiles are often farmed commercially in high densities in outdoor ponds, yet the social needs and welfare are often ignored except when excessive deaths reduce profits (example reviewed in Arena et al. 2014). Conservationists often head-start populations *ex situ* to bolster or reintroduce populations. However, many head-starting programmes fail because released individuals are unable to avoid predators, select appropriate habitats, or find food (Einum and Fleming 2001; Jule et al. 2008; le Gouar et al. 2012). Captive rearing conditions can improve success of head-starting (Swaisgood 2010; Tetzlaff et al. 2019), including consideration of communally housing conspecifics to promote social skills (Reading et al. 2013). For the relatively few species engaging in post-ovipositional/birthing parental care (e.g. Alexander 2018), keeping neonates with their mothers, even for a few weeks, could improve both survival and welfare. Future

experimental research could reveal the best social experience for young captive reptiles that would result in successful head-starting.

Future directions for relevant research should target improved welfare assessments including identifying behaviours that correlate with both positive and negative outcomes. Importantly, experimental research testing the effects of social context on welfare by manipulating groupings and various modulating factors is needed for each species. For example, although housing territorial species together can be detrimental for reasons stated above, positive social interactions could result, given enough space and access to resources (e.g. environmental diversity, food, and water). Another useful approach would be to use social network analysis to inform husbandry practices (Krause et al. 2009; Koene and Ipema 2014; Rose and Croft 2015). To this end, using social network analysis for wild populations would not only be inherently invaluable but also necessary to match captive social contexts to those in the wild (Schuett et al. 2016). Finally, our knowledge of social behaviours of reptiles in nature, in general, remains relatively poor, and a framework for social repertoires is absent (Doody et al. 2021); pursuing the natural history of reptilian sociality remains important to the welfare of captive reptiles.

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Brains, Behaviour, and Cognition: Multiple Misconceptions

7

Enrique Font, Gordon M. Burghardt, and Manuel Leal

The vision of reptiles as unimportant, simplistic, peripheral, and expendable proto-animals remains strongly rooted in society. (Miranda 2017)

Abstract

Despite abundant evidence to the contrary, non-avian reptiles are widely considered as behavioural and cognitive underachievers. The persistent myth of the sluggish, primitive, stupid reptile can be traced, at least in part, to long-standing misconceptions about reptilian brain size and organisation. Historically, reptile brains have been considered small and lacking the neural structures that support complex cognition in other vertebrates. In particular, the notion that reptiles lack a cerebral cortex has led to expectations that their behaviour and cognition should be simple and unsophisticated in comparison with birds and mammals. However, it was shown several decades ago that reptiles possess a large pallium comprising three–four distinct cortical areas and a dorsal ventricular ridge that may be functionally equivalent to parts of mammalian neocortex. In fact, forebrain organisation conforms to a common plan in birds and reptiles, which may seem surprising given the recent trend to put the cognitive achievements of birds above

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those of reptiles yet on a par with mammals. Moreover, the view that reptiles do not exhibit complex cognition faces a growing list of exceptions. Reptiles are capable of spatial, social, reversal, problem-solving, and many other types of learning and cognitively demanding behaviours provided that experimental designs account for some peculiarities of their biology involving their morphology, physiology, and ecology. Unlike frequent caricatures that depict reptiles as clumsy, inflexible, and instinct-driven, much reptile behaviour is precisely performed, delicate in appearance, readily modified, and contextually determined. Recent work has shown that reptiles can show elaborate communication and social systems, parental care, social learning, and play. Although such research is sparse compared to endothermic vertebrates, and the diversity among them immense, captive reptiles also benefit from enrichment, recognise their caretakers individually and form bonds with them, and are affected by early social isolation in ways similar to birds and mammals. Still, the gap between what we know and what we would like to know about reptilian behaviour and cognition is enormous.

Keywords

Brain · Brain size · Cerebral cortex · Cognition · Learning · Behaviour · Complex behaviour · Social behaviour · Parental care · Play

7.1 Introduction

Let us face it: reptiles have always had a public image problem. Even Carl Linnaeus, the father of scientific taxonomy, referred to them in a much-quoted passage as ‘foul and loathsome’ (1758), which has not helped their bad reputation. Reptiles are often portrayed as having small, primitive brains lacking a cerebral cortex. Their behaviour is reportedly sluggish, clumsy, and stereotyped. As far as their cognitive abilities are concerned, reptiles are widely assumed to be poor learners with reduced or nonexistent complex cognitive abilities. Even from a welfare and conservation perspective, reptiles are still considered, in some quarters, to deserve less attention than other vertebrates, such as fishes, amphibians, birds, or mammals (e.g. Czech et al. 1998; Clark and May 2002).

Those familiar with reptilian biology will recognise the above characterisation as a highly distorted caricature of ‘real’ reptiles. With over 11,000 known species and many more possibly awaiting discovery, reptiles as a group include a huge range of morphological, behavioural, and ecological variation that defies simple generalisations. Some reptiles, such as venomous snakes, large constricting snakes, large lizards and crocodiles are potentially dangerous to humans, which may explain their bad reputation, but to a large extent, public attitudes towards reptiles are based on ignorance and prejudice. However, myths and misconceptions about reptiles are increasingly out of step with growing evidence that reptiles have relatively complex

brains that support sophisticated cognitive abilities and a rich behavioural repertoire. Several recent studies have noted the social, cognitive, and behavioural complexity found in many species as well as the importance of personality and individuality across and within taxa and even families (Burghardt 2013; Doody et al. 2013; Gardner et al. 2015; Schuett et al. 2016; Matsubara et al. 2017; Waters et al. 2017; Whiting and While 2017; Lapedra et al. 2018; Font 2020; Doody et al. 2021; Doody 2023; Burghardt and Layne-Colon 2023).

In 2004, a group of leading neuroscientists joined forces to revise the nomenclature that had been in use during most of the twentieth century to describe cell groups and fibre tracts in the avian forebrain. They replaced the standard neuroanatomical nomenclature—based on erroneous assumptions regarding homologies with the basal ganglia of mammals—with new terms reflecting well-supported homologies between avian and mammalian brain structures (Reiner 2005). The revised terminology highlights the parallels between avian and mammalian brains and has gone a long way to dismiss the myth that bird brains are ‘primitive’ compared to mammals. Along with this reinterpretation of the avian brain came a reassessment of their cognitive abilities (Emery and Clayton 2004, 2005). Although those familiar with the animal behaviour literature already knew that birds, such as parrots and corvids, excel at many tasks requiring advanced cognitive skills (Heinrich 1999; Pepperberg 1999), in the public’s eye, the expression ‘bird brain’ was still synonymous with stupid or lacking intelligence.

Following the concerted effort of neuroscientists and bird cognitive scientists, such misconception started to give way, resulting in an altogether improved public perception of bird cognitive abilities (Roth et al. 2019). However, the effort was incomplete because it did not include non-avian reptiles, and thus unwittingly contributed to reinforcing the notion that there exists a chasm between avian and non-avian reptiles in terms of brain structure, cognition, and behaviour. By pointing out the overlap between birds and mammals, they effectively increased the perceived gap between them and the rest of vertebrates.

A recent review of the neurobiological underpinnings of the reptile-brain transition stated that ‘Numerous behavioural phenomena indicate a high evolutionary level of the avian brain, in some respects comparable, or even superior to that of most mammals . . . Such key elements are visual acuity, colour and stereoscopic vision, cognitive and learning abilities, elaborate vocalisation, communication, imitation, advanced social behaviour, nesting and nursing, prolonged family partnership, migration and homing, colony formation, food-storing. In reptiles, similar phenomena are absent, or rather infrequent and less elaborate’ (Kalman 2009). Such claims are all the more surprising considering the similarities in brain structure between avian and non-avian reptiles and the evolutionary relationships between non-avian reptiles and other amniotes (Nomura et al. 2013) and are clearly at odds with recent empirical findings regarding non-avian reptile behaviour and cognition.

Our aim here is to discuss what we consider are some of the major and more widespread misconceptions regarding reptile brains, cognition, and behaviour. An assessment of our current understanding of non-avian reptile (which we will refer to as reptile for the remaining of this chapter) cognition and behaviour is relevant to

issues of welfare in as much as the moral status we accord to animals often depends on the extent to which we perceive them as sentient, cognitively adept and complex beings. However, this may not be the only ruler for moral treatment of nonhuman phenomena (Burghardt 2009; Dawkins 2017). Aesthetic, ecological, rarity, commercial, and other traits also affect our treatment of other species (Burghardt and Herzog 1980; Herzog 2010).

7.2 Misconception 1: Reptile Brains Are Ten Times Smaller than Those of Birds and Mammals of Similar Body Size

The myth of the sluggish, primitive, witless reptile can be traced, at least in part, to long-standing misconceptions about reptilian brain size and organisation. Furthermore, their ectothermic physiology and lower metabolic rate often translate into slower and more deliberate behaviour that contrasts with our endothermic nature and anthropocentric/anthropomorphic tendencies (Rivas and Burghardt 2002).

The reptilian brain has often been stereotyped as small, simple, and lacking a cerebral cortex—a characterisation that is incorrect and based on outdated evidence. Let us consider brain size first. Across all vertebrate radiations, brain size varies approximately 30-fold for a given body size (Northcutt 2002). This means that it is possible to find vertebrates of similar body size whose brain weights differ by a factor of 30. Brain size varies in an orderly manner both within and between vertebrate radiations, suggesting that brain enlargement and elaboration has occurred independently multiple times in vertebrate evolution (Northcutt 2002). Birds have brains that are as large as or even larger than those of mammals of similar body size. Reptiles and other vertebrates, on the other hand, have brains that are smaller—both in relative and absolute terms—than those of birds and mammals. But, how much larger are bird brains compared to reptilian brains? Published estimates range widely, but most authors state that the average difference is tenfold, i.e. a bird or a mammal has a brain ten times larger (i.e. heavier) than a reptile of similar body size (e.g. Hurlburt 1996; van Dongen 1998; Northcutt 2011; Dicke and Roth 2016; Güntürkün et al. 2017; Shimizu et al. 2017).

The tenfold figure can be traced back to the work of Harry Jerison, who conducted the first serious attempt to quantitatively compare brain size across different vertebrate lineages. Jerison (1973) plotted brain and body weight data on a log-log scale and drew minimum convex polygons enclosing the data points for different groups of vertebrates. Anybody with even a passing interest in brain evolution is bound to have seen Jerison's polygons, which have been reproduced in countless publications, often used to justify the presumed cognitive superiority of birds and mammals: whilst the polygons for birds and mammals show almost complete overlap, a conspicuous gap separates the bird-mammal polygon from the polygon representing the remaining vertebrates (e.g. Striedter 2005). Jerison (1973) estimated the average difference in brain size between 'higher' (birds and mammals) and 'lower' (fishes, amphibians, and reptiles) vertebrates to be one order of magnitude (i.e. $10\times$). Jerison used brain and body size data for a mere 20 species of

reptiles. More recent analyses have relied on larger sample sizes, but the basic conclusion regarding overall differences in brain size across vertebrate groups remains unchanged, and the tenfold figure continues to be authoritatively quoted to describe the gap between reptiles and birds (e.g. Northcutt 2011; Roth 2013; Dicke and Roth 2016; Güntürkün et al. 2017; Shimizu et al. 2017).

Recently, an extended dataset that raises the number of available reptile species to 175 has become available (Fig. 7.1). Figure 7.2a shows the corresponding polygons and reduced major axis regression lines for reptiles and for a sample of over 900 bird species. For all body sizes, bird brains are heavier than reptile brains, but there is considerable variation within both groups. Thus, the brain of a 160 kg ostrich weighs 26 g, whilst that of a 120 kg crocodile weighs 13 g—i.e. less than a twofold difference. The crocodile brain represents a mere 0.1% of its body weight; in contrast, the brain of a 0.5 kg macaw accounts for 2.5% of its body weight. However, on average, the difference in brain size between birds and reptiles is 7.4-fold (the difference is even smaller if a phylogenetic correction is applied to account for the

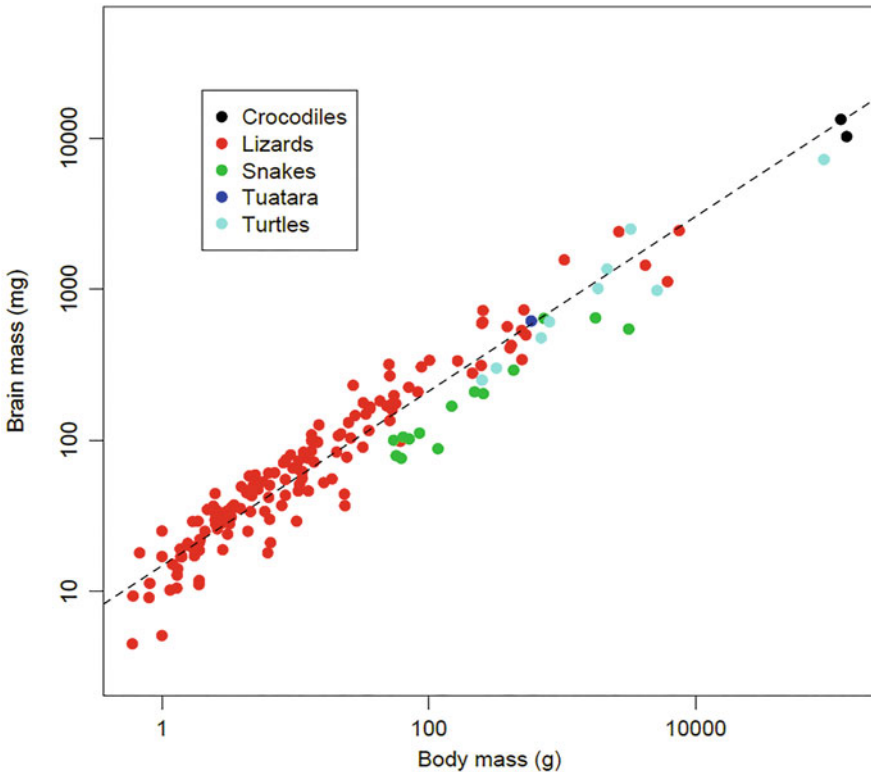


Fig. 7.1 Brain-body scaling in a sample of 175 species of living reptiles. Brain and body weight data were retrieved from published literature sources (Font et al. 2019). Only adult individuals of either sex were considered. The dashed line indicates the best-fit allometric line calculated using reduced major axis regression

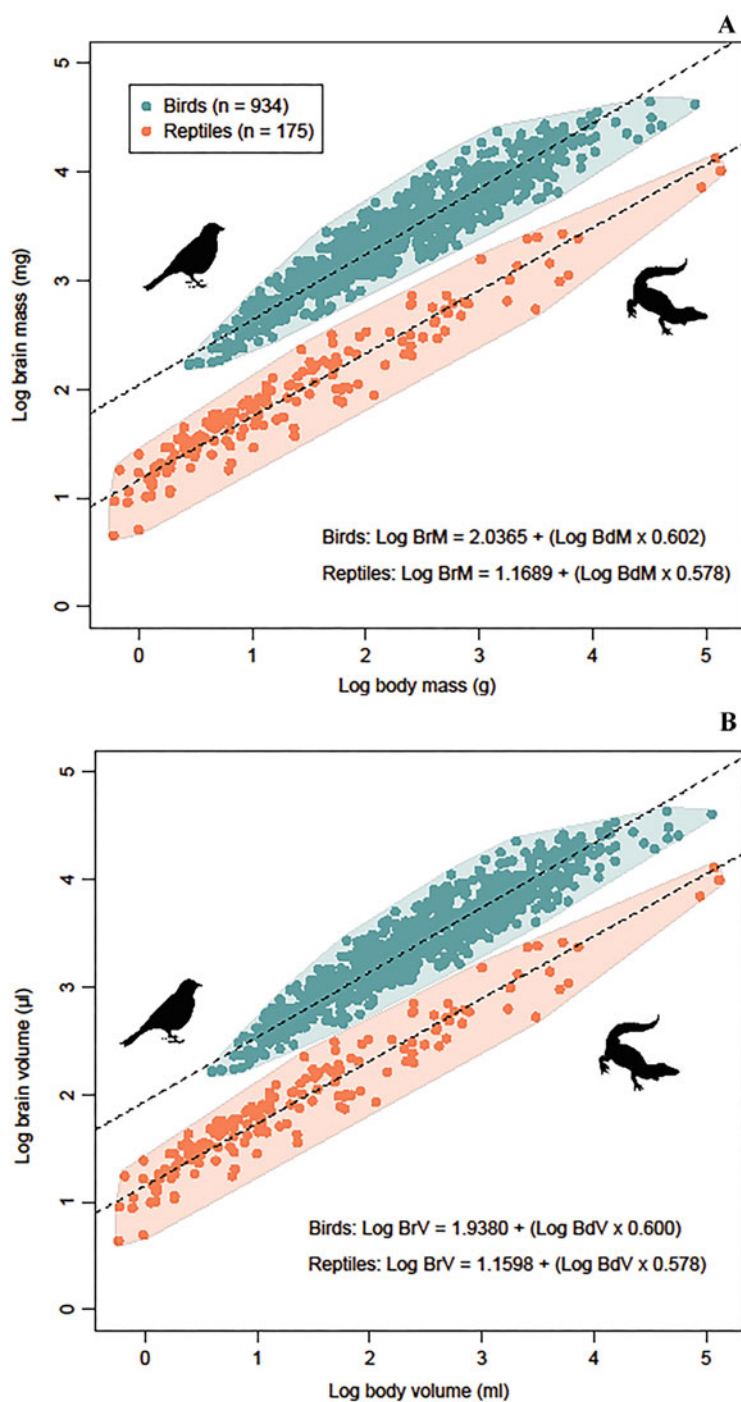


Fig. 7.2 Polygon plots showing the distribution of relative brain size in birds (upper polygon) and non-avian reptiles (lower polygon) using weight (a) and volume (b) data. Brain and body weight

lack of independence of species due to their shared evolutionary history; Font et al. 2019).

Nevertheless, even the 7.4-fold figure can be misleading. The problem with a comparison based on weight should be obvious but has generally escaped the attention of researchers interested in brain evolution: in a comparison between a reptile and a bird of similar body weight, the bird tends to be considerably larger than the reptile. For example, a pond slider (*Trachemys scripta*) and a mallard duck (*Anas platyrhynchos*) have similar body weight as adults (if anything the turtle may be heavier, particularly if it is a female), but the duck is larger—more voluminous—than the turtle. This is not surprising considering that bird anatomy has been under selection for flight, where lighter is better. Birds, for example, have an extensive system of air sacs extending into the viscera, muscles, and under the skin. As a result, the density of body tissue in birds is lower than in reptiles or mammals. In contrast, brain tissue has roughly the same density across all vertebrates (e.g. Iwaniuk and Nelson 2002). Add to that the different Bauplan ('body plan') of birds relative to reptiles. Most lizards and crocodiles have a tail that accounts for a large percentage of their total body weight (close to 50% in some cases); the tail of a bird is mostly feathers and, therefore, very light in comparison. Many turtles possess a dense and heavy carapace that increases their weight beyond what one would expect for a reptile of its body size (note that most data points for turtles in Fig. 7.1 fall below the regression line). So perhaps the gap between the bird and reptile polygons could, at least in part, simply reflect the fact that the bodies of birds are lighter than expected given their brain weight.

Figure 7.2b shows the polygons for birds and reptiles using brain and body volume rather than weight. Using volume brings the two polygons closer to each other, and the gap separating birds from reptiles all but disappears. In fact, the average difference in brain size between birds and reptiles using volume data shrinks to sixfold (further reductions can be obtained by including differences in body design in the calculations). Substituting the often cited tenfold brain size difference for a more realistic sixfold difference may seem a modest change, but worth stressing considering that the literature misrepresents reptiles by describing the differences between reptiles and birds as more dichotomous and functionally important in stereotype-consistent ways than is warranted. It is also important to note that the sixfold difference between reptiles and birds is less than that between different



Fig. 7.2 (continued) data for birds and non-avian reptiles were retrieved from published literature sources (Font et al. 2019). Log-log standardised major axis (model II) equations are also shown. The reptile slope of 0.578 has 95% confidence limits of 0.556 and 0.602, which overlap the bird slopes of 0.602 (weight) and 0.600 (volume). Brain volumes for birds and non-avian reptiles were calculated from brain weight using a common specific gravity of 1.036 g ml^{-1} . Body weight was transformed to volume using available data on specific gravity of body tissue in birds (0.718 g ml^{-1}) and reptiles (1.025 g ml^{-1}). The separation of the intercepts of the reduced major axes (dashed lines) corresponds to a 7.4-fold difference in brain weight between birds and reptiles (a); the average difference using volume rather than weight is only sixfold (b)

species of birds or between different species of mammals (note that the bird polygon in Fig. 7.2b is much taller than the gap separating it from the reptile polygon).

A related misconception has to do with the size of the reptilian brain relative to the size of the braincase. In birds and mammals, it is generally assumed that the brain fills all or most of the endocranial cavity. However, in non-avian reptiles, particularly lizards and snakes, there is a trend towards the loss of cranial elements, resulting in skulls that are lighter and less ossified than those of birds and mammals, and the brain fills only part of the endocranial cavity, the remainder being occupied by connective tissue, venous sinuses, and cerebrospinal fluid. For studies on brain size evolution that include fossil reptiles, an estimated brain: endocranial cavity ratio of 0.5 is commonly used, which assumes that the brain occupies approximately 50% of the endocranial volume (Jerison 1973). However, studies using modern imaging techniques have found that the average brain: endocranial cavity ratio is closer to 0.7 and in some species, the brain nearly fills the endocranial cavity (a 0.97 ratio in the false monitor lizard *Callopiastes maculatus*, Kim and Evans 2014). Many discussions of brain evolution in extinct reptilian lineages (e.g. dinosaurs) are flawed due to this misconception alone.

Is size all that matters? Honeybees, with their diminutive brains, are capable of cognitive feats beyond the capacity of virtually all vertebrates (e.g. symbolic communication, tool use, numerical abilities, complex problem-solving; Chittka 2017). On a comparative level, then, does the difference in relative brain size justify the expectation that birds are much more behaviourally complex and intelligent than reptiles? A large brain size is thought to confer more intelligence because more brain tissue increases the computational capacity of the brain supporting behavioural and cognitive complexity. However, the correlation between brain size and cognitive ability is weak both intraspecifically and interspecifically (Healy and Rowe 2007; Herculano-Houzel et al. 2014), and the link between brain size and intelligence remains one of the thorniest issues in comparative neurobiology (Roth and Dicke 2005; Chittka and Niven 2009). Olkowicz et al. (2017) showed that birds have roughly twice as many neurons in their forebrain as mammals of similar brain weight. This suggests that the packing density of neurons in some telencephalic areas, rather than brain size, may explain the sophisticated cognition found in birds such as parrots and corvids. More recently, a comparative study across amniotes revealed that birds and mammals have, on average, 20-fold more neurons in their brains than equivalently sized reptiles (Kverkova et al. 2022). Intriguingly, the largest difference is found in the cerebellum, which may have some role in cognition but is mostly involved in motor coordination and control.

Recent studies have begun to evaluate patterns of brain evolution in reptiles and the potential role of species ecology within a phylogenetic framework. For example, in anole lizards (*Anolis* sp.), changes in the relative size of different brain regions have occurred in a coordinated manner (Powell and Leal 2012), and although different species use habitats that vary in complexity, this complexity does not correlate with differences in neuroanatomy across species (Powell and Leal 2014). More recently, it has been proposed that species differences in locomotor mode, particularly those related with the use of arboreal, terrestrial, or fossorial habitats, are associated with differences in neuroanatomy across squamates (Macrì et al. 2019).

7.3 Misconception 2: Reptile Brains Lack a Cerebral Cortex

Size differences notwithstanding, many consider that the brain of reptiles is a depauperate mammalian brain, that is, a mammalian brain that is missing some parts (e.g. Rial et al. 1993; Amiel et al. 2011). Particularly persistent is the misconception that reptiles lack a cerebral cortex, or specific cortical areas such as the hippocampus (e.g. Mueller-Paul et al. 2012; Wilkinson and Huber 2012; Tye 2017). This idea can be traced back to the work of neuroanatomist Paul MacLean and his influential triune brain hypothesis (MacLean 1990). MacLean's triune brain hypothesis has been described as the 'new scoops on an old cone' model of brain evolution because it postulates that vertebrate brains evolve by sequential addition of new brain areas onto pre-existing ones (Striedter 2007). The model specifically claims that the reptilian forebrain is dominated by structures homologous to the basal ganglia of mammals (the first and oldest ice cream scoop). As the basal ganglia are involved in the control and initiation of voluntary movements and are considered the substrate for instinctive behaviours, reptilian behaviour is, by MacLean's view, deemed essentially instinctive in the sense that it is pre-programmed, rigid, impervious to experience, and lacking positive emotions. The model further postulates that reptiles lack a limbic system and a neocortex (the second and third, more recently evolved scoops), which are found only in mammals. Because the hippocampus is considered an essential component of the limbic system, the inescapable conclusion is that reptiles do not have a hippocampus.

MacLean's ideas about brain evolution became extremely popular, thanks in part to the writings of astronomer Carl Sagan (1977). In fact, a search through the Internet using 'reptile' and 'brain' as keywords returns far more hits on triune brain gibberish than on reptilian neuroanatomy. However, the triune brain hypothesis does not hold up under scrutiny and is, despite its intuitive appeal, essentially wrong. Vertebrate brains do not evolve by the addition of new scoops to an old ice cream cone but, as with other parts of the body, by the modification of pre-existing scoops (Jacob 1977; Dawkins 1986). The three scoops implied by the triune brain hypothesis were already present in the common ancestor of all living vertebrates and can be found, in modified form, in all its descendants (Butler and Hodos 2005; Emery and Clayton 2005). Detailed morphological and behavioural analyses have highlighted the structural homology and functional equivalence between forebrain structures in reptiles and other vertebrates, including mammals. In fact, reptiles and mammals are the only vertebrates with a clearly laminated (i.e. multilayered) cerebral cortex (Nomura et al. 2013; Dugas-Ford and Ragsdale 2015; Briscoe and Ragsdale 2018). Reptiles have, not one, but four distinct cortical areas: the medial, dorsomedial, dorsal, and lateral cortices (ten Donkelaar 1998). The medial and dorsomedial cortices are considered homologous to the mammalian hippocampus (e.g. Tosches et al. 2018) and, like the mammalian hippocampus, they play a crucial role in spatial learning and memory (Salas et al. 2003; LaDage et al. 2009; Holding et al. 2012; Striedter 2016; Reiter et al. 2017). The dorsal cortex is the target of ascending auditory, visual, and somatosensory projections and is homologous to mammalian neocortex. Finally, the lateral cortex of reptiles is homologous to the olfactory cortex of mammals

(Butler and Hodos 2005; Northcutt 2013). Of course, this is not to say that sophisticated cognition requires a laminated cerebral cortex, as the work with invertebrates and fishes amply demonstrates (Brown et al. 2011; Chittka and Niven 2009).

In addition to these cortical areas, reptiles have a unique pallial structure that they share with birds: the dorsal ventricular ridge (DVR). The mammalian homologues of the DVR are highly controversial, but this intriguing structure contains auditory, visual, and somatosensory regions and is thought to be responsible, at least in part, for the complex cognitive abilities of birds (Butler and Hodos 2005; Reiner 2009; Naumann et al. 2015). Lizards and snakes also have a discrete structure in the posterior subdivision of their DVR called the nucleus sphericus that receives input from the accessory olfactory bulb (Halpern 1980; Lohman and Smeets 1993). Surprisingly, these findings are not all entirely new. The shortcomings with MacLean's hypothesis were exposed over a quarter of a century ago (Reiner 1990), yet the triune brain is still widely cited as the state-of-the-art in vertebrate brain evolution (e.g. Linden 2007; Kean 2014) and continues to misinform discussions of reptile cognition and behaviour (Roth et al. 2019).

7.4 Misconception 3: Reptilian Behaviour Is Simple, Stereotyped, Uninteresting, and Primitive

For us, a sunny summer afternoon is full of colours, sounds, smells, and perhaps the feeling of a warm breeze against the skin. For a turtle, alligator, lizard, or snake, the same experience might be additionally characterised by sensing of magnetic field properties, polarised light patterns, or even seismic cues. It is somewhat ironic that our own inability to perceive the diversity of stimuli that pepper the sensory systems of reptiles is largely responsible for the misconception that reptiles exhibit simple, uninteresting, and stereotyped behaviours. This type of uncritical anthropomorphism is all too common and led to considering how other species, such as rattlesnakes, perceive us (crotalomorphism; Rivas and Burghardt 2002). Below we provide a few examples, ranging from communication to foraging behaviour, illustrating the richness and complexity of reptilian behaviour (see also Lillywhite 2023; Crowe-Riddell and Lillywhite 2023; Gillingham and Clark 2023; Doody 2023).

Communication is a central aspect of social interactions, and we often marvel at the diversity and complexity of signalling behaviour in birds and mammals. However, the ability of reptiles to modulate their signals depending on context rivals that of endotherms, and the sensory modalities used for signalling are perhaps more diverse in reptiles. For example, with the exception of electric signals, all other sensory modalities (e.g. visual, chemical, vibrations, auditory) are used by reptiles for signalling, often in conjunction with one another (Pianka and Vitt 2006; Fleishman and Font 2019). In fact, multi-modal signalling has been reported across the major clades of lizards [chamaeleons *Chamaeleo calytratus* (i.e. vibratory and visual; Barnett et al. 1999), flat-lizards *Platysaurus broadleyi* (i.e. chemical and visual; Whiting et al. 2009), desert iguanas *Dipsosaurus dorsalis* (i.e. chemical and visual; Alberts 1989), dwarf geckos *Sphaerodactylus* sp. (i.e. chemical and visual; Regalado 2012), long-necked freshwater turtles *Chelodina oblonga*

(i.e. sound and tactile; Giles & Davis 2009), and snakes (e.g. chemical and tactile; Greene 2000; chemical and visual; Terrick et al. 1995)]. Alligators, on the other hand, are well known for producing a diversity of mating calls, which is as rich as that observed in some bird species (Reber et al. 2017). Furthermore, in the case of motion-based signals, which are relatively common and highly salient in lizards (e.g. dewlap extension/retraction, head bobs, foot shakes), experimental evidence has demonstrated that individuals can adjust the physical properties of those signals in response to abiotic conditions (e.g. Fleishman 1988; Ord et al. 2007) and social interactions (e.g. Steinberg and Leal 2013) in order to increase the visibility of the signal. This level of plasticity is not associated with simple or stereotyped behaviours and speaks volumes about the ability of reptiles to modulate their behaviour.

Reptiles have been viewed historically as exhibiting a relatively simple foraging behaviour. However, whilst most reptiles are insectivores or omnivores (whether intentionally or incidentally), many others are herbivorous, raid bird nests, consume aquatic prey, including fish that they capture under-water, or even subdue large mammals (Greene 2000; Leal et al. 2002; Pianka and Vitt 2006; Maslanka et al. 2023). Furthermore, the means of finding and then consuming prey vary dramatically. Reptile foraging tactics vary greatly; for example, some lizards, snakes, and turtles use lures to attract prey (e.g. Drummond and Gordon 1979; Murray et al. 1991; Leal and Thomas 1994; Hansknecht 2008). Several gecko species can hunt for crickets by locating their mating calls and ambushing them once they emerge from their burrows (Sakaluk and Belwood 1984). Similarly, amphisbaenids, with their highly specialised fossorial morphology, use the vibrations of potential prey items to assist in foraging (Gans 1978). Even snakes exhibit a great variety of prey-handling behaviour. The colubrid *Alsophis portoricensis* uses different strategies depending on the type of prey it must subdue, from envenomation when handling relatively large lizards to constriction when handling small mammals (Rodríguez-Robles and Leal 1993). Similarly, snakes that specialise in eating crabs remove the potentially dangerous legs of the crabs before consuming the body—a unique and complex behaviour indeed (Jayne et al. 2002), and one species of blindsnake (*Indotyphlops braminus*) has been found to frequently decapitate its termite prey before ingesting them (Mizuno and Kojima 2015). Again, such diversity and flexibility in foraging behaviour rivals what is commonly associated with birds and mammals, yet is usually overlooked when discussing the complexity of reptilian behaviour.

7.5 Misconception 4: Reptiles Are Cognitive Underachievers

Cognition, broadly defined, encompasses all the ways in which animals acquire, process, store, and act on information, either from the environment, social interactions, or daily activities (Shettleworth 2010). The neurophysiological mechanisms governing basic cognitive processes such as perception, learning, memory and decision-making are probably similar across vertebrate groups. However, an influential trend in comparative psychology claimed that vertebrate classes could be arranged in hierarchical levels with reptiles incapable, as a group, of

learning at the mammalian level (Bitterman 1965; see also Thomas 1996). Indeed, reptiles are often depicted as the cognitive morons of the vertebrate lineage, their cognitive abilities considered inferior to those of other groups, including, more recently, fishes (Bsharry et al. 2002). Jerison (1973) described reptiles as ‘... essentially reflex machines with few requirements for plasticity or flexibility’. One hypothesis about the extinction of dinosaurs proposed that their ‘dwindling brain and consequent stupidity’ was the cause of their demise (Benton 1990). According to Vitti (2013), ‘...reptiles are classic underperformers on the most commonly used cognitive tests’, whilst Roth (2015) reports that ‘... ‘higher’ intelligence has not yet been convincingly demonstrated in ‘reptiles’’. In a recent paper, Güntürkün and Bugnyar (2016) stated that ‘although reptilian cognition should not be underestimated, nothing at the level and scope of bird cognition has been reported for this animal group so far’. This is typical of much current thinking in comparative cognition, likely stemming from the misconception that a tenfold difference in relative brain size between reptiles and birds will necessarily lead to a tenfold difference in cognitive ability (e.g. Güntürkün et al. 2017).

However, the views expressed in the above quotations are inconsistent with the available empirical evidence. Reptiles display a startling array of cognitive abilities, which at times are on a par with those of birds or mammals (see Wilkinson and Huber 2012; Burghardt 1977a, 2013; Northcutt 2013; Font 2020; Szabo et al. 2021, and references therein). Consider learning; Table 7.1 shows a list of different

Table 7.1 Learning types identified in reptiles

• Habituation
• Classical/instrumental conditioning
– Maze learning
– Detour problems and delayed reaction
– Food aversion learning
– Predator avoidance learning
– Target training
• Discrimination learning
– Visual/colour discrimination
– Chemical discrimination
• Imprinting-like phenomena and critical periods
– Food imprinting
– Geomagnetic imprinting
– Navigation cues
• Spatial learning
• Latent learning
• Probability learning
• Reversal learning
• Social learning
– Social facilitation
– Local enhancement
– Stimulus enhancement
– Copying-imitation

learning types that have been identified in reptiles. The list encompasses most currently recognised types of learning, and many entries in the list reflect not one but several studies addressing that particular learning type, often in different species. Some types of learning, such as maze learning, visual discrimination, and spatial learning, have been the focus of many studies. This is worth stressing because, particularly during the last decade, the media have hailed each new discovery as if it were the first of its kind, effectively creating the false impression that evidence of reptile cognition is rare or nonexistent. For example, Mueller-Paul et al. (2012) trained four red-footed tortoises (*Chelonoidis carbonaria*) to navigate an eight-arm radial maze. When the news hit the media, the discovery was presented as if it was the first time a turtle had been shown to learn a maze. In fact, Burghardt (1977a) lists 24 maze studies in reptiles, of which six (involving eight species) were done with turtles.

Turtles, crocodiles, lizards, and snakes have all been shown to be quite adept at most traditional learning tasks provided that the problem accommodates the peculiarities of reptilian biology, such as their body temperature at the time of testing (Burghardt 1977a, 2013, 2018; Fig. 7.3). In fact, if anything, research in this field has been marked by the notorious inability of several generations of researchers to reveal the real extent of reptiles' cognitive abilities. But when experimental designs are ethologically informed (Greenberg 1995, 2023) and take account of the diversity of

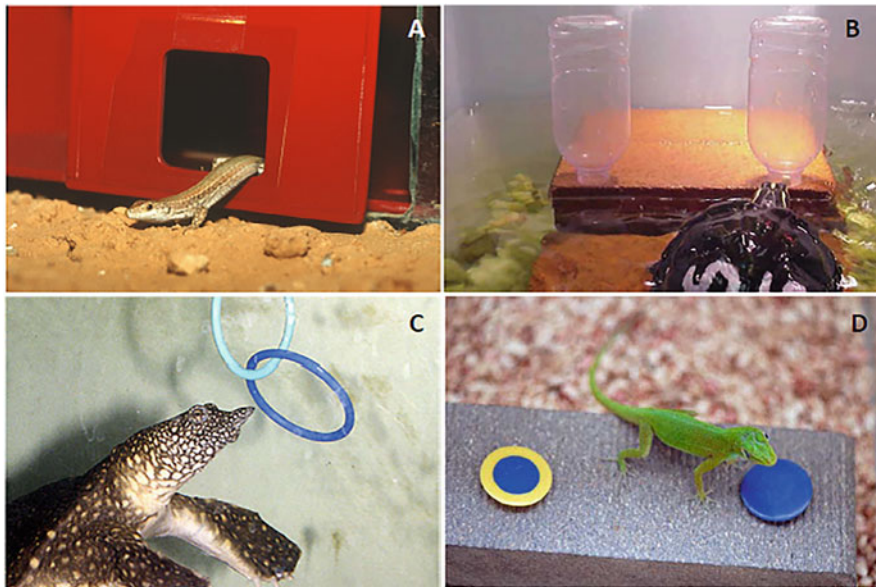


Fig. 7.3 Some examples of learning and play in reptiles. (a) Lizard (*Podarcis liolepis*) pushing a hinged glass door (a microscope coverslip) to exit a Y maze and return to its home terrarium; (b) training of turtle (*Pseudemys nelsoni*) to topple a plastic bottle to obtain a food reward; (c) soft-shelled turtle (*Trionyx triunguis*) playing with plastic rings; (d) lizard (*Anolis evermanni*) performing a reversal learning experiment

sensory abilities and behavioural repertoires found in reptiles, the conclusion put forward by Burghardt more than 40 years ago still holds: ‘... there is no type of problem learned by all birds and mammals that is beyond the ability of all reptiles’ (Burghardt 1977a, p. 665). This, of course, reflects the reality that all organisms are ‘decision makers’ in many realms of their lives and these choices must be largely adaptive for them to survive. Gross measures of ‘intelligence’ often poorly reflect what animals need to do to be successful and cognitive mechanisms work best when tuned to the problems related to survival and reproduction. This is a major point made by the early ethologists such as Tinbergen (1951).

Often, negative results are a consequence of trying to force reptiles into the straightjacket of experimental procedures and reinforcers designed for other animals (Roth et al. 2019). For example, a device widely used for the study of spatial learning is the Morris water maze, essentially a small circular pool with platforms hidden under the water surface that the animals have to learn to locate. This device may be appropriate for rats or mice, who are in fact very good swimmers, but perhaps not for fully terrestrial lizards that never, or rarely, enter the water. Yet, some studies have probed the spatial abilities of lizards by dropping them inside a pool and forcing them to swim to reach a platform hidden under the surface (Foà et al. 2009; Beltrami et al. 2010). This seems questionable even if such studies show some evidence of learning, because assessing the performance of terrestrial lizards in a task that requires swimming may grossly underestimate the lizards’ real spatial cognitive abilities in an ecologically relevant context. Alternative, more ethologically realistic procedures are available and have been successfully used to probe spatial learning and memory in terrestrial lizards (e.g. LaDage et al. 2012; Font 2019). Conversely, aquatic or semi-aquatic turtles and snakes may perform poorly when tested in terrestrial set-ups.

Although learning some tasks may require hundreds of trials, reptiles also show evidence of rapid learning (Burghardt et al. 1973; Terrick et al. 1995; Davis and Burghardt 2007; Manrod et al. 2008; Leal and Powell 2012a). For example, the agamid (*Japalura swinhonis*) learns to avoid weevils after only a single encounter and maintains aversive behaviours for more than 3 weeks (Tseng et al. 2014). Reptiles can also remember a learned task for long periods of time (Carazo et al. 2008; Soldati et al. 2017). As a case in point, turtles (*Pseudemys nelsoni*) show memory retention of a food acquisition task (knocking over a bottle for a food pellet) for an impressive 36 months without any training (Davis and Burghardt 2012; Fig. 7.3).

Besides learning, reptiles have been shown to be capable of other cognitive feats, such as individual recognition (Kramer 1989; Carazo et al. 2008), picture-object recognition (Wilkinson et al. 2013), gaze following (Wilkinson et al. 2010), abstract concept formation (Leighty et al. 2013), quantity estimation (Miletto Petrazzini et al. 2018), problem-solving, including solving non-natural tasks (Manrod et al. 2008; Leal and Powell 2012a, b; Pérez i de Lanuza et al. 2018), and possibly even tool use (Dinets et al. 2013). Evidence also suggests the existence of self-recognition abilities mediated by chemical cues (Alberts 1992; Chiszar et al. 1995; Aguilar et al. 2009). Still, the number of studies exploring cognition in reptiles is small by comparison

with those conducted for fishes, birds, or mammals, and we are still far from being able to make an accurate assessment of reptile cognition.

Although there has been some renewal of interest in reptilian cognition during the last decade, reptiles continue to be given short shrift in studies of comparative cognition. A well-known volume on fish cognition spanning close to 500 pages covers at length topics such as learning, personality, social recognition, social learning, cooperation, Machiavellian intelligence, and lateralisation (Brown et al. 2011). In contrast, a chapter entitled ‘How intelligent are vertebrates’? in a volume devoted to the evolution of brains and cognition in vertebrates covers fishes, amphibians, mammals, and birds, but not reptiles (Roth 2013).

7.6 Misconception 5: Reptiles Are Solitary, Lack Parental Care, and Do Not Form Stable Social Relationships

The idea that reptiles are generally loners and lack parental care and complex sociality is one of those claims that, when pushed, most ethologists, animal behaviourists, comparative psychologists, as well as herpetologists will demur, especially when faced with some specific examples, such as crocodylian hatchlings staying with parents for months if not years. However, the fact is that stereotyping is at work and what seems to be almost universal outcompetes facts. This was pronounced in the ‘hot-blooded dinosaur’ controversy, where dinosaurs were considered far removed from any behavioural link with those sprawling lethargic ‘traditional’ reptiles (Burghardt 1977b). Nevertheless, herpetologists themselves often have shown limited appreciation of the cognitive, social, and emotional lives of reptiles due to anthropocentric bias fostered by the lack of facial expressions, lower metabolism, and deliberate behaviour. This led to the dismissal of many early reports of behavioural complexity in reptiles. W. T. Neill, considered the dean of crocodylian biology, dismissed the evidence for parental care by McIlhenny (1935) as a mere fable with these statements as late as the 1970s: ‘In reality an alligator inherits its patterns of actions, just as it inherits its anatomical structure ... it is absurd to think that an alligator on the one hand had evolved a pattern of action involving intensive care of the young and on the other hand a pattern involving predation upon these same young’ (Neill 1971). Such attitudes by many zoo curators and herpetologists, often uninformed and uninterested in behaviour, led to views of them as not needing the types of housing and social stimulation common with most bird or mammal or even fish exhibits. The earlier mentioned triune brain ideas of P. MacLean (a true myth) were largely predicated on the presumed absence of any parental care and family life in reptiles (MacLean 1985). He absorbed too readily the standard views of mainstream herpetologists of the time, even though crocodylian parental care was by that time repeatedly documented, even in popular articles (Pooley and Gans 1976).

Studies by L. T. Evans beginning in the 1930s, and the head-bob communication display research pioneered by C. C. Carpenter in the 1960s ushered in many new findings on social behaviour and social aggregation in turtles, lizards, snakes, and

even the truly cool-living reptile, the tuatara. Important new discoveries on the social lives of reptiles are being made almost monthly by a new generation of herpetologists and others going into the field with new ideas and technology or into the laboratory with creative insights and experimental methods. A plea for appreciating these findings with examples appeared recently (Doody et al. 2013). However, even those studying reptile cognition have the tendency to emphasise that they are finding such remarkable abilities in ‘cold-blooded’, ‘asocial’ animals (Wilkinson and Huber 2012; Burghardt 2018), and thus unwittingly help to perpetuate stereotypes.

Certainly, there is great diversity among reptiles; many are highly precocial at birth or hatching and no postnatal parental care occurs. However, the exceptions are most illuminating and these are prime sources for understanding the evolutionary processes underlying postnatal parental behaviour, which is universal in other amniote vertebrates. Being universal, the origins of the behaviour are thus largely obscure and difficult to probe with no outgroups within birds and mammals. Although all turtle and tortoise eggs have long been viewed as being completely abandoned by mothers after nesting, new studies are showing that adult river turtles may return to the nest near hatching time, communicate with the hatchlings vocally, and guide them downriver many kilometres to suitable habitat (Ferrara et al. 2013, 2014). Even in the absence of parental care, hatchlings can show remarkably complex sociality (Burghardt et al. 1977; Rivas and Levin 2004). Similarly remarkable are the long-term monogamous and multi-generational colonies of some Australian skinks, recently reviewed extensively (Leu et al. 2015; Bull et al. 2017; Whiting and While 2017). In short, the social lives of reptiles have many secrets to divulge (Doody et al. 2021), such as the recent description of adults using their body as a bridge to facilitate the movements of juveniles in the gecko (*Hoplodactylus maculatus*) (Hoare and Nelson 2006) and provide important scientific entry to some important aspects of behavioural and social evolution in vertebrates.

7.7 Misconception 6: Reptiles Do Not Play

For many decades play was considered found virtually only in mammals and some birds, apparent exceptions being, as with Neill and crocodylians, rather absurd or misinterpreted (Bekoff and Byers 1981; Fagen 1981). Even apparent examples were based on brief observations and undocumented (i.e. no photos or video). Of course, all animals, including reptiles, explore new habitats and investigate objects. Burghardt filmed wild hatchling green iguanas (*Iguana iguana*) in groups exploring his camera equipment during field work in Panama in the early 1970s and newborn African chamaeleons (*Chamaeleo* sp.) wrestling in 1963. However, play was not something readily attributed to animals not already considered playful due both to our anthropocentric biases as well as the lack of a useful definition or criteria for identifying play. Burghardt has developed and refined relevant criteria over the last 20 years (Burghardt 1999, 2005, 2011). A brief summary statement would be ‘play is repeated, seemingly non-functional behaviour differing from more adaptive

versions structurally, contextually, or developmentally, and initiated when the animal is in a relaxed, unstimulating, or low stress setting' (Burghardt 2014).

Using these criteria, play has now been found in numerous species other than birds and mammals, including reptiles, amphibians, fishes, and some invertebrates (e.g. octopus, spiders, wasps) (Burghardt 2005, 2014). Among reptiles, Nile soft-shelled turtles (*Trionyx* sp.), geckos, monitor lizards, and various crocodylians engage in recognisable play activities (reviewed in Burghardt 2005; more recent examples in Augustine et al. 2015; Barabanov et al. 2015; Burghardt 2015; Dinets 2015). Such activities can include pushing and manipulating balls and rings, playing tug of war and fetch with keepers, shaking old shoes like a dog, sliding down slopes, and other behaviour that would readily be considered play if seen in a mammal (Fig. 7.3). Part of the reasons for discovering these examples is the increasing recognition, and use, of environmental enrichment as important for the well-being of reptiles as well as birds and mammals (e.g. Londoño et al. 2018).

However, the question arises as to why, even with the provisioning of toys and other objects, most reptiles do not engage in recognisable play, or play in as extended or complex manner as, for example, mammals. The reasons are several, but among the most important are the physiological constraints limiting sustained vigorous activity, the often lack of flexible and dexterous limbs used in much play (certainly pronounced in snakes!), and the lack of parental care that buffers young reptiles from the demands of foraging, defence, and protection from inclement weather when young. Together, these factors underscore that any playful activities that are not of immediate survival value may not occur unless the animal has surplus resources of time, energy, and behaviour (Burghardt 1988). This Surplus Resource Theory helps us understand that play emerges only when a constellation of life history, physiological, ecological, and behavioural factors are conducive for such behaviour. Even in mammals, for example, play is much more common in well cared for captive animals than their wild counterparts, who have more demands for their survival (Burghardt 1988). That being said, with the increased popularity of reptiles as companion animals and pets, many fascinating anecdotal examples of reptile play, including interspecific social play with other pets, such as cats and dogs, are proliferating on YouTube and other internet sites, contributed by the general public. Such video documentation is far more persuasive evidence than the verbal reports of play in many animals, including mammals and birds, in prior decades (e.g. Fagen 1981).

Also, it is interesting to note that whilst play in many mammals occurs primarily in juveniles, a period which may not be that conducive to play in many reptiles, it is in older and adult long-lived reptiles that play is most often reported. This, along with adult play in some, but not all, adult birds and mammals, supports the generality of the tenets of Surplus Resource Theory in relation to play, and the often less complex play found in reptiles (Smaldino et al. 2019).

7.8 Misconception 7: Reptiles Do Not Dream

Sleep and dreaming may seem rather peripheral to a discussion of behavioural and cognitive complexity, but some have claimed that the absence of electroencephalographic patterns typical of mammalian sleep may be a reflection of the limited connectivity and relative unsophistication of the reptilian brain (Rattenborg 2006; Rattenborg et al. 2009). Two distinct sleep states are recognised in birds and mammals: slow wave (SW) sleep, also known as non-REM sleep, and paradoxical or REM sleep. It is during this latter stage of sleep that most dreaming takes place in humans (Nir and Tononi 2010). Behaviourally, REM sleep is characterised by rapid eye movements and twitching of the limbs and tail in birds and mammals. Although eye and limb movements were described in sleeping reptiles a long time ago (e.g. Tauber et al. 1966; Ayala-Guerrero et al. 1988), the prevailing opinion until recently was that reptiles lack mammal (or bird)-like SW and REM sleep (e.g. Rial et al. 1993; Kavanau 1997). In fact, REM sleep was thought to be a trait exclusive of homeothermic vertebrates that evolved independently in terrestrial birds and mammals (Libourel and Herrel 2016). However, a recent study by Shein-Idelson et al. (2016) has convincingly shown that sleeping bearded dragon lizards (*Pogona vitticeps*) alternate between phases of SW and REM sleep (see also Libourel et al. 2018). This suggests that sleep states and their electrophysiological correlates evolved early in amniote evolution, in a common ancestor of reptiles, birds, and mammals. Whilst this is not conclusive evidence that reptiles dream, it certainly casts doubts over assertions that reptiles definitely cannot dream (e.g. Sjölander 1995).

Cabanac (Cabanac et al. 2009) not only concedes that REM sleep may be found in reptiles, but he also considers it a marker of consciousness. The possibility that the lives of animals, including reptiles, are attended by subjective experiences of the type we associate with human consciousness has generated, and indeed continues to generate, much controversy (Allen and Bekoff 2007; Dawkins 2017; Tye 2017). Firm, conclusive evidence for consciousness in other species is lacking, although an increasing number of researchers agree that subjective experiences, far from being a uniquely human attribute, probably evolved gradually over the last several billion years and are present in a broad range of species (Burghardt and Bekoff 2009). In as much as state-dependent changes in brain electrical activity are considered a necessary requirement for consciousness (Seth et al. 2005), the demonstration of REM sleep in lizards adds to other evidence concerning consciousness in reptiles (Butler and Cotterill 2006; Cabanac et al. 2009; Boly et al. 2013; Feinberg and Mallatt 2013). We take no firm position on the level and types of consciousness and subjective states that non-avian reptiles may experience as compared to other nonhuman animals, but we hold that they should not be viewed as possessing less sentience than birds and mammals in relation to captive welfare and treatment.

7.9 Further Directions on the Study of the Reptile Brain and Cognition

Much of the rhetoric against reptiles is based on gross misunderstandings concerning basic aspects of their biology. Here we have reviewed seven widespread misconceptions regarding reptiles, but, unfortunately, others also exist. Persistent claims regarding the small size and apparent simplicity of the reptilian brain have led to expectations that reptiles should have correspondingly unsophisticated behaviour and cognitive abilities. Such expectations have often coloured the interpretation of observations and experimental results and have effectively hampered progress in our understanding of reptilian behaviour and cognition. We should abandon our prejudices and overcome the inferiority complex that accompanies some work with reptiles: reptiles have a complex brain with a large pallium that performs functions similar to those attributed to mammalian cortex. Although the reptilian brain may not be as large or in certain respects as structurally complex as that of birds and mammals, these differences make the study of reptiles even more interesting. These differences also focus the challenge to explain how such relatively small and simple brains are capable of supporting the sophisticated behaviour and cognition we find in many reptiles.

Reptiles are notoriously difficult subjects to work with, particularly in a laboratory setting. As a result, the cognitive abilities of reptiles are rarely tested. When they are, it is often with a relatively small number of species that are less challenging to maintain in artificial conditions. Considering the great diversity of reptiles, studies of their cognition would benefit by moving away from laboratory settings to semi-natural and/or natural conditions for a slew of reasons. First and foremost, it has become clear that the evolution of cognitive traits has been shaped by the demands of the environment where species are found (Shettleworth 2010; Auersperg et al. 2011). Thus, studying reptiles, particularly free-ranging animals, under conditions where they can have access to the full repertoire of stimuli available in nature should provide the best opportunity to ascertain the full range of their cognitive abilities. Second, by evaluating cognitive abilities in the wild, we should be able not only to increase the numbers of individuals tested for a given experiment, but also the number of species evaluated (Steinberg and Leal 2018). When also taking into account the diverse ecology (e.g. habitat preference, social structure, foraging behaviour) found in reptiles, such an expansion of our understanding of reptile cognition would contribute to the development of a cohesive framework to explain the evolutionary forces at work on cognitive traits across vertebrates. Third, conducting experiments within the natural habitat of a species would force researchers to become familiar with the natural history of the organism in question, which should lead to experiments with more appropriate—i.e. ethologically informed—tests or tasks (Steinberg and Leal 2018). It should be noted that our best insights into the cognitive abilities of reptiles have resulted from experiments in which an understanding of the species' natural history played a major role in the experimental design. Finally, conducting experiments in the field can prevent the repeated use of the same individuals in multiple cognitive experiments. These

experimental challenges are certainly not unique to reptiles. However, in the case of reptiles, particularly for long-lived species, it is naive to assume that experience in previous experiments will not bias the performance on future experiments. Such a problem is likely to become amplified by the fact that, regardless of the species, only a few individuals typically acclimate to laboratory conditions, which already might bias our sampling of cognitive abilities.

The familiar view of the dumb, lumbering, instinct-driven reptile is slowly being replaced by a more realistic, evidence-based appraisal of reptilian behaviour and cognition. This evidence is painting a picture of reptiles as smarter and having a richer and more diverse behavioural repertoire than most people seem willing to recognise, and we have described only a small sample of this diversity here. Reptiles have an important role to play in comparative behaviour and cognition research, and their study can contribute to our understanding of the selective factors that promote independent origins of cognitive abilities across vertebrates (e.g. Whiting et al. 2018). We should also strive to eschew typological and model species thinking: there is enough variability among living reptiles as to render most broad generalisations about their behaviour or cognitive abilities useless. In the first edition of this volume, Gillingham (1995: 150) concluded that 'Reptile behavioural diversity approaches, parallels and often surpasses that seen within the birds and mammals'. As has been the case with birds, research in the field or using ethologically relevant laboratory tasks will likely reveal hitherto unsuspected cognitive abilities and behavioural sophistication in reptiles.

7.10 Animal Welfare Implications

From an animal welfare perspective, the findings reported here should raise our awareness that the needs and wants of reptiles are as deserving of attention as those of birds, mammals, and other animals. Welfare concerns are often biased in favour of species considered sentient, intelligent, and behaviourally complex, which usually includes birds, mammals, and some big-brained invertebrates, but not reptiles. It is time we recognise that the behavioural and cognitive divide between reptiles and other vertebrates that many take for granted is largely based on ignorance, prejudice, and misunderstanding and that we urgently need to re-evaluate the ways in which we maintain and study reptiles in captivity. Poor welfare is incompatible with good research and, increasingly, with public display of animals as conducted in zoos. The plight of reptiles held in captivity as pets or for research, conservation or educational purposes is often aggravated because the misconceptions reviewed here conflate to produce management practices that do not take into account the diversity and complexity of reptilian behaviour and cognition (e.g. Warwick 1990; Chiszar et al. 1995). Many chapters in this book echo this concern in their discussions of the biology and behaviour of the diverse groups labelled 'reptiles'.

Enrichment is a case in point. Studies of environmental and behavioural enrichment for reptiles are still scarce and most zoos and research facilities focus their enrichment and welfare efforts on mammals and birds, rather than reptiles

(de Azevedo et al. 2007; Melfi 2009; Maple and Perdue 2013). This taxonomic bias is grounded on the false belief that all that a reptile needs to be happy is food, a heat source, and a refuge. However, the limited evidence available shows that, when correctly implemented, enrichment improves reptile welfare and performance in cognitive tasks (Burghardt 2013; Londoño et al. 2018; Nagabaskaran et al. 2021). This area is one in which much fascinating and important progress is both possible and needed to enhance the lives of all captive animals.

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Psychological and Behavioural Principles and Problems

8

Clifford Warwick

Abstract

Psychological and behavioural attributes form the biological tools between a reptile and its environment, and are as important in life as any aspect of natural history. Behaviours such as limping, lethargy, and other signs are frequently used as indicators of physical injury and disease in reptiles. However, behavioural signs are less commonly interpreted to indicate or demonstrate psychological and ethological problems. For too long reptiles were, and sometimes still are, presumed relatively unsophisticated in their cognitive, psychological, and ethological development, and thus associated husbandry and welfare needs. Encouragingly, nowadays, major scientific interest exists in understanding reptilian mental and behavioural complexities related to their well-being in captivity. Psychological stress and behavioural frustration seem common even in the most well-considered artificial environments, and there is a range of abnormal behavioural states associated with captive reptiles. Assessments of captive reptiles should question constantly all behavioural activities, which in normal animals should not only be unmodified reflections of those in nature, but also should be seen in a holistic context. This chapter aims to provide readers with guidance and relevant background for observing and interpreting psychological and behavioural problems in all scenarios affecting captive reptiles.

Keywords

Psychological · Mental · Abnormal behaviour · Captivity stress · Adaptability · Non-adaptability · Maladaptation

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8.1 Introduction

Since this chapter was first published in 1995, much has changed, but much has not. At that time, reptile behaviour, psychology, and welfare had received little academic study, and only very sparse literature existed to support the concepts, ideas, and principles presented. Steadily, academic interest, research, and scientific literature in relevant areas—including reptiles' mental abilities, recognition of captivity stress, and explanation of biological responses—has burgeoned and continues to do so.

Psychological and behavioural attributes form the biological tools between a reptile and its environment—connecting the animal with the world around it—and as such are as important in life as any aspect of natural history (Warwick 1990a, b; Gillingham 1995; Chiszar et al. 1995; Mendyk and Augustine 2023; Greenberg 2023; Gillingham and Clark 2023; Font et al. 2023; Doody 2023; Burghardt and Layne-Colon 2023; Arena et al. 2023). Behaviours such as limping, lethargy, and other signs are frequently used as indicators of physical injury and disease in reptiles. However, behavioural signs are less commonly interpreted to indicate or demonstrate psychological and ethological problems.

For much of history, enquiries into reptilian ethology seem to have aspired to little more than the servicing of human-interest values, such as the encouragement of reproduction and pure ethological research. Until recently, reptile behaviour, insofar as connotations for animal welfare are concerned, attracted almost no studies. This lack of investigation, and often even discussion, was all the more disappointing in view of the abundant opportunities that existed for study as a consequence of the vast number of reptiles in both formal and informal collections worldwide (Warwick 1990b; Mendyk and Warwick 2023). That said, previously and now, studies into wild versus captive reptiles may be considered as holding potentially overlapping yet distinct characteristics and values because wild animal data are universally relevant and imperative to captivity, but captive animal data are relevant only to this specific situation (Moore and Jessop 2003; Martinez-Silvestre 2014; Warwick and Steedman 2023).

For too long reptiles were, and sometimes still are, presumed relatively unsophisticated in their cognitive, sentient, psychological, and ethological development, and thus associated husbandry and welfare needs (e.g. Rivas and Burghardt 2002; Burghardt 2013; Lambert et al. 2019; Learmonth 2020; Szabo et al. 2020; Font 2020; Font et al. 2023). Also, there have existed long-standing prejudices against conducting open-minded evaluations of psychological stress, behavioural 'frustration', and related issues using a welfare-centric approach (Warwick 1990b; Mendyk and Warwick 2023). These points arguably contributed to these prejudices becoming well-grooved unfortunate views, leading into self-perpetuating investigative lethargy. Psychological and behavioural assessments for reptiles are nowadays encountered more frequently, but are not universal or routinely comprehensive.

Embarrassingly present in many early husbandry concepts and philosophies resided the assumption that the lifestyle of an animal in nature is somehow not essential to life quality in general. Fortunately, this perception has been almost

extinguished amongst professional biologists in recent decades. Most encouragingly, nowadays, major scientific interest exists in understanding reptilian cognitive, psychological, and behavioural complexities related to their well-being in captivity. The primary aims of this chapter are to raise awareness of a once little and now emergently studied subject and to offer concepts, principles, and guidance on recognition of psychological and behavioural states relating to reptile welfare. Ultimately, the intention is to assist towards a better understanding of reptiles' needs and the problems presented by captivity. Much of this chapter offers conceptual perspectives and, hopefully, some constructive speculation to convey its messages. Because of this, a certain amount of leniency is requested of the reader regarding both the ideas being promoted and the terms used.

8.2 Living Wild and Noticing Captivity

Whilst reptiles are credited with sufficient awareness to detect major alteration of their environments, often they are wrongly perceived not to notice subtle environmental changes. However, it is becoming increasingly clear that reptiles are, in fact, highly aware of both gross and subtle factors within their surroundings. Recognition of conspecifics, predators, seismic, chemical, and other cues, and food types, for example, are all dependent on reptiles being aware of their world. This includes animals making detailed assessments of their environment and carefully monitoring other animal (and human) presence and intention (Burghardt 1991; Burger et al. 1991, 1992; Burger and Gochfield 1993; Holtzman et al. 1999; Burghardt 2005; Manrod et al. 2008; Leal and Powell 2012; Phillips et al. 2012; Wilkinson et al. 2010a, b; Wilkinson and Huber 2012; Burghardt 2013; Warwick et al. 2013; Bashaw et al. 2016; Font et al. 2023), as well as registering and remembering original and altered object arrangement and recognising changes taking place in their home environments—whether wild or captive.

However, the degree and complexity of environmental awareness in reptiles is heavily underscored by innate (i.e. unlearned) aspects of their biology. This is not, as will become clear later, meant to suggest that reptiles occupy either a primitive or 'instinctive' lifestyle, nor does this imply that reptiles lack adaptive flexibility to novel challenges, as pointed out by Font (2020). Rather, it is intended to imply that their innate physiological, psychological, and behavioural conditioning sets inherent 'expectations' more precisely for an existence in the natural world—or 'naturalness'. Indeed, even investigations into humans suggest that there is an innate biological need to experience natural—'wild'—conditions to aid welfare (Ross and Mason 2017). Given their highly innate biology and perceptive attributes, it is reasonable to presume that reptiles may at some fundamental biological level notice differences between the natural world and captivity and register that they are not where they should be. Frustrated drive states may contribute to psychological or behavioural maladaptation to captive environments. No matter how well-conceived, spacious, and diverse a captive environment may be, it is also probably the most profound divergence from a natural lifestyle within which an animal could be expected to survive.

8.3 Domestication and Non-Domestication

There are no domesticated species of reptile. Multi-generational captive-bred reptile ‘morphs’ may result from specific selection of superficial genetic lines, and some biologists and others speculate that certain genetic changes in captive-bred individuals of particular species suggest degrees of domestication. However, hypothetically, even if future elements of true domestication enter captive reptile biology, this is not the same as inactivating inherent traits integral to welfare needs. The concept of domestication is widely misinterpreted or confused to refer to animals that have been bred or raised in captivity over many generations (Serpell 2015; Décorcy 2019). Domestication of some animals, notably dogs and cats, arises for multifactorial reasons primarily related to their genetic make-up including pre-adaptive traits, affiliative attributes, and secondarily to their particular human associated histories; life in or near human habitations suits these species (Serpell 2015; Décorcy 2019). Adaptive plasticity to atypical environments varies widely amongst organisms. Whereas some species are highly adaptable to unusual environments and thus to captivity, others seem not to possess traits that lend themselves to such artificial conditions (Price 1984). Reptiles possess few traits essential to domestication, and such natural features as docility do not imply domestication or adaptability to captivity, as evidenced amongst cetaceans and other animals. Furthermore, species, group, generic, sexual, and individual adaptive potentials also may be highly variable. Exploration of the diversity and variation of these adaptive potentials is beyond the scope of this chapter. Many, if not most, captive animals, no matter how seemingly habituated to captivity, are stretched (or perhaps more accurately ‘shrunk’) versions of their natural selves and if ‘released’ from unnatural influences many revert to their fundamental ‘wildness’.

In any event, domestication, even where genuine, does not offer a panacea for addressing the ills associated with depriving an animal of its evolved life in the wild. Despite domestication, many dogs and cats for instance continue to suffer captivity-related psychological and behavioural problems, some of which are serious (Howell and Bennett 2017). Further, domestication has resulted in the production of these animals for human convenience and curiosity, which frequently leads to them becoming surplus to requirements and being denied fundamental value. The humane and ethical advantages even for successfully domesticated species are far from clear and certainly not universal. Close ethical scrutiny is required before modern society should embark on domestication of wild species.

8.4 Maladaptation to Captivity

In herpetology, the focus on this issue has largely centred on the so-called maladaptation syndrome, presented and discussed by Cowan (1980). Here, the emphasis is on non-specific degenerative conditions and diseases attributable to adaptational failures—coping mechanisms that could not cope. Maladaptation syndrome, therefore, refers largely to clinically identifiable deterioration and related pathological

consequences of reptiles failing to harmonise with their captive conditions. Maladaptation syndrome does not necessarily include behavioural signs of psychological and ethological compromise related to general maladaptation. Nevertheless, ethological aspects are probably also implicated in the classic maladaptation syndrome. Specific behavioural manifestations of maladaptation to captivity are outlined later.

Several abnormal and problematic behaviours in reptiles are similar to those known in other animals. However, certain behaviours, such as interaction with transparent boundaries (discussed in more detail later), highlight conditions that can be more particular to reptiles, and also indicate a general adaptational deficiency.

8.5 Stereotyped Behaviours and Maladaptive Stereotypies

In reptiles, naturally occurring stereotyped (grooved and repetitive) behaviour includes the ritualised courtship and combat routines of many species (Carpenter and Ferguson 1977; Gillingham and Clark 2023). Although such stereotypical behaviour is normal in nature, in captivity a raft of abnormal (captivity stress-related) stereotypies occur in animals in general, and there is good evidence to show that a number of birds and mammals develop stereotypies in which precise locomotive and other routines are observed (e.g. Garner 2005; Rose et al. 2017). The nature of captivity-associated stereotypies is complex, and little has been published on such phenomena in reptiles. Broadly, abnormal stereotypical behaviour derives from conflicts between natural biological needs and poor environments, and includes a range of states and severities from initial coping strategies involving minor behaviour, to major psycho-behavioural and even genetic damage, with consistent negative connotations (Garner 2005).

Several captivity-related repetitive ‘stereotypical’ behaviours, such as pacing along or interacting with transparent boundaries (ITB) and regular exploratory and locomotor activities, are frequently documented for reptiles, in particular in association with spatially over-restrictive and understimulating environments (e.g. Warwick 1990b, 1995; Warwick et al. 2013; Rose et al. 2014; Benn et al. 2019; Loughman 2020; Spain et al. 2020; Michaels et al. 2020; Stockley et al. 2020). At least some of these behaviours (e.g. hyperactivity and ITB) may be separate and distinct from classic abnormal repetitive behaviours or otherwise maladaptive stereotypies in that despite being repetitive and captivity stress associated they may reflect normal animals experiencing thwarted escape, roaming or other activities, and related drives. In some reptiles, ITB rapidly resolves when individuals are placed in improved (typically spacious and habitat-diverse) conditions. In other cases, stereotypical behaviour (ITB) has been noted as resistant to improvement through enrichment, which could indicate that some animals become ‘de-normalised’ similar to states recorded for birds and mammals (Michaels et al. 2020).

It may be that for those animals (e.g. amongst birds and mammals) where captivity stress-associated maladaptive stereotypies genuinely manifest, the phenomena occur in the context of a partial (and poorly successful) adaptational strategy amongst animals with a greater soft-wired psycho-behavioural scope—i.e. greater

adaptive mental plasticity. Whereas others (e.g. amongst reptiles), which have greater hard-wired psycho-behavioural profiles—i.e. inherited mental expectations, may be less malleable to coping with captivity.

8.6 Recognising and Interpreting Signs of Psychological and Ethological Well-being and Poor Welfare

This chapter focuses on reptile psychology and behaviour related to captivity, captivity stress, and associated problems. It is also intended to examine aspects that are not widely known, published, or discussed. Therefore, presentation and evaluation of classical signs of injury or disease, although commonly most apparent through behaviour, are not intended considerations here.

Knowledge of species-specific natural histories is essential in assessing many aspects of normality, abnormality, well-being, and poor welfare in reptiles. Also, both conspicuous and subtle behaviours and patterns need to be considered. In addition, a mindset should be adopted that is open to considering that causes of stress in reptiles may be beyond human perceptions, and include factors of sound, light, and chemistry (see Lillywhite 2023, Crowe-Riddell and Lillywhite 2023; Mancera and Phillips 2023). It may be worth emphasising that in the following sections ‘normality’ implies activities that are compatible with those found under natural conditions. Proper insight into normality may be distinctly different from, for example, popular perceptions of how a species or individual lives in nature. However, it has to be recognised that although increasing, relatively little data exist on reptilian behaviour in the wild to enable detailed comparisons.

8.7 Ontogenetic Processes and Innate (Unlearnt) Traits in Nature

It is well known that inherent physical and ethological traits that are either latent or of minimal influence during early life may later appear or exert an increasing influence. When viewed in parallel as physical/psychological/ethological phenomena, the role and strength of ontogenetic processes and delayed traits in general can be appreciated. Primarily physical considerations include thermoregulatory requirements, food selection, and sexual maturity (Hart 1983; Burghardt 1988; Burghardt and Layne-Colon 2023; Arena and Warwick 2023). Primarily ethological considerations include courtship and combat behaviours, altered social structures, migratory tendencies, and habitat selection (Hart 1983; Burghardt 1988; Doody 2023). In both these categories, largely predetermined development of physical, psychological, and behavioural traits can be highly subtle and critical, such as temperature-dependent sex determination (e.g. Bull 1983, 1987), and recognition of specific prey cues (Burghardt 1988; Chiszar et al. 1995). Development can undoubtedly also be modified through experience (Wilkinson et al. 2010a, b; Ballen et al. 2014; Burghardt and Layne-Colon 2023). Relatedly, physical (physiological

and morphological) and ethological factors are often clearly conjoined—for example, in thermoregulation, where a remarkable degree of homeostatic precision may occur.

8.7.1 Anticipating Ontogenetic Processes and Traits in the Captive Environment

Ontogenetic processes and traits have several implications for captive reptile husbandry and welfare that are seldom properly acknowledged. Many of the more conscientious reptile keepers develop captive conditions that are at least intended to go some way towards accommodating perceived key ethological needs. Commonly, though, these protocols seek to make some provision for natural history profiles based on, at best, an informed caricature of the species' behaviour. Some endeavours try to cater for behaviours that are apparent or anticipated during a particular period in the animal's life history. Consequently, many management protocols effectively aim to address set behaviours in a rigid regime rather than being flexible with inherent changes. It is important to recognise that psychological and behavioural development and related problems potentially arise at different stages in life. In wild crocodylians, for example, territoriality arises during several years post-birth; in captivity this can lead to stress and fighting, as well as management difficulties. Consequently, what seems fine at one time may not be so in the future. Therefore, it is wise to review constantly the potential for ontogenetic change.

8.8 Psychological, Ethological, Physiological, and Physical Interrelationships

Psychological, ethological, physiological, and physical aspects are so fundamentally interrelated that it is impossible to consider any area in true isolation. Indeed, stimuli and an animal's responses can flow in different, sometimes opposite, directions. Stimulation arising from, for example, a perceived predatory threat can produce physiological responses, and physiological stimulation, for example, due to seasonal hormonal alteration, can cause behavioural responses. Thus, it is important when considering matters concerning stress to maintain constantly the perspective that the individual organism is a complex biological whole and to view all matters with a holistic approach.

8.9 Stress and Stressors

It is beyond this chapter's remit to discuss at length the already considerable and expanding definitions of the term 'stress'. In this chapter, stress is used to refer to a discomforting or traumatic psychological, emotional, or physiological state or response in reptiles that is the result of perceived, potential, or actual harmful stimuli,

and threats to homeostasis. This is not intended as yet another offering to the current collection of descriptions, but to select familiar language that hopefully conveys the salient message. Stressors are essentially those stimuli that result in stress responses.

Despite having been studied for many decades, stress physiology—and our scientific understanding of it—remains in its infancy. Several important reviews of stress physiology in reptiles are available (e.g. Guillette Jr et al. 1995; Moore and Jessop 2003; Martinez-Silvestre 2014; Gangloff and Greenberg 2023). However, applying stress physiology to everyday scenarios that may impact on the welfare of reptiles has yet to be meaningfully outlined.

In comparison, behaviour as a natural window into the state of animal well-being is something we use every day, and as a paradigm this has stayed solid for as long as organisms have existed. Behaviour reflects the multifactorial stimuli perceived by an animal, as well as the gross and subtle biological responses of an organism that culminate in a particular state. As such, behaviour can provide highly revealing insights into an individual's holistic condition. Recognising behavioural signs and their possible meaning is, therefore, highly important in assessing both positive and negative states. Even if many do not yet utilise behaviour to assess stress and welfare, the behaviours themselves are there for all to see.

There is a long-running debate regarding the validity of physiological versus behavioural indicators and measurements of stress in animals (Barnett and Hemsworth 1990; Rushen 1991; Warwick et al. 2013, Martinez-Silvestre 2014; Warwick et al. 2019; Gangloff and Greenberg 2023). However, in several respects behavioural signs are superior indicators of normal and abnormal states, not least because they are typically the first indicators of an animal's welfare, and because behavioural observation is the most widely accessible approach. In many cases, the use of clinical and physiological welfare assessment can and will be concomitantly applied to behavioural assessments. Nevertheless, for reasons of its relevance to the subject matter of this chapter, as well as this author's own preference, behaviour is favoured over physiology as an indicator and measure of reptile well-being.

8.9.1 Behavioural Indicators of Stress

It is commonly presumed that reptiles show few behavioural signs of stress. However, signs of stress in reptiles are not only often similar to those in other animals, but also frequently abundant.

8.9.1.1 Signs of Positive and Negative Psychological and Behavioural States

It is arguable that, at least in some instances, the evaluation of positive behavioural signs in captive reptiles might be best achieved by looking for signs compatible with those exhibited by conspecifics in nature. Negative behavioural signs similarly might

be gauged by considering behaviour under natural conditions, and in adverse situations. Context is an important consideration here. For example, animal fighting in the wild can be normal. However, fighting amongst captive animals can be highly negative, not least because unlike in natural conditions, where victimised individuals have almost limitless space allowing opportunities for withdrawal or escape, captive animals are confined and conflicts less avoidable (Gillingham 1995; Martinez-Silvestre 2014).

Signs in the following lists (Tables 8.1 and 8.2) have been selected as key examples that, whilst also occurring in a variety of contexts, can be used when assessing possible stress in reptiles associated with human contact, for example, handling and inspection as well as during general passive observation. It is important to appreciate that these points offer only a broad guide relating to the more usual indicators of primarily psychological and to some extent physical states. Whilst behaviour is integral to the next two subsections, ethological considerations are focused on more specifically later. Unsurprisingly, behavioural signs of captivity stress appear largely similar (and related) to natural cautionary, anti-predator, or fear responses or escape activities, whereas signs of psychological quiescence and comfort appear largely similar (and related) to natural environmental investigation, food search, and rest activities. Acute and chronic stress has long been known to have potentially lasting effects on health (see Gangloff and Greenberg 2023). However, recent research into fear in particular suggests that some predator-prey interactions may have life-changing, lifelong, effects on individuals, including reduced long-term food intake and fecundity (Zanette and Clinchy 2017). Given that captive reptiles may be housed in the presence of perceived predators (which may include humans), then the potential long-term consequences of such situations should not be taken lightly.

Handling Although it can be important to handle and inspect reptiles, for example, in relation to some health and welfare assessments, certain conditioning protocols, or relocation, handling per se may often be a negative practice. Handling by humans is widely used as a specific stressor for many animals, including reptiles in ecological and physiological studies, and results in stress (e.g. Bailey et al. 2009; Agha et al. 2015; Acaralp-Rehnberg 2020). Some authors have also proposed that from the individual animal's perspective, handling may be perceived as being subdued by a predator. Borgmans et al. (2018) concluded that capture, transport, and temporary housing conditions within the pet store environment caused considerable stress for anole lizards (*Anolis carolinensis*). Stockley et al. (2020) found that handling of bearded dragons (*Pogona* sp.), normally regarded as a highly docile and 'handleable' species, resulted in increased tongue-flick rate, suggesting stress. Accordingly, for many, if not most or even all, reptiles, including those that for most observers appear quiescent, handling probably involves causing stress.

Table 8.1 Behavioural signs of stress or captivity stress (in alphabetical order). (Derived from Warwick 1990a, 1995; Warwick et al. 2013, 2019; Martinez-Silvestre 2014; Bashaw et al. 2016; Benn et al. 2019)

Behaviours	Signs	Aetiologies
Anorexia	Loss of appetite, emaciation, weakness, inactivity	Hypothermia; disease; injury; pain, co-occupant harassment, too low temperature; infection/organic dysfunction; co-occupant attack; transport trauma
Atypical locations	Reptile occupies an atypical location for an unusual amount of time or other unusual contexts (e.g. an arboreal chamaeleon on cage floor or not spending as much time as expected in normal locations)	Often related to disease, injury, discomfort, co-occupant aggression, hyperthermia, hypothermia
Cloacal evacuations when handled	Urination, defecation, excretion of malodorous substance from cloaca	Often related to anti-predator or fear responses
Clutching	Snake or lizard tightly grasps human or object	Often related to anti-predator or fear responses or ambient light/photo stress behaviour. Common in overly restrictive and exposed (including light for nocturnal species), deficient, and inappropriate environments
Co-occupant aggression	Aggressive or defensive displays, biting, chasing cage mates	Often related to courtship routines, inability to avoid cage mates when required, overly restrictive, and exposed deficient and inappropriate environments. Hunger
Death-feigning	Animal (commonly snake) appears unconscious, limp, upside down	Often related to anti-predator or fear responses
Escape attempts	Animal observed clawing, climbing, or snout-rubbing at boundaries, corners, and other points	Related to entrapment and exploratory activities. Often associated with ITB. Overcrowding. Self-compounding and frequently injurious. Overly restrictive, deficient, and inappropriate environments
Flattened body posture	Flattening of body against a surface often combined with hyperalertness	Often related to anti-predator or fear responses. Common in overly restrictive and exposed, deficient, and inappropriate environments

(continued)

Table 8.1 (continued)

Behaviours	Signs	Aetiologies
Freezing in non-relaxed posture	Eye contact with or general presence of observer results in freezing tonic posture	Often related to anti-predator or fear responses or ambient light/photo stress behaviour. Common in overly restrictive, deficient, and inappropriate environments
Grating of jaw	Turtles and tortoises tightly rasp together ramphotheca causing an abrasive grating sound	Often related to anti-predator or fear responses or light stress behaviour. Common in overly restrictive and exposed (including ambient light/photo for nocturnal species), deficient, and inappropriate environments. Pain
Head-hiding	Deliberate seclusion of head including under objects or substrate	Often related to anti-predator or fear responses or ambient light/photo stress behaviour. Common in overly restrictive and exposed (including excessive ambient light for nocturnal species), deficient, and inappropriate environments
Hesitant mobility	Animal uncharacteristically moves in 'fits and starts'	Often related to anti-predator or fear responses. Common in overly restrictive, inappropriate
Hissing	Hissing sound, accompanied by deliberate repeated inflation and deflation of the body	Often related to anti-predator or fear responses, defence and escape behaviour. Common in overly restrictive and exposed (including excessive ambient light for nocturnal species), deficient, and inappropriate environments
Human-directed aggression	Mock/real strikes using jaws or tail	Often related to anti-predator or fear responses, defence and escape behaviour. Common in overly restrictive,= and exposed (including excessive ambient light for nocturnal species), deficient, and inappropriate environments
Hyperactivity	Abnormal high-level physical activity, surplus or redundant activity	Often associated with ITB. Overcrowding. Self-compounding and frequently injurious. Overly restrictive, deficient, and inappropriate environments
Hyperalertness	Abnormal high level of alertness 'nervousness' to environmental stimuli	Often related to anti-predator or fear responses, defence and escape behaviour. Common in overly restrictive and exposed, deficient, and inappropriate environments

(continued)

Table 8.1 (continued)

Behaviours	Signs	Aetiologies
Hyperbasking	Atypically long (for species, individual, or clusters of animals) basking periods	Inappropriate thermal gradient/ low ambient temperature, or overly minimal basking source resulting in inability for animal to heat its entire body
Hypoactivity	Reduced activity relative to normal	Hypothermia; disease; injury; pain, co-occupant harassment, too low temperature; infection/ organic dysfunction; falling; dropping; co-occupant attack; transport trauma
Inflation of the body	Deliberate (often repeated) inflation and deflation of the body. May or may not be associated with 'hissing' sound	Often related to anti-predator or fear responses. Common in overly restrictive and exposed (including light for nocturnal species), deficient, and inappropriate environments
Interaction with transparent boundaries (ITB)	Highly persistent attempts to push against, crawl up, dig under, or round the transparent barriers of their enclosure	Related to exploratory and escape activity. Self-compounding and frequently injurious. Inherent psychological organisation and adaptational constraints result in failure to recognise invisible barriers
Loop pushing	Snake uses 'arch' of body to resist/deflect physical contact from cage mate or human	Often related to anti-predator or fear responses or ambient light/ photo stress behaviour. Common in overly restrictive and exposed (including light for nocturnal species), deficient, and inappropriate environments
Open-mouth breathing	Sporadic, usually slow, open-mouth respiration or gasping	Hyperthermia; infection/organic dysfunction/disease; major head/ neck injury; co-occupant attack; transport trauma
Panting	Rapid open-mouth breathing, sometimes accompanied by extension of dewlap (skin flap under lower jaw in some lizards). Also, cloacal evacuations may occur	Hyperthermia
Pigmentation change	Typically some lizards (especially chameleons) change colour—may be rapid or slow	Often related to anti-predator or fear responses, pain, hyperthermia; hypothermia; overly restrictive, deficient, and inappropriate environments; injury, disease

(continued)

Table 8.1 (continued)

Behaviours	Signs	Aetiologies
Projection of penis or hemi-pene	Projection of penis or hemi-pene associated with human presence or contact	Often related to anti-predator or fear responses
Prolonged retraction of head or limbs; reluctance to extend neck	Tortoises and turtles retracting head, limbs, or tail for periods of minutes or longer	Often related to anti-predator or fear responses, pain, disease
Pseudovocalisation	Crocodylians, some lizards, and turtles producing squeaks or whines (aside from sexual or other social communication context)	Often related to anti-predator or fear responses, physical irritations, pain, injury, disease
Rapid body movement	Abnormal 'jerky' locomotor or jumping actions	Often related to anti-predator or fear responses, common in overly restrictive and exposed, deficient, and inappropriate environments
Squirting blood from eye	Some lizards eject blood from eye associated with human presence or contact	Often related to anti-predator or fear responses
Tail autotomy	Voluntary autotomy of tail (some lizards) associated with human presence or contact	Often related to anti-predator or fear responses
Venom spitting	Venomous snakes ejecting venom associated with human presence or contact	Often related to anti-predator or fear responses
Voluntary regurgitation of food	Regurgitation of food associated with human presence or contact	Often related to anti-predator or fear responses
Wall-climbing	Common attempts to push against, crawl up, dig under, or round the general barriers of their enclosure	Related to exploratory and escape activity
Wincing	Hypersensitivity to minor physical stimuli causing retraction of head, limbs, or tail	Often related to anti-predator or fear responses. Common in overly restrictive, inappropriate environments. Pain, disease

Table 8.2 Behavioural signs of quiescence and ‘comfort’ (Derived from Warwick 1990a, 1995; Warwick et al. 2013, 2019; Martinez-Silvestre 2014; Bashaw et al. 2016; Benn et al. 2019)

Behaviours	Signs	Histories
Normal/relaxed alertness	Relaxed interest/awareness in proximate or novel objects, relaxed visual explorations	Normal environmental investigation
Calmly smelling or tasting objects or air	Calm chemical sampling of surroundings	Normal environmental investigation; food searches
Subtle changes in body posture and orientation	‘Stretching out’ of limbs whilst basking; rectilinear postures in snakes; relaxed adoption of body angles using furnishings	Normal thermoregulatory behaviour and rest
Unhurried body movements and locomotion	Relaxed environmental exploration; rectilinear movement in snakes	Normal environmental investigation; food searches
Moderate to relaxed grasp on handler or object	Snake or lizard maintains relaxed (but possibly firm) grasps human or object	Normal relaxed behaviour and rest
Relaxed drinking	Unhurried drinking	Normal maintenance behaviour
Relaxed feeding	Unremarkable feeding habits	Normal maintenance behaviour
Relaxed breathing	Unremarkable breathing habits	Normal relaxed behaviour
Physical quiescence	Unremarkable relaxed activity—e.g. free from apprehension and fear activities	Normal relaxed behaviour
Sleep	Naturally contextualised sleep pattern	Normal maintenance behaviour
Social behaviour	Positive interactions with co-occupants	Normal behaviour
Absence of signs of stress or captivity stress		

8.10 Consciousness and Self-Awareness

Consciousness and self-awareness in general are issues of considerable scholarly debate. Loosely speaking, at one end of the scale of reason, consciousness and self-awareness are taken by many philosophers and biologists to infer a biomechanistic ‘neurological’ capability to sense or conceive the environment (e.g. Descartes 1644; Searle 2005). At the other end of the scale are ideas that consciousness is a state entangled with, yet independent of, brain anatomy and physiology, although potentially actioned through the medium of neurological structures (Penrose 1989; Hameroff 1994; Hameroff and Penrose 2014; Penrose 2014). Traditional biology and common thinking are somewhat adherent to the first of these perspectives, whereas quantum mechanics and emergent neuroscience are inclined, if not adherent, to the second of these perspectives (Penrose 1989; Hameroff 1994; Koch and Claus 2006; Hameroff and Penrose 2014; Penrose 2014; Jedlicka 2017).

In many cases, sensory perception, including amongst reptiles, can be superior to humans (Chiszar et al. 1995; Font et al. 2023; Crowe-Riddell and Lillywhite 2023; Mancera and Phillips 2023). Self-awareness may be the most obvious branch of consciousness to independently observe. For example, in deer, male competitive behaviours include walking side by side to ‘size up’ the opposition and ascertain whether an all-out fight is warranted or whether such an encounter is likely to go the way of the bigger animal. Also, in snakes, a small python does not attempt to eat something impossibly large that it may tackle in several years’ time. Intelligence is another topic of considerable debate and, where reptiles are concerned, this issue has for centuries been majorly under-appreciated, with historical perceptions undervaluing the reptilian brain and intelligence (see Font et al. 2023). There is no objective scientific evidence to suggest that reptiles or any other animals are less conscious than humans. Given the above, perhaps unsurprisingly, this chapter will assign full benefit of any doubt to reptile consciousness and self-awareness, and assume these to be no less significant for these animals than they are for others.

8.10.1 Awareness of Self-Preservation and Well-Being

Psychological and behavioural acts or actions performed by animals are commonly survival (self-preservation) related. In nature, the location that an animal chooses (assuming choice is available) to occupy during its rest phase is obviously essential to the individual’s chances of survival. Risks to survival in such cases are presented mainly by predatory threats and climate extremes. In captivity, some large outdoor facilities may offer close comparisons with these factors. Indeed, it may be only in such conditions of spaciousness and environmental diversity that reasonable evaluation of self-preservation outlook becomes possible, and this section relates mainly to such conditions. Consequently, the location that an animal selects in a captive environment, for example, for its main sleep period, is suggested here as a potential indicator of its state. This consideration can be summarised by saying that sleeping in exposed places is potentially negative, whereas sleeping in sheltered places is potentially positive. However, in exemplary captive situations it is conceivable that reptiles may learn that they can sleep anywhere without predatory or climatic risk, in which case sleeping in exposed places would not necessarily be potentially negative.

The concept, therefore, involves animals making ‘sensible’ decisions on matters of survival and safety (such as location selection), and that better decision-making may reflect better holistic state. It may be that a greater number of subtle behaviours combined with, for example, good site selection for rest are the more positive states for animals, and fewer subtle behaviours combined with poor site selection for rest are the less positive states.

8.11 Specific Psychological and Ethological Problems

Reptiles seem to have two particular fundamental threads running through their responses to inadequate environments: first, exploratory, search, and escape behaviours; and second, biological shut-down behaviours to withdraw from their surroundings. Exploratory, search, and escape (and also hyperactive) behaviour seems most often to be associated with species that are natural wanderers or transients, such as large lizards (e.g. *Varanus* spp.) and box turtles (e.g. *Terrapene* spp.), whereas biological shut-down behaviour seems most often to be associated with species that either are frequently more sedentary in their habits or naturally hibernate or aestivate, such as rattlesnakes (e.g. *Crotalus* spp.) and Mediterranean tortoises (e.g. *Testudo* spp.). Whilst these strategies are natural enough, maladaptation to unnatural environments and general captivity-related complexities usually render such responses incomplete or ineffective. Broadly speaking, to prevent, reduce, or remedy commonly encountered abnormal and problematic behaviours, two requirements are essential: space and appropriately diverse naturalistic (where possible natural) furnishings; it should be noted that the boundaries of enclosures can also be effectively furnishings. Managers must assess both the interactions between reptiles, co-occupants, and their environments and the organisation of behaviours in the individual animal (Waters et al. 2017).

It is worth considering that even an apparent complete lack of signs indicating psychological or behavioural problems does not confirm their absence. Frequently, normal behaviour in captive reptiles lasts only as long as an animal basks, feeds, or interacts socially. Therefore, when such a major activity ceases (whether voluntarily or because, for example, the heat source is turned off) reptiles may again commence displaying captivity stress-related signs, such as exploratory and escape behaviour. Also, an animal's focus on basking or other fundamental activities might arise from psychological and behavioural frustration related to other under- or overstimulation. One could add that relatively straightforward problems of the thermal environment can have similar results, where low ambient temperatures or heat sources that do not radiate across an animal's entire body cause prolonged basking—or 'hyperbasking' (Arena and Warwick 2023). Consequently, whilst behaviours may be normal, their context may be abnormal and mask other underlying stimulatory deficiencies. Evaluating a holistic picture of reptile ethology is therefore important in lending context to even apparently normal behaviours. Selected below are key examples of psychological and behavioural problems and their possible aetiologies. However, these examples do not present all potentially problematic considerations. The following signs and their histories are derived primarily from Warwick (1990a) and Warwick et al. (2013), and some are discussed in more detail in those references.

8.11.1 Exploratory, Search, and Escape Activities

Reptiles are commonly seen engaged in exploration of their environments, interacting with boundaries and repeatedly trying to escape. The term 'escape'

requires brief explanation. Here, the word is used deliberately to infer that activities such as climbing corners and attempting to push through air vents, as well as those that involve regular interaction with any boundary, are probably related to endeavours to leave the current environment, especially if those features have already been thoroughly explored many times. The major clinical signs include friction lesions on the rostrum, damaged claws, and abrasions to (usually) forelimbs. Exploratory, search, and escape activities are subtly different from ‘hyperactivity’ because there may be no apparent excessive locomotor and other physical activity.

Frequently, this situation seems to be associated with searches for more appropriate environments and food sources, because when these are available the activities diminish or cease. Whilst boundaries in nature are normal, such as a steep rock face or a fallen tree, they are usually avoidable or passable. In captivity, the confining walls of an enclosure may in some respects approximate a natural boundary, but enclosure walls are usually unsurpassable and unavoidable. In nature, the closest comparison to a reptile cage might be when an animal falls into a deep crevice and cannot escape. However, the enclosure situation does not ‘holistically’ equate even with the crevice in nature. Consequently, the association between an enclosure and its occupants could be viewed as a device with animals trapped inside.

Exploratory and escape behaviour may not always be apparent, especially where observers and animal activity habits differ such as in nocturnal species. However, investigation of substrate and other environmental feature conditions for evidence of disturbance patterns (‘occupancy evaluation’) such as tracks or grooves may indicate exploratory behaviour (see Arena et al. 2023). Figure 8.1 provides examples of exploratory behaviour and occupancy evaluation evidence.



Fig. 8.1 Exploratory, search, and escape behaviour in an iguana (*Iguana* sp. Credit: [iStock.com/UPiJ](#)) and in a bearded dragon (*Pogona* sp. Credit: Amelia Benn)

8.11.2 Interaction with Transparent Boundaries

Reptiles are often seen trying to crawl up or push against the transparent boundaries of their enclosures. The major clinical sign involves friction lesions on the rostrum. In some cases, this behaviour can occupy almost 100% of a reptile's activity period. This is in contrast to many mammals and birds, which quickly learn that a transparent boundary is impenetrable and soon refrain from attempts to get through. Indeed, anecdotal instances seem to confirm that many endotherms respond to transparent partitions in much the same way as humans respond to them.

Interaction with transparent boundaries (ITB) is one of the most frequently observed maladaptive behaviours in captivity and seems to relate largely to exploratory and escape activities. Inherent psychological organisation and adaptational constraints in reptiles, together with the fact that transparent boundaries simply have no corresponding natural phenomena, appear to result in the non-recognition of transparent barriers. Indeed, innate influences probably signal to the effect that anything invisible simply is not there. The problem is often self-compounding because associated psychological stress can result in increased escape attempts and hyperactivity, which incur further interaction, and so on.

In this author's experience, alteration of existing enclosures (for instance, by masking previously transparent walls) has varied results and often limited or no positive conclusion, because in many cases animals appear to remember where perceived escape routes (transparent boundaries) were previously located. ITB can be prevented, reduced, or remedied by providing alternative, spacious, well-furnished environments that do not contain invisible barriers. Figure 8.2 provides an example of ITB.

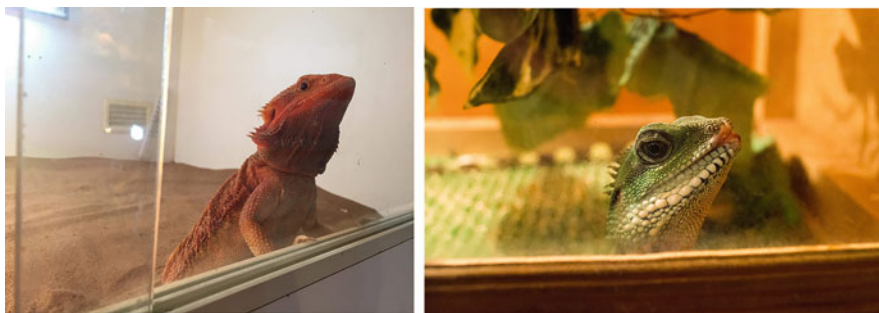


Fig. 8.2 Interaction with transparent boundaries in a bearded dragon (*Pogona* sp. Credit: Amelia Benn) and water dragon (*Physignathus* sp. Credit: [iStock.com/Maksim Lobanov](https://www.iStock.com/MaksimLobanov))

8.11.3 Hyperactivity

A distinction should be recognised between normal high levels of activity—for example, prolonged activity in relation to nest-site searches—and hyperactivity in the sense of an abnormal surplus or redundancy of activity. Although excessively high temperatures, persecution from co-occupants, and other environmental and physical factors can lead to hyperactive behaviour, these causes usually result in escape attempts rather than merely high levels of activity. Hyperactivity in this context is intended to infer a state in which an animal may engage in greater than normal exploration of boundaries and other furnishings’ or even excess locomotor activity with no apparent motive. As such the state is characterised by general excess locomotion (including swimming), interaction with boundaries (especially where transparent), and prolonged burrowing efforts, all of which may be accompanied by regular attempts at escape. Various clinical signs are commonly found, such as friction lesions on the rostrum and ventral surfaces in particular.

Hyperactive behaviour appears largely or totally associated with enclosures where poor (usually small) environments and related stress are involved. The problem, and compounding factors such as the usual increased interaction with transparent boundaries and frustrated escape attempts, results in a progressive and clearly negative condition. Spacious, well-furnished environments may prevent, reduce, or eliminate hyperactivity. Figure 8.3 provides an example of hyperactivity.



Fig. 8.3 Hyperactivity in a royal (‘ball’) python (*Python* sp. Credit: Catrina Steedman)

8.11.4 Hypoactivity

Whilst undoubtedly sedentarism can be related to, for example, normal digestion, ecdysis, and disease, as well as be forced by low temperatures, it can also relate to maladaptive states. Problematic sedentarism or hypoactivity in this context is characterised by long periods of highly reduced or no locomotor activity, and often little sensory activity such as tongue-flicking, in captive reptiles. Clinical signs can be present and include dermal lesions related to prolonged contact with substrata, anorexia, and emaciation. The condition is not necessarily season-related or associated with the thermal environment, because it occurs even at random intervals and in carefully regulated, warm environments. Adequate provision of food and water may also be present. As such it seems free from key initiating influences of hibernation, brumation, or aestivation.

Reptiles developing a hypoactive state sometimes initially display tendencies similar to animals seeking sites for hibernation, brumation, or aestivation and ‘go to ground’. This is often dependent on particular environmental features being available; for example, deep substrata and areas for seclusion that reptiles can explore before adopting a ‘dormant’ phase. However, in relatively clinical enclosures, where provisions might not allow such site searches, animals may still become sedate without obvious preliminary signs. Similarly, tropical zone species may not show obvious signs of impending hypoactivity. Recently, Szabo et al. (2020) suggested that in some situations reptiles may become habituated not to respond with overt stress-associated behaviours, again potentially indicating that apparent sedentarism may not infer quiescence.

Hypoactivity has been presented as a biological shut-down strategy (derived from hibernative, brumative, and aestivative states) to avoid the rigours of a hostile environment (Warwick 1990a, b). As mentioned previously, although the phenomenon seems unrelated to hypothermia, animals may nevertheless seek out cooler temperatures. Concerns regarding this state are thus justified by the point that the animal’s attempted withdrawal from its surroundings is abnormal and incomplete, as well as the loss of physical condition through dehydration and malnutrition. Arguably, some states of hypoactivity may be linked with psychological depression, which has been identified in, for example, lizards (*Varanus* sp.) (Stanner 1999). Large, well-furnished enclosures, varied diet that also must occasionally be ‘searched out’ by the animals, and ‘prey mimicking’ to encourage predatory behaviour where appropriate will often prevent hypoactivity, and are moderately effective in reducing and eliminating it. Figure 8.4 provides an example of hypoactivity.



Fig. 8.4 Hypoactivity in a king snake (*Lampropeltis* sp. Credit: [iStock.com/JoanBudai](https://www.iStock.com/JoanBudai))

8.11.5 Restricted by Provision

Many captive environments include a range of features that are either inappropriate or inadequate for the species or individuals within. Atypical thermal gradients, basking sites, substrates, water vessels, climbing furnishings, and seclusion options are amongst numerous deficiencies commonly encountered. Such issues may result in occupants disfavours certain of these atypical and inadequate furnishings and instead favouring only those provisions with which they have stronger biological and psycho-behavioural affinity. A frequently observed example is where lizards express 'hyperbasking' behaviour because the ambient thermal environment is lower than acceptable for the species, and individuals thus occupy a small site where higher temperatures can be located. Essentially, regardless of environmental scale and complexity, animals' occupation of that environment may effectively be restricted to a small area. Figure 8.5 provides an example of lizards restricted by provision.



Fig. 8.5 Hyperbasking in bearded dragons (*Pogona* sp. Credit: Clifford Warwick)

8.11.6 Social Stress

Although reptiles are reputed to be asocial, many are highly social and gregarious (Burghardt 1977; Gillingham and Clark 2023; Doody 2023). In fact, sociality in reptiles is highly varied. There are, for example, reptiles that live in social groups and exhibit considerable post-natal parental care, others that form social groups with dominance hierarchies, and still others that lead primarily solitary lives, and a number that seem to acknowledge each other's presence on an almost incidental basis. All these categories probably involve significant social variability and some degree of overlap.

In captivity, most reptiles are not part of social groupings, partly because the particular species may not be gregarious, and partly because captive conditions may

contraindicate such arrangements. That said, some reptiles that in nature display territoriality, but not social dominance hierarchies, are reported to develop dominant-subordinate associations when placed in the captive environment (Greenberg et al. 1984; Brattstrom 1978; see also Stamps 1977; Zucker 1994; Gillingham and Clark 2023; Doody 2023). Various aspects relating to non-gregarious reptiles are presented in other sections of this chapter. However, gregarious reptiles that form social dominance hierarchies in captivity (whether or not the same occurs in nature) warrant some mention of their own. Captive reptile social dominance hierarchies have attracted a great deal of interest and research for some years. Much of this work relates to social structures of lizards and the physiological condition of individuals relative to their social status (Greenberg et al. 1984; Greenberg and Crews 1990; Gangloff and Greenberg 2023; Doody 2023). These studies are carefully controlled; keepers are usually well aware of potentially adverse occurrences, and can act accordingly to prevent them.

However, in many other situations, normally territorial and gregarious species are housed together in unusual numbers and size, age, and sex classes. Poorly conceived and designed environments, such as territories that are too small, perching site inadequacies, lack of retreat sites, or visual barriers to prevent interactions, as well as lack of separate access to heat and food sources, also may impose involuntary hypothermia and present problematic stressors. In such colonies and surroundings, reptiles can engage in excessive combat whilst trying to establish territories, which in turn can lead to depletion of energy reserves and an associated compounding deficit in time spent feeding. Relatedly, close proximity of victors and losers, post-challenge, may cause excessive stress in the defeated animals because in nature, and possibly in larger captive facilities, these individuals would normally be able to avoid the dominant animal. Consequently, great care must be taken to ensure that where several gregarious animals are concerned, social groups are either compatible in terms of the size, age, and sex of their members or the facilities they are housed in are appropriately spacious and diverse to prevent adverse interactions.

8.11.7 Aggression

Aggression between reptiles may be normal intraspecies activity—for example, in the establishment of territories—or season-related, where some courtship and combat routines are performed. Aggression directed at humans, and sometimes towards cohabitants that are not part of a specific social system, can have diverse histories including the individual's experience of noxious stimuli associated with handling, displacement of energy due to frustration of other behaviours, breeding season-related aggression, natural timidity, and defensive responses, or because of a painful disease or injury. In terms of captivity-related stressors and aggression, environments that are restrictive and poorly organised and furnished are often implicated. Relatedly, 'dead food' diets that are offered to predators (e.g. some of the more aggressive snake species), which typically eat live food are commonly associated with aggressive tendencies. In this last example, snakes may 'miss' the biologically anticipated struggle with prey. Other indications suggest benefits to reptiles from live food as an enrichment feature (Almli and Burghardt 2006). These positions obviously do not include the welfare interests of the live food, or the occasional prey-predator injury (Cooper and

Williams 2014; Warwick 2014). As with other issues, spacious, naturalistic environments offer holistic methods for reducing or eliminating numerous cases of hyperaggression. As recently emphasised (by Martinez-Silvestre 2014; Arena and Warwick 2023; Mendyk and Augustine 2023; Warwick and Steedman 2023), the wider spaces of nature allow individuals to better avoid or escape each other and conflict, unlike captivity. Where timidity is concerned, gradual habituation to disturbing stimuli can be attempted. It is worth considering, though, that desensitising aggressive animals, whilst possibly valuable to both the reptile and the keeper, may have other implications for maintaining purity of animal behaviour (Gillingham 1995). Figure 8.6 provides examples of aggression and injury.



Fig. 8.6 Aggression in sliders (*Trachemys* sp. Credit: [iStock.com/Alphotographic](https://www.iStock.com/Alphotographic)) and aggression and associated injuries in bearded dragons (*Pogona* sp. Credit: PETA)

8.11.8 Disposition-Related Voluntary Hypothermia

Another issue related to hypoactivity concerns the idea of a state of ‘disposition-related environmental temperature preference’, perhaps more succinctly called ‘mood-related voluntary hypothermia’. Conceptually, the idea may be aligned as the opposite of ‘emotional fever’, where reptiles are thought to select higher thermal conditions in response to stress. This topic refers to the frequent selection of apparently sub-optimal temperatures in captive reptiles. In some respects, this seems similar to hypoactivity, but is particularly associated with animals making determined efforts to occupy the cool areas of their enclosures. Season-related hibernative tendencies are usually not implicated, a wide thermal gradient may be available, and no disease may be present, amongst other significant points. Typically, but not always, animals have a history of stress-related behaviours, and space-restrictive and poorly furnished enclosures often are involved.

Instead of a reptile deliberately using temperature variation to make the most of its environment, these cases may involve a reptile’s disposition leading it to make the least of their surroundings. This situation closely approximates with voluntary hypothermia during disease (Warwick 1991; Arena and Warwick 2023), but here the condition presumably arises due to environmentally induced shut-down, rather than a disease-induced shut-down. In short, a reptile may seek an environmental temperature to match its mood, and such a shut-down could be due to conditions causing disease or to inappropriate environmental conditions.

All-warm enclosures can assist in avoiding the onset of disposition-related voluntary hypothermia, but this does not, of course, resolve the reasons for its stimulation in the first place. Also, ‘all-warm’ environments should not be considered as a remedy to this problem for the additional reason that, as stated elsewhere in this book, constant set temperatures may have deleterious consequences.

8.11.9 Feeding Behaviour and Problems

There are a few general points concerning behaviour in the context of food, activity, and energetics that are worth re-emphasising here due to their relation to captivity stress, which can cause or accentuate certain situations.

8.11.9.1 Excessive Weight Gain and Loss

Excess food intake and obesity can be a problem in captive reptiles. Although imbalanced diets and insufficient exercise are classic husbandry problems implicated in obesity, psychological and behavioural aspects can also be involved. Unnatural environments and understimulation related to social stressors seem also to be associated with too great an interest in, and intake of, food. Animals that are less active in captivity (either normal ‘sit-and-wait’ predators or abnormal hypoactive individuals) may store surplus energy as excessive amounts of fat. Regardless of whether or not an animal consumes normal amounts of food, adverse effects can still occur if a relatively high food intake to low exercise

ratio exists. Also, behavioural considerations such as captivity-related hyperactivity and unusually long reproductive interactions can result in excessive weight loss. Animals may, therefore, be feeding normally, but are adversely affected by a low food intake to high exercise ratio. It is important to make careful assessment of possible weight gains or losses that may in part arise from both normal and abnormal behaviour. Consequently, appetite and being a good feeder or weight-gainer may not imply healthy appetite or a psychologically or physically healthy animal (Broom and Johnson 1993; Frye 1991a, b; Moore and Jessop 2003; Warwick et al. 2013, 2019).

8.11.9.2 Co-Occupant Harassment and Competitive and Non-Competitive Feeders

Feeding regimes in captivity are often poorly organised or monitored, or involve offering food to animals in high stocking densities. Most solutions to the problems described below are found either by referring to the species' natural lifestyle or by simple management rules (see also Frye 1991a, b; Mendyk 2018).

Injuries related to feeding frenzies are widely recognised, but even in far less competitive situations animals may have their feeding routines adversely affected. Examples include individuals that are relatively timid or slow feeders that do not compete well against even a single stronger or more forceful co-occupant; animals that are intimidated by competitive feeding and subsequently learn to avoid it by becoming 'select, run, and hide' feeders; and individual animals that are themselves subject to aggressive attacks as possibly an unusual or incidental food source. Where aggressors are suspected, but not identified, persecutors may be indicated by examining the responses of injured animals; victims sometimes appear to recognise individuals that attack them and withdraw when they approach.

Individuals having acquired food can be subject to its theft by another, a behaviour known as kleptoparasitism (Burghardt and Denny 1983). In captivity, reptiles, especially freshwater turtles and crocodylians, will often grasp an item of food and then move away from others to avoid losing it, and snakes can often lose their catches to competing others (Burghardt and Denny 1983).

Clearly, these situations can contribute to feeding deficiencies because even where animals successfully acquire a food item, they may be pressured to spend long periods defending their meal from others, which may be almost impossible in the confines of an enclosure. Consequently, avoiding intimidating encounters, attempting to protect a food item obtained, and evading being treated as food may result in insufficient or no nutrition or may lead to animals expending excessive amounts of time and energy trying to avoid losing acquired food and therefore not gain sufficient sustenance.

Captivity-related problems can turn a feeding session, intended as a nutrition and energy provider, into a significant energy consumer. Therefore, it is important to consider not only species-specific feeding requirements and all the usual recommendations that are offered for safer feeding in captivity, but also to observe constantly the behaviour of the individual animal and its co-occupants for presence and development of potentially disruptive influences on feeding.

Also, if a dominant animal eats much of a submissive animal's food, the dominant individual may end up being over-fed as well as the submissive animal being under-fed.

8.11.9.3 Abnormal Ingestion of Items

Under natural conditions, various reptiles select and consume indigestible items such as small stones for various reported reasons including for ballast amongst aquatic species and as digestive aids amongst terrestrial species (Frye 1991a, b, 1995). In captivity, an associated problematic habit occurs, known as pica, in which individuals consume a variety of inorganic items, often in detrimental and dangerous quantities, possibly resulting from nutritional deficiencies (Frye 1991a, b) or understimulating environments (Nicholas and Warwick 2011).

8.11.9.4 Post-Feeding Quiescence

After feeding, many reptiles, in particular those (e.g. snakes) that may consume large meals on single occasions, often seek a quiet place to digest food away from predators or disturbances. Post-prandial quiescence is an important behaviour in reptile feeding patterns, and this should not be disturbed by either interference, such as handling and transportation, or subtle disruptions, such as highly active co-occupants and novel background stimuli.

8.11.9.5 Cannibalism

Cannibalism in captive reptiles is associated with several situations including normal species-specific behaviour, incidentally in normally non-cannibalistic animals when one (usually much larger) animal eats another holding the same food item, in highly opportunistic semi-cannibalistic feeders that are very hungry and that are attracted to another, for example, because of an open wound or similar cue, and extreme social aggression, although in some cases normally non-cannibalistic species transfer to cannibalistic behaviour for no apparent reason. Relatedly, wound healing may be slower in stressed animals (Gouin and Kiecolt-Glaser 2011). Cannibalism is avoidable in most cases. Because these considerations are mostly related to routine husbandry problems, rather than specific behavioural considerations, they will not be discussed in detail here (see instead Frye 1991a, b; Warwick et al. 2018a). However, in some cases, aggression and cannibalism become more apparent because of general restrictions on behaviour such as spatial limitations, overcrowding, lack of seclusion, and a lack of live food in hunting species (see also Martinez-Silvestre 2014; Arena and Warwick 2023) (Table 8.3).

Table 8.3 Examples of behaviour-related self-injury (Derived from: Frye 1991a, b; Warwick 1990a, 1995; Warwick et al. 2013, 2019; Bashaw et al. 2016; Martinez-Silvestre 2014; Nicholas and Warwick 2011; Benn et al. 2019)

Friction lesions, usually on rostrum, due to interaction with transparent boundaries;
Friction lesions on rostrum, damaged claws, and abrasions to (usually) forelimbs arising from exploratory and escape activities.
Friction lesions on rostrum, feet, and underside of body and tail arising from hyperactivity.
Dermal lesions arising from hypoactivity and associated prolonged contact with substrata.
Thermal burns from too close proximity or prolonged contact with a heat source (e.g. lamps, hot rocks, other radiators).
Damaged claws from trying to burrow into shallow or hard substrata; impact injuries resulting from flight responses and climbing-related rapid descents or falls.
Impact injuries resulting from rapid descents on to an insufficiently soft substrata or into an insufficiently deep water pool.
Related matters include excessive deliberate or incidental ingestion of substrata and other environmental items—known as ‘pica’.

8.12 General Considerations

8.12.1 Establishing Possible Meanings from Behavioural Signs

It is important always to apply a holistic context to an animal’s behaviour when asking questions about a sign and trying to discover its causes. It is also important to assign priorities in the order of questions and their investigation. An example for such consideration might be provided by looking at a freshwater turtle that appears, uncharacteristically for the individual, to make repeated attempts to leave water and its captive surroundings in general.

One could consider several possibilities:

1. Is the water and perhaps the entire environmental temperature too high? The apparent escape attempts could be the animal trying to avoid a thermal extreme.
2. The animal could be ill or aged and trying to leave the water to avoid drowning.
3. Are there other animals in the enclosure that might be attacking the turtle, and is it trying to avoid being harmed?
4. Hunger might be causing the turtle to mount a food search outside its environment.
5. The animal may be displaying captivity stress-related exploratory, search, and escape activities, interaction with a transparent boundary, or hyperactivity.
6. Is the behaviour related to reproductive drive factors, e.g. to find a mate, or a nest site for egg deposition? Although the season may be incorrect, searches might still occur due to forced or altered natural rhythms.
7. The animal may be ‘transient’ male or other individual responding to migratory influences.
8. Poor water quality if extreme pH or ammonia levels are present.

Where serious immediate threats to the animal's safety are involved, for example, in 1–3, obviously the best practical method is to observe briefly and act quickly. Other aspects can be observed more fully when the higher priorities have been evaluated. Tracking the reason for the behaviour is highly important, but the overall result should be the same: the animal should be enabled to leave the water and its environment, at least temporarily. Behaviours can be regarded as indicators of the highest integrity in reflecting what an animal wants to do, for whatever reason. If an animal tries to escape an enclosure, it is a reasonable probability that either something is driving it to escape some factor(s) of the environment or it simply wants to get out! One must pay heed to such signs and quickly resolve their causes. Finally, yet of high importance is the issue that human diurnal lifestyles frequently conflict with those of crepuscular or nocturnal animals, and this may imply that opportunities for observation of signs pertinent to welfare assessments may be compromised or overlooked and animal condition underascertained (Warwick et al. 2018a). To better assess reptile welfare, observers need to be active during the animal's activity period.

Cameras can also be used to augment monitoring of behaviour or used without observer presence.

8.12.2 Body Posture and Position

A reptile's postural and positional orientation and associated voluntary movements (such as resting with part of the body in the sun and part of it in the shade, straight-line posture, and selection of angles by resting on inclines) are widely accepted to relate to behavioural thermoregulation (Warwick et al. 2019; Arena and Warwick 2023). Because of this, postural and positional orientation is implicated in normal health, but sometimes may also be associated with injury, disease, and discomfort (Warwick et al. 2019; Arena and Warwick 2023). However, this topic usually receives little or no consideration. Perhaps more often than not, when environments are suited to an animal using these strategies, it is due to incidental provisions rather than carefully thought-out conditions.

Many examples could be cited to emphasise both the prevalence and the potential importance of positional-postural considerations to reptile well-being, but perhaps a particularly pertinent case involves snakes and the facilities that are often provided for them. Snakes are frequently housed in enclosures that have linear measurements far less than the sometimes very long individuals. Enclosures with greater lengths than (especially large) snakes are regularly seen as inconvenient, prohibitively expensive, and unnecessary.

As a result, snakes of perhaps 3 m in length are often confined to enclosures where the greatest linear dimension is approximately 1.5–2 m length. The rationale for this perspective is usually based on three presumptions: that resting snakes tend to be coiled; that even mobile snakes do not adopt a 'straight-line' position; and that snakes are generally inactive and consequently do not need much space anyway. Snakes do, in fact, commonly adopt straight-line 'rectilinear' postures during locomotion and at rest (reviewed in Warwick et al. 2019). There is also anecdotal

evidence to suggest that debilitated snakes may voluntarily select the straight-line posture, perhaps as a result of discomfort (Warwick et al. 2019; Arena and Warwick 2023). Observations of captive snakes at zoo facilities (Warwick et al. 2019) found that during 60-min periods, 37% adopted rectilinear or near rectilinear postures, and 45% of the 31 snake species adopted rectilinear or near rectilinear postures and a raft of behavioural and clinical problems were identified as being associated with confinement of snakes in smaller enclosures. A recent systematic review of recommendations for snake enclosure sizes concluded that all snakes should be able to fully extend their bodies in all dimensions as an absolute minimum, including in temporary environments (other than during brief transportation) (Warwick et al. 2021).

Essentially, rectilinear posturing in snakes constitutes a fundamental normal behaviour that must be provided for in captivity. Rectilinear movement and posturing in snakes, and similarly limb, head, and neck extension in chelonians and lizards, are frequently associated with relaxed states; the animals are sufficiently 'comfortable' to expose themselves in otherwise potentially vulnerable positions. Accordingly, the absence or rarity of such behaviours may indicate inadequate captive conditions and poor welfare.

Larger environments may encourage 'normal' exercise. Obviously, species that hibernate, brumate, or aestivate are subject to prolonged reduced activity, although this is matched by reduced metabolic rate. Whilst endurance studies in reptiles (e.g. animals on treadmills) have indicated that artificially sustained exercise may be physically deleterious (Garland Jr et al. 1987), physical activity appears to be important to general health and avoidance of disease (Martinez-Silvestre 2014; Husak et al. 2015, 2017; Wilkinson 2015; Warwick et al. 2019; Arena and Warwick 2023). Any environments that restrict postural and positional orientation and potentially important associated exercise should be discouraged, and appropriate alternatives routinely made available.

8.12.3 Biological and Behavioural Strategies in Health and Disease

Biological and behavioural strategies as part of health maintenance and recovery during injury and disease have been identified in numerous animals (for limited reviews, see Kluger et al. 1975; Kluger 1979; Hart 1988, 1990; Warwick 1991; Warwick et al. 2013; Breuning 2018; Warwick 2019). Biological and behavioural strategies are natural responses that allow vital energy to be directed towards recovery and regeneration (Hart 1988). These natural healing activities are temporarily utilised at the cost of less immediate requirements such as management of physical appearance and locomotion (Hart 1988; Arena et al. 2023). However, in many instances observers do not necessarily equate these highly specialised and often readily apparent behaviours with precise biological mechanisms that involve the whole animal, rather than just the immune system, in the recovery process.

Most observers would make the association that an injured, limping animal not only reduces discomfort by not using the injured body part, but also limping helps to

solve the problem generally by easing otherwise acceptable stresses on a now compromised limb. However, sick animals that are, for example, lethargic or anorexic are often thought to be simply displaying such signs because they are distressed and nothing more than that. Too regularly important behaviours linked to disease are considered incidental rather than essential. Stressed, injured, or sick animals may benefit from positively stimulating environments to enhance recovery. Such positive environments should, of course, be the mainstay of captive conditions, but where animals have been kept under inferior provisions, transfer to naturalistic environments may be regarded as *de facto* therapeutic intervention. Much needs to be done to increase awareness of behavioural strategies in injury and disease even where domesticated species are concerned, let alone reptiles.

Some behavioural strategies seem to be simple associations with problems, although the abnormalities themselves may be serious. A hypothetical but representative case is outlined here: a snake is observed adopting straight-line body postures. On closer inspection, the animal is showing other signs such as lower abdominal distension, physical sensitivity of the body, and uncharacteristic aggressiveness; the snake is probably in some physical discomfort; signs suggest an intestinal problem, such as constipation; application of an appropriate remedy clears the impaction; the animal is relieved and the straight-line posture ceases. Commonly, snakes are confined to enclosures shorter than the length of the snake where this strategy would not have been possible. The animal's distress may not have been indicated to the observer and its voluntary actions (which may have been essential to alleviating discomfort or remedying the problem) might not have been possible in a small environment.

Voluntary hyperthermia is considered to occur in reptiles with bacterial infections, whereby animals occupy specific thermal niches in the environment that raise body temperatures to a high optimum (Kluger et al. 1975; Kluger 1979; Bicego et al. 2007; Rakus et al. 2017). This 'behavioural fever' corresponds to the 'physiological fever' response produced in endotherms and raises immune competence and other disease suppressing factors. Also, a phenomenon known as 'emotional fever' has been described by Cabanac and Gosselin (1993), which involves reptiles that have been subjected to manipulation stress engaging in voluntarily hyperthermia, presumably to correct disruption of physiological homeostasis.

Empirical evidence also seems to suggest that some reptiles may opt to lower their body temperatures to near thermal minimums during infections (Warwick 1991; Arena and Warwick 2023). Here, lower body temperature reduces metabolic rate, and whilst this might reduce immune competence it may also decrease or prevent dramatic proliferation of microbes and slow the progress of the disease and its effects to a more manageable level. This strategy initially seems risky and may be a fallback one that is utilised when some other coping mechanisms have been compromised. Perhaps, unlike behavioural fever, voluntary hypothermia may also play an important role in gaining the afflicted animal some element of rest and relief from the traumas of its condition—with that rest and relief aiding recovery. There may also be energy savings and reduced risk of predation associated with reduced activity (Zamora-Camacho et al. 2016).

Although possibly incidentally rather than cognitively determined, voluntary isolation of sick reptiles from stimuli and other animals may be a common, yet little appreciated, behavioural strategy (Warwick pers. obs.). This 'self-segregation' is possibly intended to afford the individual greater quiescence, and in nature could, as a matter of incidence, go some way to preventing the spread of disease amongst conspecifics. In captivity, restrictions of space may render both intentional quiescence-gaining moves and incidental regulation of epidemic diseases through self-segregation practically unattainable.

One could take the case of an animal selecting a site away from others and develop the concept in a slightly different direction to indicate the possible variability of a superficially similar biological strategy. Arboreal reptiles suffering from advanced systemic diseases and other problems often uncharacteristically select and occupy a terrestrial location. The animal may be weak, but at the time not necessarily so weak that it is physically incapable of clinging to a branch. In relocating to the floor, the animal has (whilst it still possesses the resources to do so) removed the possibility of unexpectedly falling and incurring further harm. It also has conserved energy, which could be used for healing purposes, by not needing to hold on to the foliage. On the other hand, it may have exposed itself to greater risks of predation by its position on the ground, especially in its weak condition. The strategy, then, arguably is a self-imposed health and safety compromise. Such behaviours are, incidentally, very serious states indeed, if one appreciates the potential implications. It is not being suggested that such examples involve animals making calculated decisions to relocate, rather that inherent drives may underlie these behaviours.

It is probably appropriate to view all specific behaviours during injury and disease not as incidental to a problem, but as signs of broader biological strategies for coping with a challenge. Provision of suitable conditions to allow such strategies to be optimised is probably dependent on spacious, thermally varied, and habitat-diverse environments. This in itself presents a substantial challenge to many if not most husbandry programmes. The widely varied positional and postural orientations mentioned previously may have some, perhaps subtle, significance not only in the maintenance of health, but also in the regulation of disease.

It is reasonable to monitor behaviour for possible strategies, and make efforts to assess and enhance the animal's goals. However, recognition of, and response to, important gross or subtle cues regarding strategies outlined here may form requirements that can properly be judged and fulfilled only by the individual animal in its natural environment (Warwick 1991). At the same time, it is worth considering that the very different stimuli and stressors in captivity could present influences that compromise or negate otherwise normal and perhaps critical self-healing mechanisms.

8.12.4 Similarities and Differences Between Juveniles and Adults

The highly precocial nature of reptiles involves great ethological similarities between juveniles and adults (Burghardt 1978, 1998; Rivas et al. 2016). This allows keepers to unify somewhat their estimations of both biological needs and behavioural repertoires in captivity. However, from opportunistic personal observations of reptiles in zoological and private collections, it appears that there are certain ethological aspects in the comparison of juveniles and adults that warrant some attention, particularly spatial requirements; exploratory, search, and escape activities; social factors; and reproductive aspects.

In considering spatial requirements, it should not be presumed that juvenile or smaller individuals are necessarily less active or utilise less space than adults. For example, Bull and Baghurst (1998) report that juvenile Australian sleepy lizards (*Tiliqua rugosa*) occupy home ranges within, and therefore smaller than, those of adults, and Rocha (1998) found that juvenile Lutz's tree iguanas (*Liolaemus lutzae*) occupied smaller home ranges than for adult males, but as large as for adult females. However, Vidal et al. (2010) report no differences between adult and juvenile activity for the high-mountain lizard (*Phymaturus palluma*), and Sepulveda et al. (2014) report proportionately greater activity amongst juvenile than adult Atacamen Pacific iguanas (*Microlophus atacamensis*). Greater activity and foraging behaviour, amongst juveniles, may in part relate to highly active invertebrate prey as well as increased growth rate to adulthood and reproductive maturation (see also Arena and Warwick 2023).

Avoiding relatively greater predation threats in nature and having to chase invertebrates in food gathering no doubt have some bearing here. Aged animals of any species may conceivably become less active due to chronic debilitation, but this does not infer reduced requirements that are natural for environmental stimulation.

Significant differences appear to exist between levels of exploratory, search, and escape activities in juveniles versus adults. Whilst these activities are common in both groups, juveniles are often far more active. It should not, therefore, be presumed that small individuals or juveniles, because of their diminutive size, are suited to small enclosures. Differences between sexually active and sexually inactive adults may also be related to the reproductive influences and drives that temporarily result in psychological and behavioural attention being directed towards conspecifics, rather than to the immediate environment.

8.12.5 Reproduction

Normal contextualised reproduction and associated behaviours may signal physiological balance, homeostasis, and good health and welfare (Guillette Jr et al. 1995; Gangloff and Greenberg 2023). However, it should not be presumed that successful breeding of captive reptiles infers good welfare or adequate husbandry. Reproduction is not a reliable indicator of an absence of stressors and stress, as has been noted both in domesticated animals (Fox 1984; Broom 1988; Broom and Johnson 1993)

and in reptiles, given that many reptiles ‘breed successfully’ under manifestly poor conditions and under conditions of stress (Warwick 1990a; Moore and Jessop 2003; Warwick et al. 2013).

From a welfare perspective, one can make out a case that reptiles should be provided with opportunities to reproduce because this is a fundamental aspect of their biological, including psychological and behavioural, make-up (Gillingham 1995; Gillingham and Clark 2023; Mendyk and Augustine 2023). It is probably correct to state that under favourably accommodating conditions, facilitating courtship and mating activities, even if not reproduction (e.g. destruction of eggs and neonates), is capable of being welfare-centric, both in terms of psycho-behavioural activities and general health and prevention of certain diseases. However, a case can also be made out that in poorly contextualised captive environments directly facilitating reproduction may introduce unwanted social stressors and outcomes.

There are, in fact, numerous adverse situations arising from many instances where keepers aim to encourage reptiles to reproduce. These include male–female harassment (which can result in individuals such as chelonians being overturned or co-occupant injuries from biting); too close proximity of breeding contestants, resulting in conflicts; male–male combat in situations that do not allow escape; physical exhaustion of male and female energy reserves due to repeated courtship and mating routines and associated locomotor activity; exhaustion of females due to physical demands of too frequent offspring production; and repeated unsuccessful courtship resulting in frustration stress.

It is arguable that captive breeding can reduce the collection of animals from the wild and avoid certain pressures on natural populations, including capture, local and international transportation stresses, and poor husbandry and handling commonly inherent to commerce (Ashley et al. 2014). However, captive propagation also leads to numerous negative welfare situations, including production of ‘excess stock’ that sometimes results in the euthanasia of many animals, a general surplus of animals that become offloaded into highly speculative markets, developmental abnormalities that may be related to specific stress in earlier or later life, husbandry specific epidemics, and the common overly restrictive and clinical production and housing of both adults and offspring during breeding and rearing conditions, notably racks.

Further, providing ready sources of animals, especially to regular high-street pet stores and private keepers, frequently popularises reptile-keeping and exacerbates related problems in some keeping sectors and may actually result in increased demand for wild-caught animals including those falsely labelled as captive-bred (TRAFFIC 2012; Warwick 2014, 2015; Tensen 2016; Greggor et al. 2018). Premature mortality amongst reptiles in the domestic environment is also often high, and appears associated with both malhusbandry and poor adaptational capabilities to highly unnatural conditions (Toland et al. 2012; Warwick 2014; Whitehead 2018). Whilst the scientific community can rightly claim detachment from some of these issues, animals for zoological and laboratory facilities are often subject to the same inhumane histories, and can even arise from the same sources.

8.12.6 Disturbance of Rest and Sleep

One cannot examine reptile ethology and fail to acknowledge sleep as one of the most fundamental of all behaviours. There has been very little research on sleep in reptiles, but several studies indicate that its main features in reptilian biology are comparable to those in other animals (Hartse and Rechtschaffen 1974, 1982; Rial et al. 2010; Libourel and Hirrel 2016; see also Font et al. 2023), and probably also its role. Normal rest and sleep may also be single session or relatively scattered throughout the day or night. So, whilst sleep is undoubtedly a state that can be harmonised with varied opportunities and durations, it is also a state that requires specific fulfilment. Rest and sleep are essential to the maintenance of health and recovery from ill-health (see also Warwick 1991; Arena and Warwick 2023; Arena et al. 2023).

Although sleep in free-living reptiles is subject to disturbances, it is reasonable to assume that in nature animals will, when necessary, select the most suitable times and appropriate periods to compensate for rest and sleep deficiencies. In captivity, situations such as regular animal handling (especially during the individual's natural rest or sleep period), photo-invasive light regimes (where heat and light sources are combined and almost constantly switched on), multiple co-occupant situations, and background (outside the enclosure) environment noise, movement, and so on, as well as many other possible factors, potentially present seriously disturbing influences on reptile sleep and rest (see Arena and Warwick 2023). Indeed, it is possible that even subtle interference with normal sleep requirements may have important effects on, for instance, immune competence and reptile health and well-being. It is conceivable that a lack of rest could be a contributing factor to abnormal and problematic behaviours, and to poor health and mortalities. Assessing a reptile's quality of rest is probably impossible through general observation, but it cannot be assumed that apparent quiescent inactivity in reptiles implies that the animals are experiencing genuinely restful states.

8.13 Literature Developments

A key theme of this chapter (and indeed the entire volume), from its origins onward, has been that nature, normal biology, and natural behaviour ought to inform the foundational substance and guidance for captive reptiles. Presently, a plethora of papers exist echoing and building on this 'emulate nature' message, via provision of naturalistic enclosure furnishings to reflect the wild or offer increased behavioural opportunities (e.g. Baines et al. 2016; Bashaw et al. 2016; Oonincx and van Leeuwen 2017; Warwick et al. 2018a; Warwick and Steedman 2023). Also, it is likely that there is much about the natural world, and even transplanted segments of it, that we simply do not yet understand, thus providing natural (or at least naturalistic) facilities allows us to at least reduce incidental neglect. Larger naturalistic environments encourage mental stimulation, foraging and exercise, overall health, and longer lifespans (Wilkinson 2015). A new line of observational and preference

studies show that reptiles seek out the option of greater space and more complex and naturalistic environments where available, and display greater diversity of important normal behaviours (e.g. Case et al. 2005; Therrien et al. 2007; Moszuti et al. 2017; Burghardt 2013; Mehrkam and Dorey 2014; Rose et al. 2014; Bashaw et al. 2016; Tetzlaff et al. 2019; Bernheim et al. 2020; Spain et al. 2020; Dos Santos 2020; Loughman 2020). Diminished spatial provisions and related inability to move or be encouraged into greater activity also result in obesity (Rose et al. 2014; Dos Santos 2020). These and other studies indicate that larger and more complex environmental characteristics are important to biological needs, normality, and welfare. Such work also shows that contrary to some common claims, historical presence in more basic conditions does not suppress or negate the biological needs for greater environmental complexity (see also Greenberg 2023).

Naturalistic enclosures also, or at least should, involve greater spatial dimensions. Space is an often under-respected fundamental component of life in nature, and one that captive conditions—that are defined by barriers—cannot match, no matter how naturalistic (Arena and Warwick 2023). Greater space, appropriately furnished, increases opportunities for natural behaviour (Gillingham 1995; Gillingham and Clark 2023; Phillips et al. 2012; Warwick et al. 2018a, b), enables avoidance of otherwise stressful co-occupant encounters, such as aggression and mating pressures (Martinez-Silvestre 2014) or disturbing noises (Mancera et al. 2014, 2017a, b), and increases holistic basking opportunities (Oonincx and van Leeuwen 2017; Arena and Warwick 2023). Essentially, greater space brings greater opportunities to meet important welfare criteria.

Sociality in reptiles, including parent–offspring communication, has now been shown to involve great diversity and complexity (Burghardt 1977; Shine 1988; Sinn et al. 2008; Vergne et al. 2009; While et al. 2009; Doody et al. 2013; Ballen et al. 2014; Wilkinson 2015; Ferrara et al. 2013; Doody 2023). Play, once thought only to reside in the avian and mammalian domains, is now a well-recognised factor in reptile psychology and behaviour (Burghardt 1988, 1996a, b, 2005, 2015; Brando and Burghardt 2019).

Obvious as it now seems, knowing normal from abnormal behaviour has become a basic ingredient of reptile welfare assessments (Martinez-Silvestre 2014; Howell and Bennett 2017). Many of the criteria listed in Tables 8.1 and 8.2 have now become the staples of behavioural research (Homer 2006; Martinez-Silvestre 2014; Howell and Bennett 2017; Bashaw et al. 2016; Benn et al. 2019). Two primary behavioural indicators of captivity stress (hyperactivity as an exploratory-escape behaviour and hypoactivity as a biological shut-down activity associated with inappropriate and understimulating environments) have been separately reported in experimental conditions (Bashaw et al. 2016; Benn et al. 2019; Mason and Burn 2018). Our understanding of environmental awareness and learning in reptiles has leapt into the modern era, and parallels other animal classes once thought to hold dominance (Holtzman et al. 1999; King and Green 1999; Pianka et al. 2004; Noble et al. 2012; Wilkinson and Huber 2012; Wilkinson et al. 2010a, b; Font et al. 2023).

Controlled deprivation is a paradigm that recognises the welfare benefits of naturalistic environments and natural stimulation of psychological and behavioural

states whilst targeting the harms of failing to address important allied needs—which all too often is the result of reptile husbandry (Burghardt 1996b, 1998, 2013; Mason and Burn 2018; Mendyk and Augustine 2023). The paradigm has steadily gained traction with numerous authors, expanding on the importance of avoiding depauperate captive conditions by under-assessment of biological needs.

For some particularly helpful introductory, situation, and case-specific literature examples relevant to reptilian and allied psychological and behavioural considerations, readers' attention is drawn to other chapters in this volume, in particular: Gangloff and Greenberg 2023; Gillingham and Clark 2023; Doody 2023; Font et al. 2023; Mendyk and Augustine 2023; Greenberg 2023; Mancera and Phillips 2023; Arena and Warwick 2023; Warwick and Steedman 2023).¹

8.14 Animal Welfare Conclusions

Contrary to some common perceptions, reptiles have complex psychological and behavioural attributes, patterns, and needs. Psychological and behavioural condition is essential to biology, survival, and success, and, fortunately, this is becoming increasingly well recognised as integral to the overall well-being of an organism.

Despite similarities between reptiles and other vertebrates, there are significant differences that result in specific problems of harmonisation to the unnatural conditions associated with captivity. Reptiles are subject to specific limitations of plasticity (physiological, morphological, energetic, and ethological) in nature, and these may give rise to problems of maladaptation in artificial environments. Reptilian psychology and behaviour are variously affected by diverse environmental, social, and other factors and by understimulation, overstimulation, and poor organisation of stimuli arising in captivity. All these influences are frequently present in the captive environment at disproportionate levels, in unnatural forms and for unnatural periods. As such, these aspects form highly significant components in stress, altered behaviour, physical self-injury, and disease. Psychological stress

¹Note: Further specific publications include (in date order): Carpenter and Ferguson (1977); Burghardt (1988); Greenberg et al. (1989); Morton et al. (1990); Lance (1990); Warwick (1990a, 1990b); Frye (1991a); Burghardt (1991); Bowers and Burghardt (1992); Lance (1992); Ford (1992); Greenberg (1992); Pough (1992); Kreger (1993a, 1993b); Kreger and Mench (1993); Chiszar et al. (1993); Mench (1998); King and Green (1999); Scott and Warwick (2002); Moore and Jessop (2003); Burghardt (2005); Garner (2005); Homer (2006); Morgan and Tromberg (2007); Pianka et al. (2004); Manrod et al. (2008); Wilkinson et al. 2010a, 2010b; Mendyk and Horn (2011); Leal and Powell (2012); Phillips et al. (2012); Wilkinson and Huber (2012); Arbuckle (2013); Burghardt (2013); Arena et al. (2013); Doody et al. (2013); Kaleta (2013); Warwick et al. (2013); Ballen et al. (2014); Rose et al. (2014); Warwick (2014); Mancera et al. (2014); Martinez-Silvestre (2014); Burghardt (2015); Webster (2016); Bashaw et al. (2016); Mellor and Webster (2014); Januszczak et al. (2016); Mellor (2016); Moszuti et al. (2017); Mancera et al. (2017a); Mendl et al. (2017); Siviter et al. (2017); Frohnwieser et al. (2018); Mason and Burn (2018); Mendyk (2018); Warwick et al. (2018a, 2018b); Whitehead (2018); Benn et al. (2019); Warwick et al. (2019); Brando and Burghardt (2019); Lambert et al. (2019); Spain et al. (2020).

and behavioural frustration seem common even in the most well-considered artificial environments, and there is a range of abnormal behavioural states associated with environmental and other stressors in captive reptiles. Indeed, it can reasonably be said that captive environments that do not take account of the ethological needs—i.e. positive normal behaviour—of reptiles are likely to cause suffering. This inevitably raises serious ethical questions about the appropriateness of keeping these animals in situations where welfare may routinely be compromised.

The situation is especially worrying in relation to commercial industries, where production methods are often intensive, allowing few opportunities to include naturalistic environments, species- and individual-specific needs, and individual attention. Perhaps more disturbing is the high-street pet market, where poor welfare exists for many reasons, including relatively low levels of biological knowledge amongst keepers, and where facilities are often determined largely by issues of small budgets and space-related conveniences in the domestic environment.

Whilst improvements to all captive reptile conditions are possible, and indeed often practicable, protocols that actually eliminate unnatural stressors and stress in captivity may not be realistic. This raises particular concern regarding the most disturbing captive situations just mentioned. In these cases, weighty ethical questions should be asked and the continuance of these practices thoroughly reviewed wherever possible.

Assessment of welfare constitutes an obligatory imperative, whether from general responsibility, professional ethical code, or legal requirement. Although approaches to welfare assessment can vary according to the layperson, biologist, or clinician, all are important and should be maximally utilised. Practically, objective knowledge and observation are arguably the most essential fundamental elements for the assessment of welfare, to which the tabulated signs of positive and negative behaviours herein may go some way to aiding good evaluation. In addition, throughout this book, general conceptual and practical information for the assessment of welfare is set out to guide readers in their efforts to evaluate physical, physiological, and psycho-behavioural condition amongst captive reptiles.

Assessments of ethological condition in captive reptiles should question constantly all behavioural activities, which in normal animals should not only be unmodified reflections of those in nature, but also should be seen in a holistic context. In addition, it is important to recognise that there is a major difference between an animal's flexibility in responding to a novel experience in nature and an animal responding to an unnatural experience in captivity. Furthermore, it is probably wrong to assume that an apparent absence of signs of maladaptation in captivity suggests that an animal is in harmony with the captive environment.

Psychological and behavioural assets are not only used routinely in health, but are also employed to assist in the healing and recovery process. Thus, these features are fundamental components of biology that act as links between an animal and the external environment in which it lives, the animal and the internal environment of its anatomy and physiology, and as a conveyer of other possible issues of individuality or 'self'. To consider animal ethology holistically is to harbour respect for the organism and its natural lifestyle. Not to do so ignores much of the essence of the animal, and to its detriment.

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Effects of Ontogeny, Rearing Conditions, and Individual Differences on Behaviour: Welfare, Conservation, and Invasive Species Implications

Gordon M. Burghardt and Donna G. Layne-Colon

Abstract

The captive environments that we provide for reptiles are not ideal. This issue applies across a variety of situations, including: rearing hatchlings or neonates in captivity prior to release in the field for conservation reintroduction efforts (head-starting); maintaining population in zoological or educational exhibits; operating commercial facilities; private hobby collections; and maintaining animals for reproduction in research laboratories. To promote the welfare of any reptile species, regardless of the reason for captivity, requires learning from prior experience, natural history, and experimental research. Relatedly, released former captives also invite welfare concerns, whether due to their own possible inabilities to cope in the wild or to their fate at human hands where considered invasive species. We outline factors affecting the development of species-typical phenotypes, perceptual responses, behavioural repertoires, and individual differences across life history stages. We support calls for evidence-based solutions to provide species-appropriate environments for rearing reptiles that enhance their roles in conservation efforts, zoo exhibits, commercial facilities, and basic science.

Keywords

Captive behaviour · Ontogeny · Individual Differences · Personality · Conservation

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9.1 Introduction

Since the first edition of this book in 1995, the number of captive-bred reptiles available from pet stores, reptile fairs, and other trade shows (especially in the United States) has expanded greatly. Reptiles have also become more prominent in behavioural, physiological, and biomedical research, in part, because there is some control over their rearing and breeding history, and because the use of captive-reared animals potentially reduces adverse effects of collection on wild populations. In a review of individual differences in reptiles (Waters et al. 2017), only 24 out of 148 citations were earlier than 1990 and many of these papers used captive animals.

Captive breeding of reptiles plays a role in conservation efforts through head-starting programmes (e.g. green snakes [*Opheodrys vernalis*], Sacerdote-Velat et al. 2014; box turtles [*Terrapene* sp.], Tetzlaff et al. 2019; indigo snakes [*Drymarchon couperi*], Wines et al. 2015; water snakes [*Nerodia* sp.], Roe et al. 2015; rat snakes [*Pantherophis obsoletus*], DeGregorio et al. 2017; horned lizards [*Phrynosoma cornutum*], DeGregorio et al. 2020). Whilst the success of the many relocation and reintroduction programmes has been mixed, published and anecdotal information of such efforts adds to our understanding of development and survival. Anole (*Anolis* sp.) lizards are now major targets of studies on speciation, dispersal, and ecological niche partitioning due to the many independent radiations that have occurred in the Caribbean (e.g. Losos 2009). A number of species are also major contributors to the recent research focus on personality and individual differences in behaviour (c.f. Waters et al. 2017). Reptiles are also major convenient vertebrates for studies of plasticity and genetic adaptation to urban environments and climate change (e.g. Campbell-Staton et al. 2020). Captive studies can be significant components of such research, although fieldwork is ultimately necessary, and species can vary widely in whether and how they can rapidly adapt to changing environments (c.f. French et al. 2018). Collecting from wild populations can also have serious consequences for rare or vulnerable reptile populations (Altherr and Lameter 2020).

Species that are considered to be invasive could be useful for humane captive research because they are otherwise often culled and cruelly killed in their new habitats. If hardy in captivity, they could provide useful models for studying many behavioural, ecological, physiological, genetic, and cognitive processes. Well beyond the infamous and destructive brown tree snake (*Boiga irregularis*) in Guam (Rodda et al. 1999), there are now many other examples of invasive reptiles. Red-eared turtles (*Trachemys scripta*) are disrupting endemic turtles in many countries, and the Cuban brown anole (*Anolis sagrei*) is displacing the green anole (*Anolis carolinensis*), the only native anole in the United States, throughout much of its range (Fetters and McGlothlin 2017). In the single state of Florida, large invasive species are having major negative impacts. These include Burmese pythons (*Python molurus bivittatus*), green iguanas (*Iguana iguana*), tegus (*Tupinambis* spp.), and Nile monitors (*Varanus niloticus*), among others (Hegan 2014; Kopecký et al. 2019). Somewhat smaller, but still impressive species such as basilisk (*Basiliscus vittatus*), the large Cuban knight anole (*Anolis equestris*), red-headed agama (*Agama agama*), and even veiled chameleons (*Chamaeleo calyptrotatus*) have established

populations in Florida (Engeman and Avery 2016). Less attention is given to some of the smaller lizards and snakes that are becoming established in non-native habitats globally.

Controlling invasive species raises ethical questions that are too often ignored in developing management practices (Hegan 2014). Whilst reptiles as pets can play important roles in education and enhancing appreciation of reptiles (Burghardt 2017; Pasmans et al. 2017), species known to have invasive potential should not be promoted as pets outside of their native range, regardless of their perceived adaptability to captivity and ease of care (Stringham and Lockwood 2018; Warwick et al. 2018a; Episcopo-Sturgeon and Pienaar 2020; Toomes et al. 2020).

One could consider the option that management, removal, or reduction of invasive species might include their reassignment to captive-based research programmes rather than being killed in the field. Invasive Burmese pythons (*Python molurus bivittatus*) captured in the Florida Everglades are being used in innovative conditioning and perception studies (Emer et al. 2015) that would be difficult and expensive to carry out in their native habitat. Introduced species can also be used to study behavioural adaptations, genetics, and microevolution. This approach can be applied both to invasive species as well as to local native reptiles having to deal with invasive prey, predators, or closely related alien species such, as is frequently occurring with lizards and turtles. Distinguishing hybrids or determining the source population(s) from whence the invasive animals came are also important tools in studying behavioural plasticity and evolution. From a welfare point of view, using such animals avoids both removing individuals from their natural habitat and purchasing animals from breeders who may rear or keep animals in seriously compromised conditions that may negatively affect natural behaviour. However, more broadly, we need to recognise that keeping any wild species in captivity involves 'controlled deprivation' and a primary goal of successfully maintaining captive reptiles is to know which types of deprivation least compromise their welfare (Burghardt 1996, 2013).

There are now many books, magazines and websites (including YouTube videos) providing information on keeping and breeding reptiles. Many are produced by experienced herpetoculturists, as well as by professional herpetologists and ethologists, dealing with topics on reptile behaviour and outlining husbandry procedures and behavioural factors that need to be considered. However, there is also much erroneous information and it might behove scientific societies to provide and publicise the availability of best practices guidance at the species level (see Jessop et al. 2023; Mendyk and Warwick 2023). This approach would benefit many prospective keepers of captive reptiles, including researchers looking for new 'models'. Chapters in this book cover many relevant topics authoritatively. However, validated information for captive maintenance is, unfortunately, lacking for the vast majority of the now approximately 11,000 described reptile species.

Furthermore, it may not be enough to raise captive-bred animals to be seemingly healthy adults. Early rearing conditions and short-term interventions may have long-lasting effects on later behaviour, as well as on health and morphology. These effects may not be immediately apparent, but they can influence the well-being of animals in

captivity, as well as determine how well (or poorly) they would survive if released into the wild. Established food preferences or abilities to capture prey can be compromised in captivity, and tameness may reduce predator avoidance or escape in the wild. Furthermore, individual differences in behaviour, temperament, and personality are far more pervasive than was generally appreciated in the past, and a growing body of research documents the problems associated with a one-size-fits-all approach, even at levels of species, population, clutch, or litter (Waters et al. 2017).

In this chapter, we outline the major life history stages and classes of events and captive conditions that may affect the subsequent behavioural repertoire and perceptual responses of reptiles. Whilst some of the factors described may not have apparent practical implications, their existence should be appreciated. We concentrate mainly on squamate reptiles, numbering in the thousands and, to a lesser extent, on turtles and crocodylians. The tuatara (*Sphenodon punctatus*), will be ignored because the few institutions housing them have fairly rigorous constraints, and an excellent comprehensive source of information regarding their biology and behaviour is available (Cree 2014). Behavioural aspects of development and their consequences for behavioural competence are emphasised. Non-avian reptiles have often been ignored in such research due to their ectothermy and lack of parental care (Burghardt 1988) that appear to qualitatively render their behaviour less complex and worthy of intensive research as compared to birds and mammals. It cannot be sufficiently stressed that, to be complete, the study of development must also consider neural, endocrine, reproductive, metabolic, social, psychological, phylogenetic, and ecological factors, as discussed elsewhere in this book. Given the growth of the literature since the last edition, we have limited ourselves to a sampling of studies across diverse topics. However, most of the citations in the earlier version of this chapter remain relevant, and many are retained because progress, great as it has been, is still limited, and also to remind ourselves of the history behind recent advances (c.f. Burghardt 2020a). Many of the topics covered herein should also be supplemented by chapters in Murphy et al. (1994) and Schaeffer et al. (1992).

The cognitive abilities and emotional experiences of reptiles are also necessary considerations for enhancing the predictive power of various captive regimes in terms of breeding, exhibiting species-typical behaviour, and adapting to various settings (Greenberg 1992; Burghardt 2013; Learmonth 2020). Individual differences in behaviour are often recognised, although usually anecdotally, and are now major areas of research, frequently under the rubric of ‘personality’ (Waters et al. 2017). Thus, the interplay of genetic and experiential variation may occupy an important part in the physical and psychological well-being of reptiles in captivity. Whilst early work on reptile learning and behavioural development is reviewed elsewhere (e.g. Burghardt 1977, 1978), there has been a major upsurge in the last 20 years (e.g. Wilkinson and Huber 2012; Doody 2023; Font et al. 2023), and selected recent studies on juvenile animals will be reviewed here to illustrate phenomena and concepts that may be relevant to captive management.

9.2 The Embryonic Period

The earliest condition that all animals experience is that of the prenatal/prehatching environment. The behavioural consequences of interventions in the period in the egg or womb, have been underreported in reptiles compared with birds and mammals, but progress is being made. This progress is especially true with regard to thermal regimes, such as changes in climate; in particular, temperature may affect many reptiles, which, being ectothermic, are less buffered physiologically from such effects compared to endothermic vertebrates. Such effects can have consequences for the reproduction of captive reptiles for both behavioural research and conservation efforts. Of course, changes in climate have many ecological consequences other than on temperature, for example, on moisture and soils; and such ecological changes may also have deleterious consequences on development in all taxonomic groups.

Some early descriptive studies of stages of embryonic development are available for reptiles, such as Decker (1967) in oviparous common snapping turtles (*Chelydra serpentina*) and Holtzman and Halpern (1989) in viviparous common garter snakes (*Thamnophis sirtalis*). It is well-known that prenatal hormones are important in sexual differentiation. However, it has been shown that embryos are influenced by hormone production in adjacent embryos in rodents, with postnatal effects on behaviour and morphology (review in Yahr 1988). Although sexually dimorphic behaviour in neonate reptiles has been studied, it is possible that delayed effects from chance, non-genetic uterine position may lead to feminised or masculinised behaviour in males and females, respectively, in viviparous species. This possibility is ripe for study and we are unaware of any studies in viviparous squamate reptiles. Indeed, hormones are greatly understudied in reptiles (Kabelik and Hofmann 2018).

Being readily manipulated, temperature is one factor for which prenatal experimentation has been carried out in the laboratory, as well as through natural variation in the field. Atypical incubation temperatures (oviparous species) or exposure of pregnant females to temperature extremes (viviparous species) can prevent embryos from developing, produce developed but stillborn neonates, or result in physical abnormalities (Vinegar 1973, 1974; Burger et al. 1987; personal observation on garter snakes [*Thamnophis sirtalis*]). In our laboratory, James Schwartz and Harold Herzog held pregnant wild-caught female garter snakes (*T. sirtalis*) from the upper Midwest of North America at a constant 20, 25, or 30 °C for the final weeks of gestation, where 25 °C is the typical successful temperature for maintaining females. Five litters, at the 25 °C temperature, were born in early August with no deformities. Of 13 litters born at a constant 20 °C temperature, 20 animals out of 245 were clearly deformed with kinked bodies, flat heads, no skull or abnormally large eyes. In eight litters, all neonates were born dead; in the other five litters, only 37 out of 100 offspring were alive at birth. Parturition was also delayed until September or October. Of 12 litters held at the 30 °C temperature, all contained live animals at a rate indistinguishable from the normal temperature. Gestation was accelerated, with births occurring in June and July. However, seven litters contained deformed snakes, with mostly kinked bodies, but also including a neonate with a foreshortened snout

and one without a lower jaw. These results suggest that rapid climate warming leading to even moderate deviations from normal locally adapted successful temperature regimes may have deleterious consequences, even although populations of this species live in habitats from near tropical Florida to well into Canada. This outcome can be expected to apply to other species as well. Whilst major climate changes have occurred in the past, the current change is taking place far more quickly, and species may be less able to adapt.

In the field (and usually in our laboratory), females have the opportunity to select their own body temperatures to some extent. Nevertheless, adverse effects of temperature during development may limit the geographical range of many species and their ability to adapt to rapid warming. However, recent studies on populations of lizards in forested versus nearby urban (and warmer) environments raise additional questions. For example, eggs of two invasive anole species (*Anolis sagrei* and *A. cristatellus*) from both forested and urban environments were incubated at temperatures found in each habitat, reflecting natural diurnal variation. The urban nests were, on average, several degrees warmer than the forest nests, and eggs experienced more extreme temperature shifts. Results showed that eggs of both populations hatched sooner in the urban than in the forested habitats, but offspring did not differ in body size, survival, and locomotory measures. Their ability to do equally well in both settings may have, the authors suggest, facilitated their invasive and colonising ability (Tiatragul et al. 2017). However, in studies of the anole (*A. cristatellus*) from the same laboratory, it was found that wild-caught urban mothers were in better body condition than forest caught mothers, but the latter improved when kept at urban temperatures. Whilst offspring from both sets of mothers did not differ in size or body condition at hatching, the urban mother hatchlings grew more over 3 months than the forest mother hatchlings (Hall and Warner 2017). It appears that, as Warner (2014) proposed, reptiles can indeed be models for studying the ‘fitness consequences of maternal and embryonic responses to environmental variation’ (Warner 2014).

The role of temperature is more complicated than being a neutral factor setting a delimited range in which a given species of reptile develops normally and is born without incident. The temperature of incubating eggs has been found to determine sex in some lizards, primarily geckos, agamids, and lacertids (Gutzke and Crews 1988), several kinds of turtles (Morreale et al. 1982) and crocodylians (Ferguson and Joanen 1982; Lang 1987). These species lack sex chromosomes entirely (Bull 1980). In many crocodylians and lizards, higher temperatures frequently lead to males, lower temperatures to females, and intermediate temperatures to a mix of both sexes. In contrast, in many turtles, females are produced at higher temperatures, males at lower ones; other variants also exist (Janzen and Paukstis 1991).

If a temperature gradient exists, individuals from the top of the nest cavity may be proportionally biased to one sex and those lower in the cavity to another. There are also time periods during incubation that are more sensitive to temperature effects for sex determination; in alligators, for example, the critical period lies between 7 and 21 days of incubation (Ferguson and Joanen 1982). This phenomenon of temperature-dependent sex determination apparently eluded scientists and breeders

for many years because of the difficulty, and apparent irrelevance, of ascertaining and recording the sex of hatchling turtles and crocodylians, groups in which the phenomenon is nearly ubiquitous. However, the complete separation of genetic and environmental sex determination in reptiles has been challenged (Sarre et al. 2004).

There is little information on potential long-term effects on behaviour due to the temperature experienced prenatally independent of sex, but there are some intriguing findings. Temperature during incubation has been linked to hatchling thermoregulatory behaviour in crocodiles (*Crocodylus palustris*) (Lang 1985, 1987) and to hatchling size and sprint speed in lizards (*Podarcis muralis*) (van Damme et al. 1992). Incubation temperature has also been linked to personality differences (boldness) in bearded dragon lizards (*Pogona vitticeps*), at least in the short term (Siviter et al. 2017).

Detailed studies of the effects of egg incubation temperature on hatchling behaviour have been conducted on snakes (Burger 1989, 1990, 1991). Drinking speed, righting response, locomotion, ascending an incline, crawling through a tube, ability to bridge a gap, and antipredator responses were examined to measure the responses of hatchlings in situations similar to those that they might encounter in their natural environment (Burger 1989). Black racers (*Coluber constrictor*), incubated at 22 °C and 28 °C showed no difference in locomotor speed, but those from the 28 °C group exhibited greater manoeuvrability. In a species that relies on speed and agility in capturing prey and avoiding predators, incubation temperature probably impacts survival capabilities. Kingsnakes (*Lampropeltis getula*), incubated at 28 °C and at 32 °C, also had better hatchling performance at the intermediate temperature of 28 °C. Snakes born from the high-temperature group, although longer in snout-vent length, were less agile and not as defensive. The low-temperature group did not hatch at all (Burger 1990). Long-term effects on behaviour (up to 6 months) have been found in hatchling pine snakes (*Pituophis melanoleucus*). Again, hatchlings from the low (21–23 °C) and the high (30–32 °C) temperature conditions did not perform as well on behavioural measures as those from the intermediate (26–28 °C) temperature groups (Burger 1989).

In semiaquatic keelback snakes (*Tropidonophis mairii*) eggs were incubated at average minimum, mean, and average maximum temperatures as recorded in the field, and it was found that animals incubated at the warmest temperatures had lower viability, slower swim burst speed, and reduced swimming duration than those at the cooler temperatures (Bell et al. 2013). Furthermore, varying the behavioural testing temperature showed no evidence of embryonic temperature adaptation. Temperature variance during incubation can affect morphological as well as behavioural traits, as shown in a smooth softshell turtle (*Apalone mutica*) (Ashmore and Janzen 2003). Hatchlings of another softshell turtle (*Pelodiscus sinensis*), from a turtle farm in China, were incubated at constant or fluctuating temperatures from 23 °C to 34 °C. Results showed that the fluctuating regime led to the heaviest and most morphologically normal hatchlings, and cooler temperatures reduced locomotor performance using several measures (Du and Ji 2003). These types of findings have clear implications for captive breeding and reintroduction projects.

The incubation temperatures of eggs and the extremes that females are exposed to can be somewhat controlled in captivity, and, as noted earlier, effects of temperature on the sex, size, physical condition, and behaviour of animals are important considerations in preserving captive populations of reptiles. For example, Gutzke and Crews (1988) have shown that those few female leopard geckos (*Eublepharis macularius*) born at high temperatures (which usually produce males) are morphologically normal, but are more aggressive than 'typical' females and never breed. These results are probably dependent on hormonal changes, which are very important in courtship, dominance, and intraspecific aggression (Alberts et al. 1992; Greenberg 1992; Phillips et al. 1993).

Some factors other than temperature that affect prenatal development and post-natal behaviour include: physical contact, light, magnetic environment, maternal diet, and exposure to environmental contaminants. Doody et al. (2021) provide a comprehensive review of the phenomena of synchronous hatching and the role of communication within clutches before and after hatching. Eggs that are usually buried or incubated in enclosed spaces, experience differences in type and timing of light exposure, deposition order and proximity to other eggs. Prolonged exposure to light during this period has been shown to be deleterious for several species of lizards (Zhang et al. 2016). This issue raises cautions, because often reptile eggs are incubated in exposed substrate so that they can be monitored with little disturbance. In captivity, the incubation of eggs whilst single, as well as exposed, may be a practical means of monitoring their condition or development. Again, there are cautionary flags, for eggs of the natricine snake (*Natrix maura*), when incubated separately, produced offspring that were less social and more active than snakes from normal clumped egg clutches (Aubret et al. 2016). It has also been discovered that the magnetic environment in which eggs are incubated can affect the navigation behaviour of hatchling loggerhead sea turtles (*Caretta caretta*) (Fuxjager et al. 2014).

Both the type and amount of maternal diet have also been studied. An early study showed that maternal diet during gestation in a generalist garter snake (*Thamnophis sirtalis*), did not alter the chemical food cue preferences of offspring (Burghardt 1971). More recently, a study of pregnant multi-ocellated racerunner lizards (*Eremias multiocellata*) showed that whilst diet restriction compromised maternal immune function and other traits, including reduced litter size, the offspring were not affected in terms of neonate mass, length, sprint speed, or sex ratio (Wang et al. 2017). These authors reviewed a rather extensive number of other studies and concluded that by incurring costs of a deteriorating environment (less food), this species can still produce fit offspring, though fewer in number, and thus improve the ability of their offspring to deal with unpredictable environmental change.

Exogenous sex steroids during development may also disrupt normal processes, and endocrine-disrupting contaminants have been identified in aquatic reptiles, especially crocodylians in Florida freshwater lakes. Such contaminants may result from industrial production of pesticides and other products and lead to deformities and behavioural effects (Guillette et al. 1994, 1995; Milnes et al. 2008). Hatchling red-bellied turtles (*Pseudemys nelsoni*) found in alligator nests from some of these

same Florida lakes showed reduced defensive behaviour (Placyk and Burghardt unpublished). Field studies have identified synthetic androgens derived from fish farming supplements in a strongly male-biased population of American crocodile (*Crocodylus acutus*) embryos and hatchlings in Costa Rica (Murray et al. 2017). Experiments ruled out temperature as being a factor in the abnormal sex ratio. In short, incubation and prenatal conditions may have profound effects on subsequent behaviour in reptiles, the effects of which we are just beginning to understand.

9.3 Parental Care

Once an animal is born or hatched, it is confronted with a whole new situation. For birds and mammals, the first associations are with an adult, usually one or both parents. The general consensus appears to be that rearing by conspecifics is better for captive animals than hand-raising by humans. This matter is especially important in captive breeding programmes, because rearing experience has been shown to affect adult sexual behaviour in many mammals (Mellen 1992, and references therein), and birds (Hess 1973). For example, Mellen (1992) found that maternal-reared domestic cats (*Felis catus*), copulated more readily than those raised by humans alone.

Historically, reptiles, except for crocodylians, have not been considered as providing postnatal or post-hatching parental care (Shine 1988; Somma 1990). However, the list of exceptions is growing and the importance of studying them is being recognised (Adkins-Regan and O'Smiley 2019; Doody et al. 2021; Gillingham and Clark 2023; Doody 2023). To date, parental care has been observed in some riverine turtle species (Ferrara et al. 2012). Parental care after birth or hatching is rare in snakes but has been found in many pit vipers (Viperidae) (Hoss et al. 2014) and African pythons (*Python sebae*). Nest brooding and defence is more common. Reports of cobras defending nests, and finding newborns with, or in the vicinity of, the mother after birth are also known (reviewed in Shine 1988). Parental care has been observed in lizards, especially the skinks (*Eumeces* spp., Noble and Mason 1933; Evans 1959; Somma and Fawcett 1989; and *Corucia zebrata*, Pough 1991). Members of the former group protect the eggs from predators, and keep the eggs from moulding and drying out by turning and moving them. The prehensile-tailed skink (*Corucia zebrata*) usually produces only one large neonate at a time, who spends time with the female for an extended period. Honneger (1985) reported that a female and her young reacted aggressively toward a keeper trying to separate them. Incidentally, because coprophagy does occur in this species (Honneger 1985), it is possible that during this association, the young receive the species-specific gut microflora necessary for digestion.

Coprophagy has been documented in hatchling green iguanas (*Iguana iguana*), who may need to eat inoculated faeces from adults in order to digest food properly. It has been shown that, for a period after hatching, green iguanas are highly motivated to eat faeces (Troyer 1982, 1984). Although this acquisition of microflora by the neonate from the adult may not entail any active social relationship between the generations, it does have implications for laboratory-bred animals. Perhaps the most extreme example of long-term parental-offspring interactions is found in some

Australian skinks in the genus *Egernia* (Whiting and While 2017). Closely related skinks may differ greatly in their sociality, again indicating the problems with generalising across species. The many statements about 'asocial' or 'non-social' reptiles still found in the literature are most misleading (see Doody 2023).

The best-documented examples of reptilian parental behaviour occur in crocodylians. Crocodylians build and guard nests and patrol the shallow pool nearby where the hatchlings will swim. When the pre-hatchlings call from still within the egg, this 'pipping' brings in the mother and sometimes the father (Herzog 1975; Hunt 1980; Lang 1987), signalling to them to dig out the hatchlings and carry them to water. The hatchlings of some species remain with their parents and other adults for up to 2 years (Garrick and Lang 1977; Lang 1987). According to Lang (1987), these social interactions involve animals of different age classes and affect how individuals feed, defend themselves, and reproduce. The health and behaviour of animals raised in captivity without the benefit of such social interactions may thus be compromised. Many recent studies have expanded this early work and it is reviewed elsewhere (Doody et al. 2021).

The filial and sexual imprinting seen in birds and mammals has not been investigated in reptiles, although there are reports of paternal care of young of other species in captive crocodylians, where prolonged parental care is reported in many, but not all, species. Controlled experiments involving both adults and offspring are needed. This may include experiments exposing hatchlings to unfamiliar conspecifics as well as other species by swapping eggs across mothers and then checking for bonding at a later time, in addition to studies using humans or robotic models, as in the early studies of filial imprinting in chickens, ducks, and geese. Such investigations would be feasible in a zoo or captive breeding facility. Similarly, studies should be made of skinks that brood their eggs and may then remain with their young for a few days. Would they show parental solicitude to genetically unrelated hatchlings?

Although perhaps not normally considered parental care, when mothers of the viviparous lizard (*Zootoca vivipara*) were exposed to predatory snake chemicals during gestation, their offspring grew longer tails (useful in predator escape), and dispersed much farther from the birth location than offspring from unexposed mothers (Bestion et al. 2014). In a similar fashion, females of the Japanese snake (*Rhabdophis tigrinus*), which ate toads, provisioned their hatchlings with toxic nuchal glands (Hutchinson et al. 2013), whereas females that laid eggs without having eaten toads, had hatchlings that lacked this defence. Presumably, maternal provisioning in this manner gives the young an advantage, because it may be some time before they locate toads and have toxic bufadienolides sequestered in their glands. Associated with the glands are some distinctive antipredator behaviours such as neck arching (which puts tension on the glands and draws attention to them) and neck butting (which pushes against the putative predator). Hatchlings of this species living on islands without toads, and with only nontoxic frogs as prey, were more likely to flee than perform the nuchal gland related displays. However, if such hatchlings were fed toads, they began to perform more of the nuchal gland displays (Mori and Burghardt 2017). Experiments with prey trail following showed that

gravid females preferred to eat toads when gravid, whilst nongravid females and males preferred frogs (Kojima and Mori 2015). This difference would play a role in describing normal phenotypes and behaviours, including captive temperament, for this species. It is an example of foetal programming that is not related to a future disease risk, but to survival related to predatory risk.

9.4 Enclosure Temperature

Much research has examined the effects of body temperature on the behaviour, physiology, growth, and health of reptiles in captivity. The consensus is that a range of temperatures should be provided, especially for thermophilic species and those needing to bask, those in arid environments with high daily temperature variation and for bringing animals into reproductive condition. However, temperature during early rearing may have profound effects as well. For example, when captive-born tiger snakes (*Notechis scutatus*) were reared in cool (19–22 °C), warm (19–26 °C), or hot (19–37 °C) enclosures, after 14 months, there were no differences among the groups in preferred body temperature, locomotor speed, or anti-predator responses. However, when the snakes were then shifted to the typical yearly variation in temperature, Aubret and Shine (2010) found that snakes reared at cooler temperatures selected hotter temperatures in the hotter ‘season’ for at least 2 months, showing that rearing temperature, and not current temperature, was most important. Periods of less-than-optimal temperatures, as experienced by a temperate zone species of viper (*Vipera aspis*), does not prevent them from catching up on their development when they are able to access more favourable temperature gradients (Aïdam et al. 2013). For these young snakes in their natural environment, the authors suggested that reducing prey foraging effort could save them energy during times of low prey availability.

9.5 Handling, Enclosures, and Novel Environments

After birth or hatching in captivity, a captive neonate typically experiences being handled and introduced to some form of enclosure. Even if the adults in a collection are housed in semi-natural enclosures, the neonates are usually maintained in smaller containers with relatively simple cage furnishings (e.g. shelter, water bowl). Whilst this arrangement allows for some degree of individual care and relative ease of cleaning when caring for multiple neonates, the effects of this experience are less understood than what is known about rearing some birds and mammals in restricted versus more enriched environments (but see Almlı and Burghardt 2006).

In general, there are no specified space requirements for neonate reptiles as there are for many birds and mammals housed in a laboratory environment (but see Warwick et al. 2019; Arena and Warwick 2023). Individual aquaria, glass jars, and assorted plastic boxes (now often modified and commercially available as reptile enclosures) are chosen to provide enough space for the animal and a water dish

(Murphy and Campbell 1987). As neonates grow, they are transferred to more spacious enclosures whenever it appears that they are too large for the current one. Especially with large reptiles, such as pythons, crocodylians, and tortoises, expense and space limitations often lead to compromised conditions that interfere with normal behaviour or even the ability to move to warmer or cooler areas for appropriate thermoregulation (see Arena and Warwick 2023).

An effect of captivity, even with naturalistic outdoor enclosures, is that young reptiles may habituate to, or become positively attracted to, humans. A perceived advantage is that such captives are, as a consequence, less disturbed by humans during maintenance and research procedures. If they are also more tolerant of their cage mates (Lang 1987), then aggression in somewhat crowded conditions may be reduced. However, learning to associate certain cues with humans can be a disadvantage as seen with young Morelet's crocodiles (*Crocodylus moreleti*) described by Hunt (1980). Because individual crocodiles associated keeper presence and the sound of metal trays with food, the crocodiles 'lunged at a human figure every time one passed'. Such feeding-elicited striking can pose a problem with large and dangerous snakes, something with which most zoo curators are very familiar. Often, handling reptiles is stressful and should be avoided because this can lead to thrashing, biting, scratching, defecation, scent gland discharge, tail loss, and other potentially negative responses. However, target training reptiles have been found to have many advantages in handling, examining, transporting, and reducing food competition in socially housed animals (e.g. Augustine 2009, 2011; Augustine and Baumer 2012; Gibson 2020).

For at least two litters of captive-born rattlesnakes (*Crotalus enyo*), raising them in cages normally used to house adults did not significantly affect their performance on tests of locomotor ability or their investigation of a novel environment (Marmie et al. 1990). Both litters were also compared with wild-caught adults on their ability to strike and trail prey. The captive-born animals did not search as intensely, perhaps because they had not previously searched very far in order to find their food (but see Chiszar et al. 1985, discussed below). Individual variability in the performance on these tests was not compromised by rearing conditions. Herzog and Burghardt (1988), working with garter snakes (*Thamnophis* sp.), found individual and litter differences in defensive temperament that remained stable for up to a year. However, different housing, handling, and feeding procedures could lead to marked differences in subsequent responses to a standard antipredator behaviour test (Herzog et al. 1989; Bowers and Burghardt 1992), with more positive contact leading to calmer snakes.

9.6 Cage Structure

Clearly, reptiles in relatively large enclosures can engage in more behaviours than those in smaller quarters. Many snakes are housed in cages in which they cannot even stretch out unencumbered (Warwick et al. 2019). Such conditions are obviously very restrictive (see also Arena and Warwick 2023), but in some respects, the

size of an enclosure may not be as important as what features it contains. The type of substrate used does not appear to affect behaviour unless it interferes with, or even prevents, the animal from doing something that it would normally do, such as burrow, shed, feed, or defecate. Thigmotactic (tactile) stimuli may be needed by some species (for instance snakes), so clear (or darkly transparent) shelters may be used to provide the animal with a sense of security whilst still being visible for viewing. However, spitting cobras (*Naja mossambica pallida*), if given a choice, prefer an opaque shelter (Radcliffe and Chiszar 1983; Chiszar et al. 1987). Thus, transparent shelters may not be suitable for well-lit enclosures. They may be useful primarily for observation in dimly lit or red-light displays. In a series of experiments, it was found that spur-thighed tortoises (*Testudo graeca*) in larger more natural enclosures, exhibited far more diverse reproductive behaviours than in more restrictive settings; this was particularly true of male responses to females (Bernheim et al. 2020). So, even though mating may occur in more simple and small enclosures, the full range of behaviour may not be seen. Other studies of providing objects to enclosures have been conducted recently (e.g. Burghardt 2013; Bashaw et al. 2016; Moszuti et al. 2017; Spain et al. 2020), and this active area of research should be consulted by those designing habitats for captive reptiles.

The position of objects in a cage is important for the expression of normal behaviours. This is also the provenance of the field of environmental enrichment. Studies have shown that animals, including juveniles, can be affected greatly by their environment and enrichment opportunities, which go beyond feeding (Almli and Burghardt 2006; Bashaw et al. 2016; reviews in Burghardt 2013; Eagan 2019; Mendyk and Augustine 2023). Reptiles are ectotherms and control their body temperature (metabolic rate, activity level) largely by behavioural thermoregulation. All enclosures should be provided with a thermal gradient and zonal mosaic within the range known for that species (which may also include daily and seasonal adjustments of indoor ambient room temperatures), and it should be noted that young animals may have different preferred temperatures to adults (cf. Lang 1987, for crocodylians).

The quality and intensity of light provided may also be important in behavioural ontogeny (e.g. Moehn 1974; Sievert and Hutchison 1991; Mancera and Phillips 2023). The sources of heat and light, or the placement of shelters and other furnishings, should not force an animal to choose between security and maintaining a preferred body temperature (Pough 1991). Other behaviours, such as facilitating skin-shedding or allowing for the escape of subordinates, may be affected by the type and arrangement of cage furnishings. For example, Avery (in Pough 1991) notes that for the viviparous lizard (*Lacerta vivipara*), thermoregulation and feeding behaviour are both compromised by the lack of complexity in the cage environment.

Developmental shifts in habitat use are also important to consider. For example, juvenile Komodo dragons (*Varanus komodoensis*) are more arboreal than adults (Auffenberg 1981), and such ontogenetic shifts may be important to consider in captive settings. Shelters are important components of captive environments for almost all reptiles except, perhaps, completely arboreal and oceanic species. Developmental changes in shelter use and the types of shelter preferred can also occur and differ among species. Kolanek et al. (2019) found that young snakes of two different

species varied in their use of habitat, especially shelters, as they matured. Juvenile smooth snakes (*Coronella austriaca*) are at risk of cannibalistic predation by adults when young, and avoid being in shelters with adults, whilst the slow worm (*Anguis fragilis*), does not exhibit such avoidance. Interestingly, these two species are sympatric and similarly sized viviparous squamates with comparable morphology and habitat preferences. This is a striking demonstration of how social interactions can influence habitat use and why ontogenetic shifts need to be considered in captive settings.

The possible long-term effects of environmental enrichment on the lives of captive reptiles, so often demonstrated in mammals from rodents to primates, is a wide-open area needing urgent study, and this section only provides a sampling. Providing ‘play’ objects to a Nile soft-shelled turtle (*Trionyx triunguis*) reduced self-injurious behaviour in a long-term captive (Burghardt et al. 1996), and such enrichment may be developmentally important for many other reptile species (Burghardt 2005; Pellis and Burghardt 2017). For example, burrowing or sand-dwelling lizards may benefit in demonstrable ways when they have appropriate substrates, even if providing them precludes study or public viewing. Reviews of behavioural enrichment in reptiles are available that provide useful guidance, which certainly has ontogenetic relevance (e.g. Benn et al. 2019; Burghardt 2013). Spatial and physical enrichment, best viewed as reducing the effects of controlled deprivation (Burghardt 1996, 1998), needs to be considered along with social, feeding, and even predator-stress factors.

9.7 Social Arrangements

A decision that must be made is whether or not to house neonates together. We know that raising many mammals, from rats to monkeys, in solitary confinement is deleterious to normal development, especially for social behaviour, including how they react to others of the same or opposite sex. Whilst many reptiles seem to live solitary lives outside of mating seasons, social aggregations may be more common than expected, even in snakes, which are frequently characterised as non-social (Gillingham 1987; Doody et al. 2013, 2021; Schuett et al., 2016; Doody 2023). This issue may be especially true of neonates. Keeping more animals per enclosure reduces the number of enclosures to be maintained, the amount of building space used and, more importantly, the amount of attention each individual animal needs to receive. However, in group situations, care must be taken to ensure that all individuals have access at any one time to food, water, thermal gradient, and shelter (see Warwick 2023; Arena and Warwick 2023), because dominant-subordinate relationships can greatly affect growth, colour, and behaviour (for example, in green iguanas [*Iguana iguana*], personal observations; Phillips et al. 1993). Sufficient space, along with the proper distribution of food, water, perches, and retreats, can help to ensure that all individuals have relatively equal access to these necessities with as little stress as possible. However, group housing is probably not the best choice for delicate and socially aggressive species that require intensive

maintenance, such as many chameleons (*Chamaeleo* spp.). Captive environments may simply not be large or complex enough to facilitate normal behaviour and social spacing.

At the Oklahoma City Zoo, keepers found that neonatal chameleons of several species should be housed individually. If lizards were housed in groups of six to ten, the amount of horizontal space was more important than the vertical, because the neonates could space themselves on 'equal planes'. This prevented smaller individuals from being forced to the floor of the cage, where they did not feed or drink as well as the others (Castle 1990). As noted above, keeping juveniles and adults together may be problematic for many species, because larger individuals may outcompete smaller ones for food, shelter, basking sites, and may even regard them as prey or consume them, perhaps accidentally, when both are competing for prey, as in snakes. On the other hand, many young reptiles are rather social, such as green iguanas (*Iguana iguana*) (Burghardt 1977).

In some of the more social species, such as crocodylians and iguanas, isolation from their peers may be stressful in their first year. For example, some hatchling crocodiles are quite gregarious and tend to congregate on top of each other in group enclosures (Lang 1987). If aggressive interactions develop that may limit the feeding and growth of smaller individuals, then animals should be sorted by size and put into new groups. Juvenile iguanas (*Iguana iguana*) will similarly 'pile' on one another to maintain tactile contact at night (Burghardt and Rand 1985). There is evidence that neonate green iguanas recognise siblings (Werner et al. 1987), one of the first such demonstrations in reptiles, and this may influence both current grouping patterns and subsequent social interactions involving food and reproduction. However, kin recognition has also been documented in neonatal smooth snakes (*Coronella austriaca*) (Pernetta et al. 2009). Female, but not male, rattlesnake (*Crotalus* sp.) litter-mates reared apart from birth for 30 months recognised same-sex siblings compared to similarly aged and reared non-kin (Clark 2004). Highly social lizards living in family groups (Riley et al. 2017; Whiting and While 2017) may be particularly affected by isolation, although this has not been formally established. However, socially isolated, versus group-reared veiled chameleons (*Chamaeleo calyptratus*) showed deficits in social and feeding behaviour at 2 months of age (Ballen et al. 2014). This result was different to the previously described study by Castle (1990), and thus show how species may differ. Kin and social recognition, as well as social isolation, in reptiles is an understudied, but growing topic of interest and research in captive animal welfare (Doody 2023).

Group housing may also affect feeding. In young turtles (*Pseudemys nelsoni*), the amount of food consumed was significantly greater for animals housed together than for solitary individuals (Bjorndal 1986). In this case, the competition for food may have encouraged feeding. Social facilitation of feeding has been described in iguanid lizards (Greenberg 1976). In other cases, such as the hatchling chameleons and crocodylians previously discussed, as well as snapping turtles (*Chelydra serpentina*) (Froese and Burghardt 1974), a dominance relationship may develop that discourages some individuals from feeding and even limits access to food. In European pond turtles (*Emys orbicularis galloitalica*), animals reared in different social and feeding regime groups develop social structures which may be important

to consider in conservation approaches to this threatened species (Masin et al. 2020). Young garter snakes (*Thamnophis radix*) compete for food and recognise their competitors, and avoid them in subsequent nonfeeding encounters (Yeager and Burghardt 1991). Group-housed water snakes (*Nerodia sipedon*) fed separately, grew faster than those kept and fed in isolation or those kept and fed in groups (Burghardt 1990).

Are there long-lasting effects of social experience? As pointed out previously, no firm evidence of filial, sexual, or parental imprinting has been demonstrated. This does not mean that some kinds of bonding do not occur, or that interactions with conspecifics are not useful or facilitatory, even if not essential. Perhaps some difficulties associated with breeding reptiles in captivity are a consequence of the animals bonding with heterospecifics or lack of experience with conspecifics (Bowers and Burghardt 1992). However, it may be that too much human contact is itself disruptive of natural social behaviour, and this may interfere with normal reproductive behaviour, as in some birds and mammals (Hess 1973). With regards to environmental enrichment, the risks and benefits of social manipulation have been far more systematically addressed in primates (e.g. Visalberghi and Anderson 1993), than for reptiles.

9.8 Feeding

There are many possible welfare concerns involving feeding behaviour, diet, and possible influences on physiology, growth and survival in captive reptiles (see also Maslanka et al. 2023). Inducing neonate reptiles, especially snakes, to feed is often one of the most difficult aspects of maintaining them in captivity. Yolk storage may mean that food will not be accepted or even needed right after birth or hatching. With exotic or rare species, as well as some commonly captive examples, we often lack information on what their diet consists of in the wild. With neonates, the problem is confounded by the fact that what they can or will eat is often very different from what adults will eat. There may also be changes in what is accepted as an individual grows (Mushinsky et al. 1982). Young racer snakes (*Coluber* sp.) might eat crickets, for example, whilst adults may prefer rodents (Herzog and Burghardt 1974). In captivity, food items offered commonly reflect what is most readily available. For example, species that specialise in eating amphibians or lizards can be ‘tricked’ into accepting laboratory mice. Such mice are usually readily available and have the advantage of being relatively parasite-free. The effects of such relatively unnatural diets on growth, physiology, and behaviour are not well known. Chemical cues are major factors in food selection of many reptiles and Weldon et al. (1994) review the many ways in which chemoreception can be used to induce reptiles to eat.

Laboratory rodents and other prey items such as fish are often presented to reptiles pre-killed for health, safety, ethical, or aesthetic reasons. The effects of the lack of normal hunting behaviour on the health and welfare of reptiles are not well understood (c.f. Chiszar et al. 1985, 1993; Marmie et al. 1990; Almli and Burghardt 2006). Experience with normally available prey (Burghardt and Krause 1999) and

reactions to toxic, often invasive prey that wild captured individuals may have experienced in the wild, such as fire ants (Langkilde 2009) and cane toads (Phillips and Shine 2004) can alter predatory behaviour and prey preferences. Ontogenetic effects can be found in learned aversions to such prey in both behaviour (e.g. Venable and Langkilde 2019) and morphology (Phillips and Shine 2004).

Related to this issue are studies on the ontogeny of strike performance and prey capture in reptile feeding, which is especially evident in snakes, but can certainly affect foraging in lizards, turtles, and crocodylians. Studies of advanced colubrid snakes show that they improve their performance with experience; for example, constriction (Greene and Burghardt 1978); and prey attack and ingestion (Burghardt and Krause 1999). However, this situation is apparently not the case with pythons and boas, in terms of constriction, which, as juveniles, use the species-typical constriction mode as perfectly as adults (Greene and Burghardt 1978). An experiment with royal ('ball') pythons (*Python regius*) showed that experience with live prey over the first 10 feedings did not improve the constriction performance as compared to snakes artificially fed under sedation (Penning and Dartez 2016). Rigorous quantitative studies have shown that the kinematics of prey striking in ball pythons actually deteriorates in several measures over the first 3 years of life (Ryerson 2020). However, the author rightly noted that the snakes were only fed dead prey artificially moved to induce striking, and they did not actually have to forage for prey, which was provided to them on a regular basis. These studies suggest that developmental changes due to prey type and availability can profoundly shape the behaviour and welfare of captive reptiles and need to be considered in determining what is 'natural' and what is conducive to optimal wellness.

Whilst prior experience with one prey versus another can have consequences on food choice even of an imprinting nature (Burghardt and Hess 1966; Fuchs and Burghardt 1971; Arnold 1978; Lyman-Henley and Burghardt 1995; Burghardt 1992; Grassman 1993; see also reviews in Burghardt 1978, 1990), such altered preferences may be short-lived. In addition, individual differences in preferences may not be as suppressed or obliterated as once thought (Burghardt 1975). When tested, after 3 years on a single-prey type, several garter snakes (*Thamnophis* spp.) still showed subtle effects of their chemosensory preferences at birth (Yeager et al. unpublished). Periodic variation in prey offered may be sufficient to keep animals willing to eat a variety of prey types. However, rearing snakes on different diets did alter behaviour in dealing with other prey types as well (Burghardt and Krause 1999). Feeding regimes as well as temperature can have important effects on both captive and field (large natural enclosures) populations of McCann's skinks (Hare et al. 2012).

Nevertheless, the choice of prey items accepted by neonates such as juvenile garter snakes (*Thamnophis* spp.) can be influenced by prior exposure to prey chemicals even though they are not allowed to come into physical contact with the items (Burghardt 1992). Thus, keeping food sources in the same room as the animals may influence their feeding on such prey or, in chemosensory sensitive species, lead to (appetitive) searching behaviour with unknown consequences. This is particularly relevant in the context of commercial animal establishments, including pet stores, where predator and prey items may be kept in close proximity of one another

(Warwick et al. 2018b). Thus, keeping prey and food in different rooms with limited air exchange is advisable. In this context, we want to emphasise the nature of the differences between individuals and among related taxa. These differences may be more pronounced in generalist species that feed on a variety of prey types, each demanding somewhat different perceptual, capture and handling, and learning abilities. Closely related garter snakes (*Thamnophis* spp.) vary in their ability to capture and ingest fish, and in their ability to profit from experience (Halloy and Burghardt 1990). It is also often discovered that snakes may take prey types in some populations that are never eaten in others, such as crayfish predation in black-bellied garter snakes (*Thamnophis melanogaster*) that normally prey on fish, amphibians, and leeches (Manjarrez et al. 2020). It may also be advisable to avoid unvarying diets for both nutritional and behavioural well-being.

For years our laboratory raised litters of several species of garter snakes (*Thamnophis* spp.) on a diet of fish, earthworms or free choice of either, and have monitored growth, ingestion rates, prey preference, and chemosensory responses. Guidance is available on the kinds of data that can be gathered fairly simply by systematic feeding and record-keeping, supplemented with simple tests (see Mendyk and Block 2023). The snakes were raised on equivalent amounts of vitamin and mineral fortified earthworms (*Lumbricus terrestris*) and mosquito fish (*Gambusia affinis*) for over 8 months under controlled conditions. Two litters of both the generalist species (*Thamnophis sirtalis*), and the earthworm specialist (*Thamnophis butleri*), were divided equally into earthworm and fish diet groups, balanced as closely as possible by sex. There were significant species, litter, sex and dietary effects on growth, prey preference, and habitat choice. Interestingly, the specialist species was more affected by experimental treatments than the generalist species (Lyman-Henley and Burghardt 1995). These data suggest that heritable family and geographic differences can underlie how neonates and hatchlings from the same species may respond to different diets and other manipulations. Research on such differences should be carried out with reptiles fed insects or different types of vegetation as well as with snakes, very few of whom eat insects.

Invasive species that are toxic prey to native species is an issue of great concern. The massive number of deaths of native reptiles in Australia due to the introduced and expanding numbers of cane (marine) toads (*Rhinella marina*) is devastating populations of monitors, snakes, and other vertebrates. Experiments have shown that monitor lizards can be trained to avoid them using conditioned taste aversion, and this might have practical applications in the field (Ward-Fear et al. 2016). In the United States, fire ants (*Solenopsis invicta*) are highly toxic to insectivorous lizards and a critical question is whether through learning, ontogenetic, or evolutionary processes native species can adapt. Using naïve and wild-caught eastern fence lizards (*Sceloporus undulatus*) as a model, studies involving wild and laboratory populations from invaded and non-invaded areas produced somewhat complex results (Robbins and Langkilde 2012), demonstrating how selection regimes differed across age classes of lizards. For example, laboratory-reared lizards from an invaded area were less likely to prey on ants than similarly reared lizards from a noninvaded population, suggesting natural selection on prey choice. More naïve juveniles than

adults from invaded populations ate fire ants suggesting an ontogenetic shift. Unexpectedly, more field-caught adult lizards from invaded populations ate fire ants than did juveniles. The authors suggested that because juveniles were more likely to die due to fire ant ingestion than adults, plasticity, ontogeny, and fire ant feeding interact in complex ways.

These types of findings have ramifications for captive diets. At times, captive reptiles are fed live prey that may be mildly toxic or aversive and we need to be alert to such effects. For example, redworms (*Eisenia foetida*) are an apparently easily purchased bait worm and ideal for small snakes, but the authors have found that young snakes, whilst enthusiastically eating them initially, may reject them later or not thrive; something we did not recognise during our early studies on chemical prey recognition in garter snakes (*Thamnophis* sp.).

9.9 Antipredator Behaviour

When planning for captive maintenance, the antipredator and defensive responses of reptiles need to be thoroughly understood and accommodated. Next to feeding reliably, defensive temperament is probably the most pervasive consideration in captivity, as this can lead to undue stress for the animals. This problem is compounded with highly venomous snakes, particularly fast-moving ones such as mambas, large and potentially dangerous species such as certain boids (pythons, anacondas), varanids (monitor lizards), a few turtles (*Macrolemys* spp., *Trionyx* spp.) and crocodylians, because keepers may act hesitantly and defensively themselves, furthering the stress and defensive reactions of the animals. Flighty and defensive species, even harmless ones (such as some racers (*Coluber* spp.)), may themselves be at risk from, for example, incessantly trying to escape and rubbing their snout wire netting. Our observations of highly venomous young habu (Okinawan pitvipers [*Protobothrops flavoviridis*]) revealed their extraordinary alertness, agility, quickness, and defensive temperament, that not only make them risky captives but also helps explain why they are the source of most venomous snake bites on Okinawa.

Ontogenetic considerations can certainly play a role in habituation to conditions in captivity. One indication of this is the common experience that wild-caught adults of many species are ill-suited for captivity, whilst some captive-reared individuals become much more docile, readily feed, tolerate human viewing during normal activities, and so on; green iguanas (*Iguana iguana*) caught as hatchlings or as adults are good examples. Thus, captive-reared animals are not only desirable from a conservation standpoint (i.e. do not directly deplete natural populations), but also from a captive management and animal welfare perspective, if used in research and exhibits.

Mortality in young captive reptiles is usually the result of birth defects, failure to feed, stress, disease, and euthanasia of surplus stock, not predation. On the one hand, why worry about the competence of an animal's defensive response where there are no predators? The risk of predation may exist in captivity in the form of uneaten live

prey items or conspecifics within the same enclosure. On the other hand, exposing young captive animals to some type of predator threat harmlessly may be necessary to determine if captive rearing conditions are affecting biologically relevant responses to a threat (DeGregorio et al. 2017; Burunat-Pérez et al. 2018). These considerations help to draw conclusions about how a species responds in nature, or to find out if a component necessary for their survival were released into their natural habitat, has been compromised. Webb (2020) provides a compact and useful review of these issues.

The absence of parental or non-parental adult associations early in the life of a young crocodylian could be fatal in the wild because its main line of defence (after sharp teeth, tail thrashing, swimming away, going limp when held in jaws) is to vocalise and alert conspecifics that it is in trouble. If raised in captivity in the presence of conspecifics, a young crocodile may at least be able to compete more successfully for a territory, nest site or a mate when mature. There is a need for research on the value of youthful social experience with conspecifics on survival in the wild. Such knowledge could also inform best practices for the species in captivity.

Many young reptiles have been observed performing species-typical defensive behaviours without prior experience (Greene 1988). Neonates of some garter snake species (*Thamnophis*), when first removed from the mother's cage, will coil and strike at a human hand (personal observation). When tested in standardised trials, neonates may strike at a human finger when they are one day old (Herzog and Burghardt 1986). It appears that snakes are the most studied group of reptiles when it comes to describing and quantifying antipredator responses in the laboratory. Within the garter snakes alone there are species, population, litter, and individual differences in their responses (Arnold and Bennett 1984; Herzog and Schwartz 1990; see also reviews in Burghardt and Schwartz 1999; Waters et al. 2017). The anti-predator responses of some natricine snakes actually improve over the first days of life, probably due to maturation, and may decrease in frequency and intensity due to habituation (Herzog et al. 1989). A study of western rat snakes (*Pantherophis obsoletus*) found that anti-predator strikes were faster and initiated from greater relative distance in adults compared to juveniles (Penning et al. 2019). Learning as well as maturation may underlie these changes. Knowing the nature of antipredator tactics used by neonates in the wild (headhiding, crypsis, tail waving, striking, flight) can help inform the proper interpretation of their behaviour in captivity and appropriate adjustment to reduce stress.

Captivity and handling have been reported to reduce the defensiveness of some turtles, lizards, and snakes (reviewed in Greene 1988—most articles, expectedly, referred to recent captives, not captive-raised). Most reptiles whose captive environments are provided with hiding places and or visual barriers, do not appear to be disturbed by activity outside of their cage. These animals may become habituated to activity that is not biologically relevant or directly affecting them at that time (Hediger 1950). Wild-caught water snakes (*Nerodia*) may become more tractable when they do not have a place to hide—when they can see what is going on about them all the time (P. Andreadis, personal communication). However,

anecdotally speaking, some captive-reared animals appear to reach levels of desensitisation to elements of captive regimes that wild-caught adults do not. This may be related to ecology, body size, and especially species-characteristic antipredator behaviours that become established during ontogeny and later resistant to modification. For example, wild-caught adult green iguanas (*Iguana iguana*) and white-throated monitors (*Varanus* sp.) are shyer and more elusive, often difficult to get to feed or observe feeding, more likely to stay in retreats, and are more readily stressed and reactive to human intrusion than captive-reared animals from the same population maintained in comparable settings (personal observation; John A. Phillips, personal communication).

Responses that may be considered defensive displays may also be signs of stress. For example, a snake that strikes at the glass or a lizard that runs into a wall every time someone walks by, may endure injury or fail to eat or thermoregulate properly, thus affecting its health (Warwick 1990a, b). Handling beyond that required for normal maintenance, often recommended for young captive mammals, does not necessarily have a calming effect in reptiles, as in young garter snakes (*Thamnophis sirtalis*) (Herzog 1990). Individuals that were handled prior to presentation of a model predator had higher strike scores than controls, but not as high as those that had previously been harassed by the same model predator. Even gentle handling of rather docile lizards, such as bearded dragons (*Pogona* sp.), may be stressful, rather than calming (Stockley et al. 2020). Stress effects are described in detail (see Gangloff and Greenberg 2023) and may be particularly important with neonates of species that are shyer, more defensive, or finicky with food preferences.

Habituation to the captive environment may cause neonate bushmasters (*Lachesis muta*), to stop vibrating their tails and striking at about one month of age (Greene and Santana unpublished observations in Greene 1988). Hampton and Gillingham (1989) showed that neonate eastern garter snakes (*Thamnophis sirtalis*) that became habituated to a visual stimulus in a test situation did not become habituated to the observer who approached and handled the snakes after the test. Extensive comparative studies of habituation of defensive responses in four species of naïve *Thamnophis* found major species and individual differences in several measures, including striking, coiling, and fleeing (Herzog et al. 1989; Bowers 1992). This indicates that temperaments differ even among individuals from the same litter and reinforces the imperative for keepers of captive reptiles to view each animal (in conjunction with accurate record-keeping) as an individual with its own distinct personality that may affect its reactions to a variety of contexts.

Body pattern and colour may also be important to note, particularly in species not generally maintained in captivity. Many neonate reptiles, especially numerous snakes and freshwater turtles, have distinctive and vivid colours and patterns not found in adults. What should we make of these differences, and how are they related to behavioural differences between juveniles and adults? One hypothesis worth exploring is that such differences are related to avoiding predation rather than serving to enhance food procurement or conspecific sociality. The colours are often too vivid to be merely cryptic. For example, the pattern of striping on lizards and snakes may be related to responses to predators: striped individuals (and species)

are more prone to flee than fight than are banded, blotched or patternless animals (for example, Brodie 1989). Non-striped species are often more slender and faster moving than blotched species; but there may be more to this. Although neonate reptiles may be far more vulnerable to predation than adults, they may also be less tasty, thus colour and pattern variants could be aposematic (warning) cues. Britson and Gutzke (1993) demonstrated that neonate turtles are avoided by potential fish predators and that this response seems to be due to their behaviour (bites, scratching) rather than any toxic or noxious chemicals. The bright colours and patterns in juveniles could then be viewed as warnings to the relatively small predators that would normally eat prey weighing only a few grams.

It is possible that the rings on the neck of several colubrid snakes (e.g. ring-necked snakes [*Diadophis punctatus*], grass snakes [*Natrix natrix*], brown snakes [*Storeria dekayi*], and Japanese tiger or keelback snakes [*Rhabdophis tigrinus*]) may be related to aposematic colouring, because they are usually white, yellow, or orange against a black or dark brown background. If only the head is noticed by a predator, or the head/neck (nuchal) region is in the process of being attacked, the view of the nuchal area as an aposematic signal could cause confusion or hesitation by the predator and give the victim a little more time to escape. The possibility of a developmental component is shown by the Japanese tiger snake (*Rhabdophis tigrinus tigrinus*), in which the bright neonatal yellow or white neck band is lost in the adults. Similarly, garter snake (*Thamnophis melanogaster*) neonates are far more brightly coloured than adults, often with contrasting ventral areas that can be flashed in the vigorous defensive responses of this species (Herzog and Burghardt 1986). In the future, we may be able to make predictive statements about the temperament of species and individuals, and thus how they might initially be approached in captivity, by considering their colour and markings and the developmental changes that may occur. This is an area where those keeping various species could make important observations conducive to better designed captive habitats and husbandry procedures.

9.10 Individuality, Plasticity, and Long-Term Influence of Captive Regimes

It is apparent from the previous material that regardless of species and age differences, individual differences and plasticity are aspects of all the topics presented. Diet and foraging behaviour, antipredator strategies, sociality, and habitat preferences, among others, can all differ due to geographic, clutch/litter, sex, and genotypic factors. The recent emphasis on animal personality and individual differences in temperament are an acknowledgement of their importance, and work on reptiles is becoming prominent as well (c.f. Waters et al. 2017). Of course, evolutionary processes work through natural selection and genetic variation. However, chance processes, such as genetic drift, may underlie the establishment of new populations on, for example, islands and introductions due to pet release and other means. Thus, behavioural variation and rapid behavioural change occurring over

only a few generations may have conservation and management implications in both field and captivity (Losos 2009). Personality differences may interact with such plasticity. For example, bolder male Namibian rock agamas (*Agama planiceps*) not only retain this trait over time but also spend more time feeding and basking, leading to greater risk of predation in the field (Carter et al. 2010). Such animals may do better in captivity and as exhibit specimens than more shy animals, because their predation risk in captivity is minimal.

Behavioural variation in all the areas mentioned above may also be due to the plasticity of responses, not just innate or congenital factors. Behavioural plasticity in captivity may, as discussed with temperature, be a result of prenatal factors as well as maturation. The latter is behavioural change due to growth, nervous system, and hormonal changes that seem to be almost ‘automatic’ or hard-wired. However, experience, such as exposure to stimuli or lack thereof, can interact with such maturational change. It is not unusual to have animals that were placid and easily kept when small become difficult, even dangerous (to conspecifics and keepers), as they mature and become territorial, dominance oriented, or reproductively active. Food preferences can also change in some species and individuals whilst in others, they do not. One might view this situation as a change in personality or temperament.

We also know, as described above, that species differences are great. Plasticity due to factors such as habitat or diet changes can be distinguished, at least conceptually, from those involving traditional learning processes such as habituation, sensitisation, and association learning involving Pavlovian and operant conditioning. Target training, useful in management, is surprisingly easy to implement in captive reptiles and should be more commonly used outside of zoo management circles (Gibson 2020). The same is true of environmental and behavioural enrichment (reviews in Burghardt 2013, 2019). The application of behavioural systems research (Burghardt and Bowers 2017) is also important for understanding the organisation of animal behaviour and the best ways to implement enrichment procedures (Burghardt 2019). We are now learning much about the possibility of more complex learning and cognitive processes in all animals, and reptiles are not an exception (Wilkinson and Huber 2012; Burghardt 2020b; Szabo et al. 2020; Font et al. 2023). Some reptiles have shown reversal learning, social learning, problem box solving, picture recognition, complex maze navigation, individual caretaker recognition, and so on (see Font et al. 2023). The upshot is that each individual animal has its own way of responding that is the result of not only its genetic heritage and species-typical behavioural repertoire, but also its range of experiences. Some of these considerations can be implemented by caregivers, but many are set in motion by indirect or subtle means that we are only beginning to understand.

Ethical, legal, and perceived conservation imperatives have impacts on the increasing interest in captive breeding of reptiles relating to the pet trade, research, and for subsequent release. It is possible that over generations we will see marked changes in the behaviour of reptiles in captivity involving selection as well as life histories in captivity. Over several generations it is likely that, given the great amount of variability seen in reptiles and the substantial heritability of many behavioural traits (e.g. Boake 1994; Burghardt and Schwartz 1999, Burghardt

et al. 2000), selection will favour certain genotypes that aid survival in captivity in terms of feeding, growth, docility, readiness to mate, and production of viable offspring. It may also be that within a few generations of such artificial selection important behavioural, morphological, and physiological changes will occur that are to varying degrees incompatible with survival in the wild. Shifts in diet and foraging behaviour, and decreased anti-predator responses, are likely in some species. These may have important consequences for animal welfare in captivity, as well as for recovery and reintroduction efforts.

For these reasons, environmental means of encouraging behaviour that is inadvertently selected against or relaxed in captivity, such as feeding and antipredator responses, may need to be fostered through deliberately developed procedures to assess behavioural competence (Chiszar et al. 1993) and to develop any necessary rehabilitation procedures. Such behavioural encouragement may become a critical issue for some species. It is particularly unfortunate that amateur and professional reptile breeders and pet dealers are actually proud of producing and selling hybrids and aberrantly patterned mutants such as albino pythons (e.g. Barker 1991). This issue of breeding atypical genetic lines is as ethically and biologically irresponsible as is the marketing of white tigers in zoos. Neither the species nor the ‘freak’ individuals benefit from such practices, because the genetic changes may alter aspects of the phenotype other than the novel colour or pattern. However, we also must remember that our often sparsely furnished, cramped and unnatural housing arrangements in zoos, laboratories, breeding, ‘head-starting’ facilities, hobby collection, and private home, may be creating behaviourally distorted animals that can thwart recovery, restoration, and genetic integrity schemes, in addition to having deleterious effects on their captive lives and psychological well-being.

These considerations are embedded in both the great individuality in temperament and personality documented in virtually every species of reptile that has been systematically studied to date (Waters et al. 2017). This situation is to be expected, of course, but often not appreciated in either husbandry, developmental, or experimental research. Relatedly, plasticity in behaviour is also very common and can interact with individual differences in complex ways (Snell-Rood 2013). Furthermore, transgenerational transmission of effects, via epigenetic processes, is becoming widely documented and should certainly be expected in reptiles, as occurs in fishes (Berbel-Filho et al. 2020).

9.11 Animal Welfare Conclusions

Reptiles are dependent in many and varying ways on environmental factors and experience as well as the processes involved in growth and physiological, hormonal, and nervous system development. The life events experienced by reptiles, from the moment of conception, surely are critical to their later behavioural capabilities, preferences, temperament, growth, and reproduction, although the exact nature of the effects is still little understood or even appreciated. The developmental trajectory of any animal is also constrained, buffered, channelled, and even shaped by its

specific genetic heritage. This heritage is not only species-characteristic but also, more importantly, individualised. Thus, any guidelines and procedures for keeping and rearing, for example, ‘the’ copperhead or ‘the’ green iguana must recognise the great effects that both ontogeny and individual differences can play in the behavioural phenotype of any given representative. As captive breeding and rearing of reptiles becomes more common and is perceived as necessary for conservation, education, and basic biological research, the effects of inadvertent artificial selection in captive settings will manifest themselves in many and diverse ways. For a long time to come, our knowledge will be in a continual state of flux, even with common species. Our attention to patterns and processes of development must enter into every captive management programme. Often, it takes years for adequate husbandry procedures to be developed and implemented (Mendes et al. 2019).

Some of the most intense and often successful efforts are those to protect, conserve, and reintroduce the many endangered large iguanas, mostly limited to islands, primarily in the Caribbean, spearheaded by the IUCN Iguana Specialist Group. The many research groups have dealt with issues of rearing, head-starting, genetics, health, parasites, sociality, reintroduction, and survival in the field (Alberts 2007; Pérez-Buitrago et al. 2008; Escobar et al. 2010; Wilson et al. 2016). These efforts are all part of what is becoming known as ‘species recovery planning’. The role that zoos can play in academic, conservation, and welfare-oriented research on reptiles is important and some reptiles may be far more valuable and suitable for behavioural research than others (Mendelson et al. 2019). Indeed, the zoo community is being very proactive in many aspects of improving the welfare of captive animals, including reptiles (Kaufman et al. 2019; Melfi et al. 2020).

Undoubtedly, there are many twists and complications that we will encounter whilst endeavouring to improve the management and rearing in captivity of reptile species. Even for animals not targeted for release into the wild, anti-predator training and mild stress may contribute to captive welfare and well-being, as the ‘five freedoms’ for captive animals are being reassessed (e.g. Mellor 2016; Browning 2020). The use of species-typical field and behavioural factors are being promulgated by many as critical to best practices for maintaining, breeding, and rearing reptiles (e.g. Loughman 2020).

Today issues of natural behaviour, health, injury, and privation risks, and teleological, ethological, and subjective factors are all being debated in ongoing discussions of what best constitutes appropriate captive husbandry. To resolve these issues, we need continual scientific research on diverse species. Accumulating the necessary detailed data is a daunting task. What we need to cultivate is a questioning ethological attitude that examines a reptile’s life from the animal’s point of view, whilst realising that it is ultimately our own point of view tempered with current scientific knowledge and, unavoidably, financial constraints that underlie decisions. Regardless, we should operate from a framework of critical anthropomorphism (acknowledging the perceptual and behavioural traits of the animals), whilst still being cognizant of their sentient status and the inevitable controlled deprivation (Burghardt 1991, 1998, 2013) involved in keeping any captive animal.

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Controlled Deprivation and Enrichment

10

Robert W. Mendyk and Lauren Augustine

Abstract

Captivity places various constraints on the lives of reptiles, and despite the best efforts by caretakers, captive environments will never offer the same degree of complexity or range of choices available to free-living individuals in nature. Efforts to improve the lives of reptiles in human care may focus on increasing environmental complexity and the range of choices and opportunities available to them. Known collectively within the field of animal husbandry as enrichment, the origins and underpinnings of such efforts are deeply entrenched in the management of mammals. In reptiles, enrichment is a relatively new phenomenon, likely due to long-held erroneous presumptions that reptiles lack the cognitive or behavioural complexity to benefit from enrichment. This chapter reviews concepts of enrichment within the context of herpetological husbandry, presents a conceptual framework for developing reptile enrichment programs, and discusses ways in which captive environments can be enriched to improve the lives of these animals. Also addressed are some inherent challenges associated with the interpretation and provision of reptile enrichment that can affect its implementation and success. Through this discussion, we seek to stimulate new interest and more widespread usage of enrichment in the reptile-keeping community beyond zoological parks, where it is mostly limited to today.

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Enrichment · Controlled deprivation · Captive husbandry · Welfare · Choice · Complexity

10.1 Introduction

Captivity places various constraints on the lives of reptiles, and despite best efforts by some caretakers, captive environments will never offer the same degree of complexity or range of choices available to free-living reptiles in nature. Logistical constraints including, but not limited to space and climatic variation, and limited nutritional diversity can restrict the level of control that captive reptiles have over their own physiological, psychological and behavioural states, which can lead to both direct and indirect impacts on their welfare (Arena and Warwick 1995; Burghardt 1996, 2013). Perhaps the greatest challenge in creating captive environments that satisfy the needs of a species is that key information on crucial biological or environmental parameters may not yet be known or obtainable. Therefore, reptile keepers often use trial and error to piece together fragments of available information with their own experiences and assumptions of what may be appropriate conditions for a species. As new information comes to light and as keepers develop new and advanced husbandry practices, captive environments can be refined to better reflect the biological requirements of a species and improve overall quality of life.

Efforts to improve the lives of captive reptiles may focus on increasing the complexity of environments and the range of choices and opportunities available. Known collectively within the field of animal husbandry as enrichment (Markowitz 1982), such changes can come in many different forms, and the merits, applications and assessment of enrichment have been discussed by various authors (Newberry 1995; Mellen and MacPhee 2001; Young 2013; Londoño et al. 2018; Eagan 2019). Whilst deeply entrenched in the captive management of mammals and to a lesser extent, birds, enrichment for reptiles is a relatively new phenomenon (Hayes et al. 1998; Burghardt 2013; Kuppert 2013; Michaels et al. 2014), likely due to long-held presumptions that reptiles lack the cognitive or behavioural complexity to benefit from such efforts (Maple and Perdue 2013). Nevertheless, despite such assumptions, there is compelling evidence demonstrating that captive reptiles can indeed benefit from enriched environments (Burghardt et al. 1996, 2002; Therrien et al. 2007; Burghardt 2013; Kuppert 2013; Bashaw et al. 2016; Burman et al. 2020; Spain et al. 2020; Hoehfurner et al. 2021; Warwick and Steedman 2023).

This chapter reviews concepts of enrichment within the context of herpetological husbandry, presents a model for developing reptile enrichment programs, and discusses ways in which captive environments can be enriched to improve the lives of these animals. It also addresses some inherent challenges associated with the interpretation and provision of reptile enrichment that could be affecting the implementation and success of relevant programs. Through this discussion, we seek

to stimulate new interest and more widespread usage of enrichment in the reptile-keeping community beyond zoological parks, where it is mostly limited to today.

10.2 Controlled Deprivation

Much still remains unknown about the biology of many species maintained in captivity. Accordingly, captive environments are at best human approximations of how these animals are perceived to live in the wild (Burghardt 1996). Thus, without a complete understanding of a species' biology or environment, captive conditions are inherently incomplete. Burghardt (1996) introduced the term 'controlled deprivation' to address this issue of depauperate captive environments and the challenges they present for captive management and improving animal welfare. Under this model, it is recognised that captive environments are deprived of many physical, spatial, climatic and behavioural elements present in natural wild habitats that complement the biology of species, and that any changes to these environments should seek to counter the effects of deprivations by providing the most biologically important components of nature.

In contrast to traditional views of enrichment that did not necessarily take into consideration species-specific biological attributes or important elements of a species' natural history that may be missing in captivity (Burghardt 1996), the controlled deprivation model incorporates a more holistic view that seeks to incorporate the most critical features of nature that can influence a species' physiology, psychology and behaviour (e.g. space, nutritional diversity, climatic variables, social dynamics). The benefit of this approach is that changes to captive environments seek to avoid or remedy shortcomings in husbandry and prevent potential issues associated with them by providing conditions that are biologically relevant and innately familiar to a species, rather than some unrelated substitution or addition of unfamiliar conditions or stimuli. In this sense, the approach to enriching captive environments is more proactive than reactive and represents a long-term investment in providing animals with greater species-specific options and complexity within their environments. The controlled deprivation model focuses on narrowing the gaps between the conditions and opportunities provided in captivity and those typically available to species in the wild.

10.3 Enrichment

The concept of enrichment first emerged from efforts aimed at increasing the biological relevance of captive environments (Hediger 1950; Markowitz 1982; Newberry 1995). Although many definitions have been proposed over the past several decades (e.g. Shepherdson 1994; Newberry 1995; Markowitz and Gavazzi 1996; Mellen and MacPhee 2001; Young 2013; Michaels et al. 2014), enrichment can perhaps best be defined as 'the addition of environmental features, or changes in their method of presentation, which increase the complexity of a captive animal's

environment, resulting in beneficial effects on behaviour and other aspects of biological functioning' (Newberry 1994). Having direct implications for improving animal welfare, today, enrichment is offered to a broad range of species, including livestock, zoo, laboratory and companion animals.

With foundations in reducing negative emotional states in captive animals and keeping individuals occupied, enrichment has frequently focused on addressing captivity-related issues pertaining to physical health, boredom and frustration (Newberry 1995; Burghardt 1996). This often includes the introduction of novel objects, tasks and stimuli that are aimed at providing mental and sensory stimulation for animals that may not otherwise be receiving it (Markowitz 1982; Wells 2009), increasing activity and exercise (Shepherdson 1998), reducing aggression (Newberry 1995), or addressing other issues such as stereotypic and self-injurious behaviours (Chamove et al. 1982; Carlstead et al. 1991; Meehan et al. 2004; Flemming 2007; Mason et al. 2007; Eagan 2019). Enrichment is often viewed as a supplement to captive husbandry, or the addition of some 'extra' element, parameter or condition that may not necessarily be vital to an individual's care, welfare or survival (Burghardt 1996). To this end, enrichment is usually temporary or periodic in nature, with objects and stimuli exchanged frequently to maintain novelty (Mench 1998).

10.4 Enrichment as Applied to Captive Reptiles

Whilst vernacular usage of the term enrichment has come to represent all changes made to captive environments that are aimed at improving welfare and now dominates the field of husbandry, we recognise that Burghardt's (1996) controlled deprivation model represents a more honest and accurate approach for identifying and addressing the challenges of improving reptile welfare (Burghardt 2013; Michaels et al. 2014). Nevertheless, for the purposes of this chapter, we follow conventional usage of the term and refer to such changes to captive environments as enrichment, but keep these important distinctions in mind and view enrichment through the lens of controlled deprivation.

As ectotherms, reptiles are tightly coupled with their physical environments behaviourally and physiologically. Because of these close associations, reptiles require unique approaches to their enrichment in captivity, where traditional models and methods based on avian or mammalian subjects may not suffice. Compensating for the deprivations of captivity, reptile enrichment requires an approach that considers the unique ecology, ethology, morphology, physiology and cognitive abilities of each species (Burghardt 1996). Additionally, given the behavioural, physiological and cognitive diversity seen across the Reptilia (Gillingham 1995; Gillingham and Clark 2023), and because welfare is measured at the individual level, caretakers must avoid a standard one-size-fits-all species approach to enrichment.

Identifying specific deprivations is key to developing goals for effective enrichment programs. However, as previously noted, critical features of a species' environment may not presently be known. Furthermore, although the situation is

improving, behavioural indicators of good welfare are generally lacking for reptiles (Warwick 1990; Gillingham 1995; Warwick 2023); some information exists regarding abnormal behaviour (Warwick 1990, 1995; Warwick et al. 2013; Bashaw et al. 2016). As is the case with amphibians (Michaels et al. 2014), signs of deprivation in reptiles may not be obvious and it can be difficult for caretakers to interpret the behaviours, sensory modalities and communication channels of reptiles if using a mammalian or anthropocentric bias (Burghardt 1996; Doody 2023).

In captivity, reptiles are often housed in simplistic environments that feature a very limited set of conditions (Warwick and Steedman 1995, 2023), such as a single heat source, a single ambient humidity level, a single water bowl, a single hide box, a single substrate of uniform depth, and limited dietary variation, among others. These conditions are provided based on keepers' perceptions of the animal's most immediate needs or preferences, which are often inaccurate (Morgan et al. 1998; Gaalema et al. 2011; Mehrkam and Dorey 2014; Mendyk and Warwick 2023). Such simplistic environments offer captives limited options and control over their own physiological, psychological and behavioural needs, and probably represent the minimum threshold of survival-critical resources that can be provided (Mellor 2012, 2015).

Chiszar et al. (1993) noted that several psychobiological processes in reptiles may be altered by captivity, which can have important implications for animal welfare and the need for enrichment. These may include, but are not limited to, changes in activity cycles, refuge-seeking behaviour, deployment of anti-predation tactics, thermoregulation, humidity selection, cold response, temporal and energetic expenditures whilst foraging, responses to prey cues and chemosensory trailing ability, muscular conditioning and endurance, and detection of conspecific chemical cues (Chiszar et al. 1993; Crowe-Riddell and Lillywhite 2023). To counter these and other potential effects, enrichment should seek to enhance captive environments by providing greater variation and opportunities for captives to control some aspects of their environment, including the ability to decide when, where and how to use these opportunities (Markowitz and Aday 1998).

Unlike traditional approaches to enrichment that seek to treat the immediate effects of ongoing captivity-related issues such as reduced activity (Chamove et al. 1982) or stereotypic behaviours (Carlstead et al. 1991; Meehan et al. 2004; Mason et al. 2007; Eagan 2019) by providing captives with random stimuli to occupy their time, reptile enrichment should instead seek to expand on and enhance existing conditions in order to address the underlying deprivations responsible. For example, it is often reported that captive reptiles are less active than their wild counterparts, but what specific deprivations may be responsible for this reduction and how can these deprivations be rectified? Whilst the ultimate goal is to facilitate more natural activity levels, the underlying deprivations that may lead to reduced activity first need to be addressed by providing greater biologically relevant variation and choices in the captive environment.

10.5 Enrichment or Basic Husbandry?: A Philosophical Quandary

Although well-intentioned, the push in recent years to incorporate enrichment into the daily husbandry of reptiles, especially in zoological parks, has inadvertently created several challenges associated with its interpretation and provision. It may sometimes be difficult for reptile keepers to differentiate between enrichment and basic husbandry. Keepers may be under the impression that they are providing some extra element as enrichment that is not essential to the care of a species, when in fact, they are providing a very basic component of animal care that will allow the animal to reach a minimum standard of welfare. This may especially be true when reptile enrichment is approached from a mammalian perspective, where certain physiological underpinnings such as ectothermy, or reptile-specific sensory modalities or communication channels are not taken into consideration.

Because enrichment is often used to refer to any changes made to captive environments that seek to improve animal welfare, an important philosophical question is raised. Should a distinction be drawn between what is perceived to be enrichment versus changes to husbandry that allow for a minimum threshold of basic care to be met? For instance, does it constitute enrichment to provide an arboreal species that has been kept terrestrially its entire life with a tree branch for climbing, or a fossorial species with deep natural substrate for burrowing, or a heliothermic species with a basking spot for thermoregulation? Or, do these and similar examples (e.g. Shelley 2014) merely represent meeting a basic, minimum threshold of care that should have been provided from the start, given what is known about the most basic habits of a species?

We must be careful in the way that enrichment is defined and perceived in reptiles, because there are inherent dangers and consequences associated with claiming all corrective changes to husbandry as enrichment (see discussion below). Efforts to enrich the lives of captive reptiles should be encouraged and celebrated; however, enrichment should not be confused for, interfere with, or come at the expense of meeting the basic husbandry requirements of a species. Even though reptile enrichment is an important component of husbandry and a continuum that changes as new information becomes available, some benchmarks of foundational care based on the biological needs of a species are needed from which to build upon (Burghardt 1996).

10.6 A Model for Reptile Enrichment

Reptile enrichment should have clearly defined and measurable goals that are based on satisfying specific biological needs and facilitating natural behaviours and processes that may be impacted or inhibited by the deprivations of captivity. The flow chart presented in Fig. 10.1 outlines a general model for improving captive reptile environments through enrichment. Once specific baseline husbandry criteria are met, captive environments can then be enriched by expanding on these parameters to



Fig. 10.1 Flow chart model for developing reptile enrichment, with a hypothetical example highlighting the provision of an enriched thermal environment

offer greater variation and complexity to improve the level of control that captives have over their own behavioural, physiological and psychological needs (Fig. 10.1). Clearly defined goals and anticipated outcomes also serve as a way of evaluating whether or not enrichment has been successful and enable keepers to modify and adapt current approaches as needed (see discussion below).

10.7 Examples of Reptile Enrichment

There are many ways in which captive environments can be enriched to help counter the effects of deprivations and to improve well-being in reptiles. Examples typically fall within five main categories, including environmental, dietary, sensory, cognitive and social enrichment, but considerable overlap does occur across this spectrum. It is important to note that whilst many different forms of enrichment have been proposed and offered to captive reptiles, few have formally been evaluated in terms of their effectiveness using objective and measurable criteria (e.g. Kuppert 2013; Bashaw et al. 2016; Therrien et al. 2007; Eagan 2019). Therefore, the effectiveness of many forms of reptile enrichment in improving welfare remains largely anecdotal or speculative until further investigations can be performed.

10.7.1 Environmental Enrichment

As poikilothermic ectotherms, many essential physiological, behavioural and psychological processes in reptiles are dependent on the range of environmental conditions available to them. Therefore, as a continuous goal, captive environments should seek to build on already implemented species-specific husbandry parameters by increasing the complexity of the physical environment and climatic conditions to better reflect those of natural conditions and offer more choices in how they are utilised.

10.7.1.1 Thermal Regimes

Reptiles vary widely in their thermal biology, exhibiting a broad range of thermoregulatory strategies, preferred body temperatures and critical thermal maxima across taxa (Huey 1982). Providing a range of temperatures commensurate with an individual's needs offers more options for thermoregulation (Fig. 10.1). For example, going one step beyond a basic thermal gradient ranging from one end of an enclosure to the other, a thermal matrix comprised of multiple heat sources with different infrared wavelengths and intensities and cooler retreats located throughout an enclosure will offer numerous opportunities for thermoregulation. Additionally, rather than having to select between thermoregulation and other essential behaviours, multiple refugia with different thermal properties can enable captives to simultaneously carry out additional behaviours (e.g. foraging, feeding, refuge-seeking) whilst effectively regulating their body temperature. Similarly, heat sources situated near the front viewing windows of enclosures may force captives into situations where they are conflicted by the needs to thermoregulate and reduce vulnerability to perceived predators. By offering thermal zones away from this area, captives may feel less vulnerable and be more willing to express normal thermoregulatory behaviors.

Periodically manipulating thermal conditions by changing the locations of heat sources and varying the temperatures at each location can promote greater activity by encouraging animals to explore their environment to seek out desired thermal

conditions rather than relying on a consistent site. Changing the location of basking spots throughout the day and varying their intensities can also promote greater activity, especially for more sedentary species, and encourage enhanced natural thermoregulatory behaviours reflective of a more naturalistic lighting scheme. Similarly, manipulating thermal conditions throughout the year to reflect seasonal fluctuations experienced by wild conspecifics can also be important for facilitating normal physiological states such as periods of inactivity or brumation and reproductive cycling.

10.7.1.2 Water Relations

The ways in which reptiles access, utilise and conserve water can differ dramatically across taxa, and this can have strong species-specific implications for how water is provisioned in captivity (Boyer 1988; Frye 1995; Maslanka et al. 2023). Simply providing a water bowl may not meet the hydration requirements of a species (Mendyk 2018). For example, some arboreal species may not descend from trees to drink from pools on the ground, whereas other species may not seek out or even recognise standing pools of water at all, relying instead on rainfall, mist or dew for drinking and hydration. Once a species-appropriate source of water is accessible, variations in the source, location and volume can offer captives multiple options for water intake and submersion. Furthermore, manipulating water levels can elicit natural behaviours. For example, when provided with decreased water levels during feeding, a Mertens' water monitor (*Varanus mertensi*) at the Smithsonian's National Zoo used its entire body to corral and capture live fish in the shallow water of its pool (LA, pers. obs.), an insightful hunting behaviour also used by wild conspecifics (Hermes 1981). Manipulating water levels or rainfall could also be important for stimulating physiological processes such as reproductive cycling or aestivation in some species.

Humidity levels can also influence a species' ability to conserve water, with low or inadequate levels contributing to, or even accelerating dehydration through evaporative water loss. Access to appropriate humidity levels that minimise or prohibit chronic dehydration is another crucial element of a species' husbandry. Providing multiple areas of different humidity levels, such as within burrows and other refugia, can offer captives various options for water conservation, because many species seek out humid burrows to escape dry ambient conditions and to limit or prevent water loss (Bulova 2002). Beyond this physiological need to maintain appropriate water balance, many reptiles may also benefit from variations in the hydric environment for physical or behavioural reasons. For example, many species seek out different humidity and substrate moisture levels depending on their ecdysis cycle.

10.7.1.3 Substrates

Reptiles utilise substrates in different ways to satisfy various biological needs. However, this dependence may not be obvious or fully understood by some keepers. Morphologically and behaviourally, many reptiles are adapted for life on specific substrates which are not always known or available to keepers, where providing choice and access to an appropriate range of options in captivity can facilitate important natural activities and impact behaviour and physiology, as well as physical

and psychological well-being. Substrates that are not correctly paired with a species can impact captives' abilities to dig and construct burrows for refuge, thermoregulation, water conservation or oviposition, as well as affect normal claw growth (Mendyk 2018).

In addition to meeting physiological, behavioural and physical needs of a species, offering a choice of different substrate options can increase the likelihood of meeting the nesting preferences of gravid females and reduce the chances of nesting distress and associated complications such as dystocia, a common source of morbidity and mortality in captive oviparous reptiles (Millichamp et al. 1983; Lloyd 1990; Raiti 1995; Mendyk et al. 2013). Moreover, variations in substrate types and depths can help meet the preferences and comfort of individual captives. For example, when given a choice between different substrates, box turtles (*Terrapene carolina*) preferred resting on softer substrates (Case et al. 2005). The appropriateness of substrates should reflect features of those present within a species' natural habitat as well as variation in these substrates that may occur across a landscape.

10.7.1.4 Enclosure Furnishings

Reptiles are often equipped with specialised adaptations for utilising certain elements of their physical environment, such as rocks, trees or aquatic features, but these elements may not be known or provided for species in captive situations. Overlooking key physical components could inhibit natural behaviours that impact a species' physiological or psychological processes. For example, if the length, diameter, orientation or surface texture of perching is unsuitable for a particular species of arboreal snake, they may not choose to use this perching, which can impact their ability to thermoregulate properly if provided with arboreal basking locations.

Once basic furnishings that complement a species' ecology, morphology and habits are implemented, variations in size, thickness, texture, orientation and arrangement can be explored to increase the complexity of physical elements within an enclosure and provide a broader range of options from which to select. For example, increasing the number and orientation of appropriately-sized branches available or rendering the walls of an enclosure climbable can increase the total amount of usable surface area for an individual, which could lead to increases in activity and facilitate natural behaviours such as copulation (Mendyk 2014). Increasing the number of perches or rock outcroppings available in different parts of an enclosure as well as offering variations in their sizes and textures can provide additional choices over how and where animals can thermoregulate, communicate with conspecifics, and view their surroundings.

Changes to the physical environment such as restructuring or moving cage furnishings and changing substrates can elicit a broad range of behavioural responses. For example, Phillips (1994) noted an increase in investigative behaviours in monitor lizards when the dimensionality of their enclosures was altered; similar changes or rearrangements of enclosure elements can elicit comparable responses in other reptile groups. However, whilst observed behavioural responses to such changes may imply some enriching effect, these should be carefully evaluated in the context of each species. For instance, increased activity may represent improved

welfare in active foraging species such as varanid lizards but may indicate stress and reduced welfare in largely sedentary ambush hunters such as vipers of the genus *Bitis*.

10.7.1.5 Refugia

Reptiles utilise refuge sites to satisfy a wide range of biological requirements such as quiescence, predator or conspecific avoidance, thermoregulation, water conservation, and, in egg layers, oviposition. Shelter may also be crucial for maintaining a sense of security and psychological health, and the appropriateness of refugia will depend largely on the size, morphology and thigmotactic habits of a species (Warwick 1990; Hayes et al. 1998; Mendyk 2018). The provision of a single, arbitrarily-sized and -shaped hide may not satisfy basic requirements as it may fail to offer important specific features.

Increasing the number of refugia in an enclosure can provide multiple options for captives to satisfy various behavioural, psychological and physiological needs. For example, refugia positioned in different locations can offer different thermal or hydric conditions that animals can seek out depending on their physiological needs at any given time, whilst also offering protection against perceived threats from predators or conspecifics. Variations in (low) light intensity within hides can also provide options from which captives can select, and refugia of different shapes and sizes can offer choices in whether an animal prefers to squeeze itself into a tight-fitting hide (i.e. thigmotaxis) or a less restrictive space. Refugia with different sized entrances can also be used to exclude certain (e.g. larger, more dominant) individuals, thereby providing opportunities for smaller individuals to escape or avoid aggression or mating advances from conspecifics.

10.7.1.6 Spatial Considerations

One of the greatest limitations of captivity is the disparity in space available to species when compared to the natural home range sizes of wild conspecifics. Increasing the amount of space available to captives can allow for greater variation in thermal and hydric conditions and other environmental parameters discussed above, as well as allow for greater activity levels and the range of natural behaviours that can be exhibited (see Arena and Warwick 2023). In the case of snakes, which are frequently maintained in physically restrictive, mentally unstimulating enclosures that may not allow captives to fully stretch out or exercise, increased space can have important beneficial effects on the physical health and psychological well-being of captives (Warwick et al. 2019; see also Mendyk and Warwick 2023). However, increasing the footprint of enclosures may not always be possible. Nevertheless, enclosures can still be improved on to create more biologically relevant environments by maximising the total amount of usable surface area available to captives (Mendyk 2014). This may include adding three-dimensional wall treatments to enclosures, or increasing the complexity of enclosure furnishings to provide multiple levels or tiers of surfaces that can be used for different activities, and should be based on the unique morphological attributes and habits of a species (Mendyk 2014).

10.7.2 Sensory Enrichment

The ways in which reptiles experience, process and interact with their environment can vary greatly across taxa, and are heavily influenced by their unique sensory modalities (see Crowe-Riddell and Lillywhite 2023). However, it is less common for captive reptile environments to take into consideration the sensory modalities of a species, which may impact an individual's ability to perform certain tasks and behaviours, communicate with conspecifics, or process their environment (see Doody 2023). Here, providing a range of conditions that enable or encourage the use of a species' senses can offer more biologically appropriate and engaging captive environments.

10.7.2.1 Chemoreception

For many reptiles, chemoreception plays important roles in sourcing food, communicating with conspecifics, and making sense of the physical environment (Madison 1977; Schwenk 1995). Captive environments are inherently deprived of many of the chemical cues that would normally be present in a species' natural habitat that could convey important information about an individual's surroundings. In captivity, the paucity or removal of familiar chemical cues, such as through over-cleaning and disinfecting enclosures, can have negative effects on the behaviour of snakes (Chiszar et al. 1995) and possibly other reptiles. The use of different natural substrates and other enclosure furnishings may be important for retaining familiar chemical cues that a species can use for chemoreception and communication.

The introduction of novel scents to an animal's enclosure can have marked effects on its investigatory behaviour, especially in highly olfactory-driven taxa such as snakes and lizards, but also in chelonians. Many different forms of scent enrichment have been offered to captive reptiles, including those of familiar and unfamiliar conspecifics, predator and prey species, different substrates and inanimate forms (e.g. perfumes, aromatic oils, detergents; Burr 1997; Xiaoyi and Cheng 2011; Londoño et al. 2018). Shed skins, fur and fecal matter from conspecifics or other species can be introduced to enclosures to provide opportunities for captives to carry out natural investigative behaviours, as can rubbing these scents on enclosure furnishings and substrates. Novel scents have the potential to increase natural investigatory behaviours and alertness, provide mental stimulation, and possibly even stimulate reproductive cycling or courtship behaviour. Even 'bad' scents that could signal danger, such as light smoke can illicit natural behaviours (Mendyk et al. 2020), although the potential psychological and physiological impacts of such stimuli and their welfare implications remain unclear.

10.7.2.2 Visual Considerations

Captive environments may also be deprived of visual stimuli that wild individuals would normally experience and rely on, such as communicative displays from conspecifics, predatory stimuli, and environmental cues such as daily and seasonal photo- and scoto-periods. Introducing new visual stimuli to enclosures can bring about behavioural changes in captive reptiles. For example, mirrors have been introduced to several species, including tortoises, iguanids, varanids, gekkonids

and chameleons (Bashaw et al. 2016; Mendyk and Augustine unpublished), often resulting in defensive or agonistic responses that could be important for developing or practising communicative displays in the absence of conspecifics. Moving enclosures so that conspecifics are visible to one another can serve similar purposes. At the same time, adding visual barriers to enclosures can increase the number of options available to captives to avoid agonistic visual displays from conspecifics, as well as reduce stress caused by human keeper activities.

Light cycles can have profound effects on the activity, behaviour and physiology of reptiles (Cowgell and Underwood 1979; Tosini et al. 2001; Ferguson et al. 2014; Augustine 2017). For example, many diurnal and nocturnal reptiles maintain activity during crepuscular periods and may rely on these periods for carrying out necessary behaviours and physiological functions such as foraging, thermoregulation or vitamin D3 synthesis. Yet, most captive lighting schemes do not allow for such natural transitionary periods and instead utilise 'on/off' timers for controlling daily photoperiod. Providing crepuscular periods, as well as manipulating the length of photoperiods throughout the year to reflect natural seasonal changes, could bring about important natural behaviours and facilitate various physiological functions.

With at least some reptile groups known to possess tetrachromatic vision and thereby able to see beyond the human-visible light spectrum (Fleishman et al. 1993; Loew 1994; Ellingson et al. 1995), reptiles perceive light differently than mammals. Providing variations in light wavelengths may offer important visual cues for thermoregulation and UV photoregulation, and can be important for various physiological processes (Adkins et al. 2003; Perry and Fisher 2006). Moreover, the provision of UV light can provide conditions needed by some biofluorescent species to express and/or visualise fluorescent cues that could be key to their sociality and behavioral ecology (e.g. Prötzel et al. 2018, 2021; Sloggett 2018; Top et al. 2020; Mendyk 2021; Paul and Mendyk 2021) which would otherwise not be expressed in the absence of such wavelengths.

10.7.2.3 Tactile Considerations

Thigmotaxis, the motion or orientation of an animal in response to tactile stimuli, appears to play an important role in the movements and refuge-seeking behaviour of many reptiles (e.g. Chiszar et al. 1987; Mendyk 2018). Environments that do not offer options for captives to utilise tight-fitting shelters or physical objects during locomotion and rest may alter the activity, behaviour and movement patterns of some species. Providing opportunities for animals to come into contact with surfaces of different textures and hardnesses or tight-fitting spaces to squeeze inside can be important for facilitating anti-predatory behaviours, offering security, or providing guidance during locomotion. However, the tendency to seek out tight-fitting spaces for refuge should not be misconstrued as support for housing reptiles in physically restrictive enclosures (see Warwick et al. 2019). Tactile variation also allows captives to select conditions based on their own personal preferences and physical comfort. For example, sea turtles have been provided with materials in their aquaria, such as running water currents and plastic pipes that they can rub against whilst swimming (Therrien et al. 2007); different surface textures can also provide relief

from physical discomfort and also aid in ecdysis. Ground vibrations are used by some reptiles to detect prey (e.g. Martinez-Vaca Leon et al. 2020), and although it has yet to be explored in captivity, such behaviour may offer opportunities for tactile enrichment with certain taxa.

10.7.2.4 Acoustic Considerations

Reptiles exhibit a broad range of auditory capabilities (Weaver 1978; Dooling et al. 2000; see also Mancera and Phillips 2023); however, captive environments rarely take into consideration how a species may utilise auditory stimuli in its everyday life. In zoos, many reptiles are known to hone in to various auditory cues associated with daily husbandry rituals, such as the jingling of a zoo keeper's keys, the turning of an enclosure lock (Procter 1928), or even the voice of familiar caretakers (see Murphy and Walsh 2006). Hill (1946) reported that a Komodo dragon (*Varanus komodoensis*) appeared to respond inquisitively to the scraping sound of a metal shovel as the lizard pushed it across a concrete floor, providing mental stimulation for the animal. For taxa that rely on vocalisations for communication, such as crocodylians (Herzog and Burghardt 1977; Frankenberg and Werner 1992; Vergne et al. 2012) and some gekkonids (Marcellini 1977; Frankenberg and Werner 1992), acoustic enrichment introduced through audio recordings offer opportunities for stimulating natural communicative, social and courtship behaviours. Additionally, some captive crocodylians have exhibited strong behavioural responses to anthropogenic sounds, including jet planes (Murphy et al. 2016), large vehicles, portable generators, lawnmowers, and leaf blowers (Mendyk personal observation; Augustine unpublished), suggesting the possibility for other forms of acoustic enrichment. Recent studies have also identified vocalisations in aquatic turtles that have a communicative basis (Ferara et al. 2013), which could offer opportunities for enrichment applications that stimulate natural social behaviours in this group.

When developing auditory enrichment for reptiles, it is important to consider the auditory ranges and sensitivities of species. For instance, certain sounds perceptible to humans may not register with reptiles, and similarly, reptiles may hear or respond to sounds that the human ear is incapable of detecting. Some caution is advised with regards to the types of sounds and their intensities to ensure that acoustic enrichment stimuli are safe for all recipients.

10.7.3 Dietary Enrichment

Captive diets rarely reflect the nutritional diversity of those in nature and are seldom offered in ways that encourage or require natural foraging and food handling behaviours (see also Maslanka et al. 2023). Accordingly, captive reptiles may experience nutritional imbalances (Donaghue and McKeown 1999; Mans and Braun 2014) because captive diets may not be nutritionally equivalent to those in the wild (Dierenfeld et al. 2009; Sweeney et al. 2017). Many natural dietary items may not be commercially available or locally sourced, thus captive diets require enrichment by incorporating alternative items that are nutritionally similar to wild

components. Enriching captive diets by including novel and infrequently offered food items that share some resemblance to the natural diet can also help prevent captives from developing single item dietary preferences as well as provide more nutritionally complete diets that improve nutritional balance (Newberry 1995). For example, for insectivorous species, insect attracting devices can be used to help introduce a broader diversity of prey items than may be available commercially (Hayes et al. 1998).

Novel or infrequently offered food items similar to those eaten in the wild can also encourage natural foraging and prey-handling behaviours that would not otherwise be expressed in captivity. These behaviours can be important for increasing activity, providing mental stimulation, and strengthening muscles that would otherwise rarely be used. For example, adult Komodo dragons (*Varanus komodoensis*) in zoos tend to be fed prey items such as rodents that are substantially smaller than the large ungulate prey they typically feed on in nature. As a result, captives may not utilise the same neck, jaw, shoulder and forelimb muscles that would normally be used in the wild use to tear off pieces of flesh from large carcasses, and tend to have lower bite and pulling forces (D'Amore et al. 2011; Veasey 2017). Although rarely explored in reptiles (but see Meers, in O'Regan and Kitchener 2005; Drumheller et al. 2016), studies on captive mammals, including large felids, have noted remarkable skeletomuscular differences between captive and wild individuals that are attributed to the reduced usage of certain jaw and skull muscles when fed dietary items that do not require their regular usage (O'Regan and Kitchener 2005). Offering large carcasses and prey items to sizable varanid lizards and other large carnivorous taxa such as crocodylians and large constrictors could help strengthen rarely-exercised muscles, prevent potential skeletomuscular aberrations, and improve overall physical condition.

Whereas food resources in nature are often inconsistent and unpredictable, captive reptiles are usually fed the same quantities on regular schedules (Hayes et al. 1998), sometimes to the point where feeding times can be anticipated by captives. Variation in feeding schedules can potentially prevent feeding aggression and other food-associated anticipatory behaviours such as pacing or escape attempts. Extended fasting periods could potentially offer some physiological benefits as well, such as preventing obesity, realigning energetic balances, or conditioning animals for reproductive cycling.

The manner in which dietary items are presented to reptiles in captivity can affect the expression of natural behaviours, as well as offer many opportunities for enrichment. For example, instead of provisioning food in a single location, scattering food items in different areas that require active searching, or broadcasting live prey throughout an enclosure can provide for mental stimulation, exercise and encouragement of natural foraging and hunting behaviours (Phillips et al. 2011). Providing areas that live prey can escape to may encourage some reptiles to utilise novel or insightful behaviours for sequestering hidden prey (Hayes et al. 1998). This has been widely observed in varanid lizards, with several species employing specialised prey extraction techniques involving the forelimbs or tail (Gaulke 1989; Eidenmüller 1993; Horn 1999; Patanant 2010; Mendyk and Horn 2011; Mendyk 2012; Fig. 10.2).



Fig. 10.2 When presented with hidden insect prey inside a tree hole that is too narrow to be accessed with the jaws, black tree monitors (*Varanus beccarii*) and other members of the tree monitor (*V. prasinus*) complex switch to an alternative method of prey extraction utilising coordinated probing with the forelimbs (see Mendyk and Horn, 2010). Photograph by Robert W. Mendyk

Extractive foraging may be possible in other lizard and snake groups in captivity when provided with such opportunities. The use of tongs or forceps to move pre-killed or immobile prey items around the enclosure can stimulate a range of natural behaviours, including prey chasing in active hunting species, or careful coordination and calculation of the timing of strikes in more sedentary, ambush-hunting species such as boids, pythonids and viperids. In both scenarios, such movement and stimulation may be important for the development and refinement of motor skills and coordination, which would be less likely to occur under more sedentary prey offerings.

The provision of live prey can offer various benefits to the health and welfare of captive animals (Newberry 1995), including reptiles (Burghardt 1996). For example, snakes fed live prey have been shown to demonstrate greater competency in natural hunting and prey-handling behaviours than those only offered pre-killed animals (Almli and Burghardt 2006). In addition to diversifying the behavioural repertoires of captive animals to include a broader array of natural hunting and prey-handling behaviours, offering live prey and allowing captives to hunt for their food can provide mental stimulation that may be important for learning, coordination and cognitive development, as well as reducing aggression between individuals (Warwick 1990). Because injuries can be inflicted by certain prey species, some caution and oversight with live prey offerings may be necessary. Although it is beyond the scope of this chapter, the welfare of prey species should also be considered when offered alive to captive reptiles; additionally, the standards and legality of this practice may vary by country and should also be taken into consideration (Cooper and Williams 2014; Warwick 2014).

10.7.4 Cognitive Enrichment

Various studies conducted over the last two decades have challenged long-held preconceptions that reptiles are limited in their behavioural and cognitive complexities by describing a suite of remarkable behaviours and abilities in the group, including problem-solving (Manrod et al. 2008; Gaalema 2011; Mendyk and Horn 2011; Leal and Powell 2012), social learning (Kis et al. 2015; Wilkinson et al. 2010), play behaviour (Burghardt et al. 1996, 2002; Augustine et al. 2015; Dinets 2015; Murphy et al. 2016), and tool use (Dinets et al. 2015; see also Font et al. 2023). Therefore, although very little is presently known about the cognitive development, learning capacities and psychological needs of reptiles, simplistic captive environments deprived of mental and sensory stimulation may not be offering the range of stimuli that would naturally challenge animals to learn new tasks and behaviours or provide them with the stimulation needed for optimal brain development and psychological health. Thus, cognitive enrichment, which seeks to engage 'evolved cognitive skills by providing opportunities to solve problems and control some aspect of the environment' (Clark 2011, 2017) represents a grossly under-utilised tool that can be used to improve the lives of captive reptiles.

10.7.4.1 Novel Objects

Many reptile species appear to possess remarkable spatial memories of their home ranges and immediate surroundings (Holtzman 1998; Day et al. 1999; Holtzman et al. 1999; López et al. 2000, 2001; Wilkinson et al. 2007; LaDage et al. 2012), and are likely attentive of changes in their environment. Such awareness can be important for identifying potential threats or the availability of new resources (food, water, shelter). In captivity, the introduction of new objects may stimulate a range of investigatory behaviours in reptiles. Although Glickman and Sroges' (1966) early investigations into the behavioural responses of some 20 species of reptile towards inanimate objects introduced to their enclosures yielded limited data suggestive of such a level of interest or interaction, subsequent investigations, particularly in zoological parks, have shown that many species of reptile including lizards, snakes, chelonians and crocodylians will investigate and interact with new and unfamiliar objects (e.g. Burghardt et al. 1996, 2002; Burghardt 2013).

Although provisioning of novel objects in captivity is widely applied to lizards and chelonians, snakes have largely been overlooked, perhaps due to perceptions of lower cognitive abilities (Maple and Perdue 2013). Yet, many species of snake appear to be inquisitive and will investigate new objects introduced to their environment. For example, an adult anaconda (*Eunectes murinus*) at Audubon Zoo seized a long skimmer net from keepers and stayed with the object for several hours, periodically 'gumming' the net pole in what appeared to be some form of focused investigatory behaviour (Mendyk, personal observation). Beyond offering mental stimulation, introduced objects should have some biological relevance to a species; simply adding a cardboard box or tube to an enclosure may offer little benefit to an animal if it lacks in functionality or relevance to the species (i.e. why would an animal interact with an object with these qualities in the wild? what is the biological

basis?). Care must also be taken when considering objects for introduction, as some inedible objects may be mistaken for food and accidentally ingested (Baer 1998; Nicholas and Warwick 2011).

Novel objects in some cases may also stimulate reproductive behaviours and provide opportunities for individuals to learn, practice or refine these behaviors. For example, in captivity, male chelonians are known to attempt to mate with various inanimate objects including rocks, logs and balls, and male iguanas (*Iguana iguana*) have been observed attempting to copulate with towels and blankets (Mendyk, personal observation). In cases where animals are housed individually or without potential mates, novel objects can enable individuals to satisfy behavioural and physiological needs such as the innate drive to reproduce.

Play behaviour, or the voluntary, repeated behavioural interaction with an object in a relaxed setting (Burghardt 2005, 2013) was once thought to be limited to birds and mammals, but has since been documented in a number of reptiles, including aquatic turtles (Burghardt et al. 1996; Burghardt 2013), crocodylians (Lazell and Spitzer 1977; Augustine et al. 2015; Dinets 2015; Murphy et al. 2016) and varanid lizards (Hill 1946; Burghardt et al. 2002; Kane et al., 2019). With play behaviour recognised in most major reptile groups, this may be an incentive to provide additional species with rich, stimulating environments to encourage mental stimulation and promote cognitive development (Burghardt 2013). In addition to providing mental stimulation through play behaviour, novel objects can also help reduce self-injurious behaviour, as was the case with a Nile softshell turtle (*Trionyx triunguis*) at the National Zoological Park (Burghardt 1996; Burghardt et al. 1996).

10.7.4.2 Problem-Solving Tasks

Problem solving is an important fixture in the lives of wild animals that can facilitate learning and remembrance of biologically relevant skills and behaviours (Meehan and Mench 2007). However, captive reptiles are rarely presented with the same range of situational challenges that would normally be experienced in the wild. Some reptile groups have demonstrated remarkable problem-solving abilities in captivity, especially when presented with foraging and food handling tasks. Such challenges can be as simple as hiding food items within enclosures or placing them in areas that an animal cannot easily access. Puzzle feeders requiring animals to manipulate a device to sequester food and similar apparatuses that require insightful solutions to obtaining food have been widely used with varanid lizards (Manrod et al. 2008; Augustine 2011; Mendyk and Horn 2011; Mendyk 2012; Kuppert 2013; Cooper et al. 2019; see Figs. 10.2, 10.3 and 10.4) and may also show similar effectiveness with other reptile taxa. For example, many active foraging snakes including, but not limited to elapids [mambas (Fig. 10.5) and cobras] and colubrids (racers, rat snakes and indigo snakes) are excellent candidates for enrichment involving the hiding of prey items, puzzle feeders and related challenges (e.g. Kleinginna 1970; Vause and Jones 2009). Some aquatic turtles have also responded positively to puzzle feeder devices (Bryant and Kother 2014; Fig. 10.6), and crocodylians are prime candidates for problem-solving challenges considering their perceived intelligence and



Fig. 10.3 A puzzle feeder enrichment device for a Philippine water monitor (*Varanus cumingi*) at the London Zoo. The monitor must manually manipulate the jars in order to spill their prey contents onto the ground where it can then be consumed. Photograph courtesy of Grant Kother

complex behavioural repertoires which include tool usage for capturing prey (Dinets et al. 2015).

The success and appropriateness of problem-solving tasks and feeding enrichment devices will depend largely on the morphology, cognitive abilities, behavioural capabilities, sensory modalities and foraging habits of a species, as well as the context of any challenge, which should be relevant to the species' biology. For instance, hiding food items or the use of puzzle feeders would probably be less effective for more sedentary sit-and-wait predators than more active foragers, and what may be effective for one species may be ineffective for closely related taxa.



Fig. 10.4 A foraging apparatus developed for blue tree monitors (*Varanus macraei*) at the London Zoo. This apparatus requires active prey searching as well as focused balance and coordination for retrieving prey items given its wobbling, kinetic nature. Photograph courtesy of Grant Kother

Whittaker et al. (2005) found that a puzzle feeder device developed for large varanid lizards was successfully used by *V. komodoensis*, but not by *V. salvadorii*. Problem-solving tasks and challenges also need to be relevant to the sensory abilities of a species; for instance, some taxa may be more reliant on visual cues than olfactory cues, and vice versa.

10.7.4.3 Training

Operant conditioning is widely used in zoological parks as a behavioural management tool to work safely with formidable species and to facilitate non-invasive husbandry and veterinary procedures (Weiss and Wilson 2003; Augustine 2009, 2010; Augustine and Baumer 2012; Hellmuth et al. 2012; Augustine et al. 2013). Although training often seeks to develop and reinforce behaviours that may not necessarily have a natural basis with reptiles such as targeting and stationing, training for voluntary participation in important procedures such as physical inspections, weight measurements, blood draws and injections can eliminate the need for manual capture and physical restraint and thereby avoid potential stress and



Fig. 10.5 Black mamba (*Dendroaspis polylepis*) feeding enrichment at the London Zoo. Prey is hidden inside the bird's nest, encouraging natural foraging behaviour and hidden prey extraction. Photograph courtesy of Grant Kother



Fig. 10.6 A pig-nosed turtle (*Carretochelys inculpta*) interacts with a submerged puzzle feeder device at the London Zoo (see Bryant and Kother 2014). Photograph courtesy of Grant Kother

injuries associated with these techniques. Target training can also be used to avoid or reduce feeding aggression, especially in large carnivorous species such as varanid lizards and crocodylians that can inflict serious injuries on one another during feedings. Training can also provide mental stimulation that engages animals on a cognitive level (Shepherdson 1998; Clark 2017), which can be important for learning processes and cognitive development in reptiles. Additionally, although not yet explored in reptiles, the interactions that some captives have with their caretakers may also have some enriching psychological effects, as documented in other animal groups (Hosey 2008; Claxton 2011).

10.7.5 Social Enrichment

As a vastly improved understanding of reptilian social behaviour begins to emerge, it is now widely recognised that a broad spectrum of sociality exists across the Reptilia (Doody et al. 2021), which has important husbandry and welfare implications. In nature, more solitary species may have limited contact with conspecifics except for where home ranges overlap, at shared resources (e.g. food, water, shelter), or for reproduction. In many cases, the spatial constraints of captivity lead to higher stocking densities and unnatural social groupings when compared to the spatial dynamics of wild populations (Hayes et al. 1998). Greater population densities in captivity can lead to agonistic interactions and the establishment of dominance hierarchies (e.g. Barker et al. 1979; Alberts 1994) that can directly impact health and welfare. Maintaining animals together all of the time can also lead to reproductive lethargy and decreased breeding success (Gillingham 1987). Therefore, reductions in population densities within enclosures, even if temporary, can offer individuals relief from territoriality, dominance, or persistent mating attempts, which could reduce stress levels and improve welfare. However, it is important that animals transferred to other enclosures, even just temporarily, receive the same welfare-promoting conditions and range of choices.

Social interactions between individuals can elicit a wide range of natural behaviours that may be important for maintaining psychological health or facilitating normal physiological processes. For example, combat can be an important courtship ritual and precursor to copulation as well as the initial step in establishing dominance for many species of reptiles (Weaver 1967; Murphy and Mitchell 1974; Auffenberg 1977; Carpenter and Ferguson 1977; Thompson et al. 1992), where the introduction of new individuals or housing multiple individuals together can stimulate and initiate some of these normal behaviours. Reproduction is another key aspect of an individual's life history, where providing individuals with the opportunity to mate and reproduce (even if eggs or offspring are culled) can provide a more enriched life experience for captives and help satisfy the physiological drive to reproduce. Additionally, although similar studies are currently lacking for reptiles, it has been shown that captive females of several fish and mammal species that were not given opportunities to reproduce experienced reduced fertility and heightened risks for reproductive health complications (Penfold et al. 2014). Therefore, providing

opportunities for reproduction may reduce the likelihood of such complications in captivity.

It has been discovered that some reptiles can learn new behaviours by observing and copying the behaviours of conspecifics (Wilkinson et al. 2010; Kis et al. 2015), suggesting that social learning, at least for some species, may play an important role in cognitive development and the expression of natural behaviours. Group feeding behaviour on large animal carcasses is known for some large reptile species such as Komodo dragons (*Varanus komodoensis*) (Auffenberg 1981; Burghardt et al. 2002) and several crocodylians (King et al. 1998). Through interactions with conspecifics around a shared food resource, dominance hierarchies can facilitate defensive behaviours as well as provide opportunities for younger, subordinate individuals to learn how to interact with conspecifics. Such socialisation and learning could be important for future introductions of conspecifics, especially in species with known histories of aggression and problematic introductions in captivity (see also Doody 2023 and Burghardt and Layne-Colon 2023).

10.8 Evaluating Enrichment

Despite a growing body of literature describing new ways of enriching captive environments, few studies have formally assessed the efficacy of reptile enrichment (Case et al. 2005; Almli and Burghardt 2006; Therrien et al. 2007; Manrod et al. 2008; Rosier and Langkilde 2011; Bashaw et al. 2016; Januszcak et al. 2016; Eagan 2019). Instead, enrichment is often deemed successful simply if the animal responds to the stimulus or interacts with an object and is based largely on subjective or anecdotal criteria (Burghardt 1996). It is important to note that a behavioural response to a new stimulus or interaction with an object does not necessarily equate that it has had an enriching effect on the animal (Newberry 1995) or that it has adequately satisfied some deprivation. Further complicating matters, for reptiles that may not show overt signs of stress or behavioural frustration in response to deprived environments, it may be unclear what their behaviour would look like when provided with vastly improved enriched environments.

Part of the challenge in evaluating the success of enrichment is determining what criteria should be used for gauging success (Alligood and Leighty 2015; Alligood et al. 2017), which will depend largely on the psychobiological profile of a species and the specific goals of the enrichment. For example, if the goal of a particular enrichment program was to provide opportunities for increased activity and the expression of more natural foraging behaviours, were there objectively measurable increases in activity levels or the number of behaviours observed? Similarly, if the goal of enrichment was to diversify opportunities for thermoregulation, did the enrichment lead to measurable changes in thermoregulatory behaviours and increased opportunities to reach their target body temperatures (Fig. 10.1)?

Going one step further, enrichment must also be evaluated based on whether there was any appreciable impact on animal welfare. Reptile welfare can be measured and evaluated in many different ways using physical, behavioural, physiological or

psychological criteria (Warwick et al. 1995, 2013; Martinez-Silvestre 2014; Moszuti et al. 2017); however, it is beyond the scope of this chapter to discuss these measures of welfare. Nevertheless, sufficient evidence for improved biological functioning may include, but is not limited to, increased lifespans, decreased stress levels and abnormal behaviours, enhanced physical condition, holistic reproductive success and inclusive fitness, or a combination of these factors.

10.9 Challenges Associated with Reptile Enrichment

With enrichment becoming so engrained in the day-to-day management of zoo animals, some keepers may become so focused on providing enrichment stimuli to their animals that they overlook crucial elements of husbandry. A prime example of this can be seen with Komodo dragons (*Varanus komodoensis*) and other varanid lizards, a group whose thermal husbandry is frequently mismanaged in captivity (Mendyk et al. 2014, 2016). In zoos, varanids are often provided with a variety of novel objects and scents for stimulation and to increase activity and encourage investigatory behaviours, but at the same time may be physically unable to reach their optimal body temperatures because of insufficient thermal conditions, particularly inadequate surface basking temperatures (Mendyk et al. 2016). In such cases, keepers focusing on providing enrichment stimuli arguably overlook a fundamental physiological underpinning of their biology. As poikilothermic ectotherms, how can such enrichment be properly evaluated when captives are unable to operate at optimal physiological performance? In terms of prioritisation, ensuring that an animal can reach and maintain an optimal physiological state should take precedence over the provision of novel objects and stimuli.

Another challenge seen in zoological parks is that reptile enrichment programs are sometimes initiated without a particular focus, plan of action, or desired outcome, and in some cases, may look to benefit the caretakers rather than the animals themselves (Murphy 2007). Complicating this issue is the general lack of studies assessing the success and appropriateness of reptile enrichment programs using objective measures. Together, these conditions have created situations where zoos and related facilities are commended for their efforts to improve the lives of captive reptiles through enrichment, without knowing if these efforts have truly impacted the animals' well-being. This final point underscores the importance and need for more thorough record keeping (see Mendyk and Block 2023) as well as more evaluative studies of reptile enrichment and welfare.

10.10 Animal Welfare Conclusions

Because captive environments will never reflect the same degree of complexity or variation present in nature, enrichment, as viewed through the lens of controlled deprivation, will always provide opportunities for improving the lives of reptiles in captivity. Efforts to enrich captive environments will fall short if offerings bear little

or no functional or biological significance to a species or if they are lacking in set goals or desired outcomes. Moreover, it is crucial that reptile enrichment programs are evaluated objectively to determine the effectiveness of specific forms of enrichment with specific taxa. By determining what is and what is not effective, keepers can avoid providing folklore husbandry (see Arbuckle 2013; Mendyk 2018; Mendyk and Warwick 2023) and enrichment that has not been scientifically validated. This will undoubtedly require more focused investigations into the deprivations of captivity and their potential effects on various psychobiological processes, as well as further studies that seek to develop additional effective measures of reptile welfare.

We can only provide captives with conditions we are familiar with; therefore, it is crucial for reptile keepers to maintain relevant familiarity with current research on the biology and husbandry of the species under their care and incorporate new information and perspectives into the design and upkeep of captive environments as they become available. To help expedite this process, reptile keepers are encouraged to compile and publish their own observations and experiences, although care must be taken to ensure that this information is presented in an objective manner and within appropriate biological contexts. For reptile keepers who continually work to improve and refine husbandry practices by countering the effects of controlled deprivation, disseminating their results on a global scale will also help enrichment gain greater traction and acceptance within the broader reptile-keeping community, particularly among private herpetoculturists where it is rarely practiced today.

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Effects of Noise and Light

11

Karen F. Mancera and Clive J. C. Phillips

Abstract

Noise is a sound that is unwanted due to its frequency and amplitude, and it may be causally associated with stress. Noise adversely affects both captive and wild animals, including reptiles, whose hearing ranges are particularly sensitive to low-frequency sounds, and they can easily be affected by noise in general. Reptiles are also particularly sensitive to light, because they utilise a broader spectrum than many or most other animals. This is difficult to adequately replicate in captivity. Light can also greatly affect reptiles' physiology and well-being. Light pollution particularly affects foraging behaviour, activity patterns and orientation; hence it is important to maintain an appropriate light environment that considers UV-B and infrared provision in a gradient that allows individuals to behaviourally regulate vitamin D production and temperature. In this chapter, the basic characteristics of reptile sound, noise and light perception are reviewed. Noise and light conditions encountered in captive environments, including transport of lizards for the pet trade, are described, and recommendations are provided to minimise stress caused by noise and inappropriate light conditions.

Keywords

Sound · Light · Noise · Third eye · Stress · Reptile · Captivity · Welfare

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11.1 Introduction

Reptiles are commonly kept in zoological institutions, laboratories and households, where they are exposed to anthropogenic noise and light. In addition, noise and light are also related to transportation and a variety of human disturbances associated with reptile husbandry and the technology used in their captive environments. Because avoiding noise and to some extent, light is not an option for animals in confinement or for those confined to specific locations in the wild, understanding the effects of sound and light on reptiles is important. Therefore, this chapter aims to review the effects of noise and light on reptiles, and to discuss some possible strategies to decrease the stress that is associated with these stimuli.

11.1.1 Basic Characteristics of Sound and Noise Perception

Sound is a mechanical wave that travels on an elastic medium in a simple harmonic motion (Blauert and Xiang 2009; Franklin et al. 2010). When energy is applied to particles in a medium, a mechanical sound wave is created, and the particles will travel from one side of the initial equilibrium point (where acceleration is zero) to the opposite side (the point of maximum displacement of particles) and back, for an indefinite amount of time; this process generates oscillations or cycles. The number of cycles per time interval in the sound wave is called frequency. The maximum displacement of the particles from the equilibrium point is called amplitude (Franklin et al. 2010).

The sound wave's frequency (measured as number of cycles per second or Hertz [Hz]) is correlated with the perception of pitch; the higher the frequency (that is, the greater the number of cycles per second), the higher the perceived pitch. Despite this relationship, frequency is an objective, measurable wave property, whereas pitch only describes the subjective, psychological impression of frequency. The amplitude (measured as the logarithm of the intensity of the smallest pressure change that can be detected by the human ear [20 μ Pa] or 0 decibels [dB]) determines the sound wave's intensity, which is perceived as loudness (Haughton and Feth 2002; Franklin et al. 2010).

Sound waves trigger the subjective sensation of hearing (Haughton and Feth 2002), and they need to have enough intensity and be of a specific frequency to be detected by the listener (Franklin et al. 2010). As an example, the hearing range for humans has been established to lie between 0.2–20 kHz at 60 dB SPL (Heffner and Heffner 2007). Therefore, mechanical waves travelling through the air with these characteristics are perceived as sound by humans (Haughton and Feth 2002; Drosopoulos and Claridge 2005). Soundwaves falling outside this frequency range are considered infrasound (below 20 Hz) or ultrasound (above 20 kHz) and are inaudible to humans (Franklin et al. 2010); however, other animals are able to hear them. For example, the house mouse (*Mus musculus*) possesses a hearing range between 2.3 kHz and 92 kHz at 60 dB SPL (Heffner and Masterton 1980; Heffner and Heffner 2007) and can perceive ultrasounds but not the low-frequency sounds.

Reptiles are generally able to hear low-frequency sounds between 0.2 and 2.2 kHz and sometimes higher, such as the Australian sleepy lizard (*Tiliqua rugosa*), which has a hearing range between 0.2 to 4.5 kHz (Köppl and Manley 1992). As well as the hearing range, the interaction between an individual's frequency sensitivity and amplitude determines their perception of sound; for healthy individuals, mechanical waves that fall outside the estimated frequency hearing range can still be perceived as sound if the amplitude is high enough, making individual variation an important factor (Berglund and Hassmén 1996; Pater et al. 2009).

The best hearing sensitivity, determined from auditory brainstem responses, is extended over a wide range in lizards, more than in most bird species (Brittan-Powell et al. 2010). However, it should be noted that hearing thresholds are highly dependent on the measurement methods used and the methods of surgical preparation (Manley 2000). Human amplitude measurements use an A-weighted decibel scale (dB [A]), which corrects for human sensitivity, that is, the range of frequencies humans hear best (2–4 kHz) (Haughton and Feth 2002; Franklin et al. 2010). There are no decibel weighting methods that consider such frequency sensitivity in reptiles, partly because it requires detailed research into the hearing capabilities of each species (Voipio et al. 2006; Pater et al. 2009).

Despite the importance of acoustic cues, when sound becomes unwanted by the receiver, it is considered noise and is associated with frustration and stress (Maling 2007). Noise has three main characteristics that determine its potential to irritate the listener: intensity, complexity and degree of non-linearity. Increased intensity is the result of a greater amplitude and indicates that there is more energy contained in the sound wave, which activates hearing structures with greater strength and power, producing discomfort if concentrated within the receiver's frequency sensitivity (Cone and Hayes 1984). Complex sounds, particularly those with intricate mixtures of sounds, produce discordant mixed frequencies with excessive complexity, which are more aversive than pure tones at a single frequency (Cone and Hayes 1984). Non-linearity is the presence of unsynchronised sounds, such as hissing and clicking, forming acoustic cues with unpredictable components. Non-linear sounds are often related to distress and alarm calls, producing aversive behavioural responses (Fitch et al. 2002; Redon et al. 2006; Blesdoe and Blumstein 2014).

The perception of sound as noise depends on the frequency range, amplitude, complexity and predictability of the soundwave, making the perception of noise a subjective experience. However, once perceived, noise may result in deleterious effects in captive animals, such as increased activity of the sympathetic nervous system, the hypothalamic–pituitary–adrenal (HPA) axis and the cardiovascular system (Anthony et al. 1959; Henkin and Knigge 1963; Ames 1978), as well as suppression of the reproductive and immune systems, damage to the cochlea and related hearing structures, increased metabolism and DNA damage (Swaddle et al. 2015). Unfortunately, to this date, there is no research investigating if reptiles are also affected in the same ways as other animal groups. However, their hearing range and sensitivity indicate they are aware of noise disturbance at certain frequencies, making noise stress a clear possibility for them.

The little amount of research addressing the effects of aversive auditory stimuli on reptiles could be attributed to the fact that most research on the effects of anthropogenic noise on animals has focused on amphibians, birds and marine mammals, disregarding animals that are not obviously vocal or charismatic, such as reptiles (Shannon et al. 2015). The assessment of the effects of noise on reptiles is also made more difficult by their diverse hearing anatomy, which results in a wide variety of auditory abilities amongst reptile orders (Dooling et al. 2000).

11.1.1.1 Hearing Ranges and Effects of Anthropogenic Noise on Different Orders

The auditory apparatus for reptiles has major differences between species, particularly in the middle ear and cochlea (Kaplan 2002; see also Crowe-Riddell and Lillywhite 2023; Lillywhite 2023). Those that can hear, which includes most lizards, have a tympanic membrane, usually located at the back of the head, either superficially or at the end of a short canal, which transmits sound through the middle ear via the stapes (a small bone, alternatively known as the columella) to the inner ear. This is a combination of semicircular canals (for balance) and the cochlear duct (for hearing). The latter is filled with perilymphatic fluid, through which vibrations travel to the macula lagenae, a cluster of sensory cells from which the sensation of hearing occurs. The lagenae have cilia embedded in a membrane within the cochlear duct, and in lizards, free-standing hair cells, which are believed to enable them to hear high-frequency sound (Manley and Köppl 2008). Despite this, reptiles generally have a weaker awareness of high-frequency sounds than birds (Manley 2000). The lagenae also connect to the auditory (VIIIth cranial) nerve, which transmits sound signals to the brain. This nerve bifurcates, leading to two auditory nuclei, which code for different characteristics, sound timing and amplitude. Binaural comparisons are particularly strong in lizards, facilitating prey detection.

Snakes do not have a tympanum, but they do possess a stapes bone, which receives vibrations travelling through the ground, and it is likely that airborne (Christensen et al. 2012) and waterborne (Chapuis et al. 2019) vibrations are also perceived. Crocodiles, turtles and most lizards (except those living subterranean lives, in which case they respond to vibrations) all have well-developed hearing apparatus.

Research of the auditory brainstem response by Brittan-Powell et al. (2010) found that the audiograms for alligators and lizards both show similar sensitivity at and below 1 kHz to that of birds (budgerigars and screech owls), or it may be slightly higher for the reptiles, which probably reflects the similar organisation of their auditory apparatus—unidirectional hair cells covered by a membrane. Above 1 kHz, the sensitivity threshold for alligators is consistently higher than for geckos and the birds tested. The evolution of additional high-frequency hair cells in most lizards may have increased their sensitivity at these frequencies. However, behavioural thresholds have not been measured in most reptilian species (Brittan-Powell et al. 2010).

The hearing organs of turtles, tortoises and tuataras have not changed since Palaeozoic times, and they constitute a basal blueprint for the reptilian ear and its hearing capabilities (Manley and Clack 2004). Tuataras (*Sphenodon punctatus*) are

represented by one species and two subspecies found only in New Zealand, with hearing sensitivity and peak responsiveness of 0.1–0.9 and 0.2–0.4 kHz, respectively (Gans and Wever 1976). Testudines are believed to have similar auditory capabilities; for example, the hearing range of the red-eared turtle (*Trachemys scripta*) lies between 0.6 and 0.8 kHz at 60 dB SPL (Patterson 1966) and the desert tortoise (*Gopherus agassizii*) from 0.2 to 0.8 kHz (Bowles et al. 1999). Hearing frequencies in turtles are estimated to be around 0.5 to 1 kHz at 60 dB SPL (Dooling et al. 2000), which is probably correct for all testudines due to the anatomical similarity of their hearing structures.

There is little research addressing the effects of noise on tuataras or testudines. A study evaluating the effects of sound emitted by subsonic (peak amplitude 126 dB cumulative sound exposure level) and supersonic (ten simulated 25 psf sonic booms) aircraft noise on the desert tortoise found that, at the highest level of exposure, some animals experienced transient (c. 1 hour) temporary threshold hearing shifts of +5–20 dB SPL, but there were no permanent effects. However, it was predicted that the effects might become permanent if tortoises were exposed to this noise over a number of years (Bowles et al. 1999). The tortoises' mean hearing threshold was approximately 34 dB SPL, with a range of 20–50 dB SPL. The most common response was 'freezing' for approximately 2 hours, followed by head withdrawal. Furthermore, it is likely that tortoises and other reptiles with similar hearing capabilities can perceive noise generated by non-destructive military operations such as vehicles off-road, uncontrolled dogs or discharge of firearms, because the frequencies for this form of human-generated noise closely overlie their hearing range (Tracy et al. 2004). Noise generated by a seismic airgun has been shown to induce dive responses in loggerhead turtles, indicating an avoidance response to the sound (DeRuiter and Doukara 2012).

In the case of snakes, although commonly thought to be deaf, these members of the order Squamata can actually hear sounds within a frequency range of 0.1–0.5 kHz (Dooling et al. 2000; Young 2003). To date, there have been few studies addressing the effects of anthropogenic noise on snakes. When Young and Aguiar (2002) exposed western diamondback rattlesnakes (*Crotalus atrox*) to a synthesised tone of 0.2–0.4 kHz at 65–75 dB SPL in an acoustic chamber, animals significantly ceased body movements, and reduced or ceased tongue flicking, and displayed rapid jerks of the head and rattling, proving that snakes can respond behaviourally to sounds at these frequencies. Because most noise associated with human occupancy is highly energetic at low frequencies, snakes and lizards are likely to be negatively affected by high amplitude anthropogenic noise, and this has been pointed out by studies where reptiles elicit behavioural reactions when exposed to wind turbines, human-made noise in protected natural areas and in laboratory settings where open-cast mining noise is broadcasted (Roberts and Roberts 2009; Barber et al. 2011; Mancera et al. 2017). Therefore, it is paramount to understand how noise at audible frequencies for reptiles can trigger the stress response and affect reptile physiology, both in captive and wild environments.

Lizards, which are also members of the order Squamata, have optimal hearing range frequencies between 1 and 3 kHz (Saunders et al. 2000; Christensen-Dalsgaard 2005). Most lizards' hearing ranges are between 0.1 and 5 kHz

(Manley 2000), despite the great variability in the anatomy of lizard hearing structures (Köppl and Manley 1992; Popper and Fay 1997). For example, the tokay gecko (*Gekko gecko*), a highly vocal species with a complex vocal apparatus producing chirrups, barks, clucks and whistles (Brittan-Powell et al. 2010), is able to hear sounds between 0.5 and 5 kHz. Its optimal hearing frequency is 0.7– > 2 kHz, hence sounds at these frequencies will be perceived at low intensity (20 dB SPL) (Köppl and Manley 1992). In the gecko, the highest sensitivity appears to coincide with the fundamental frequency of their advertisement calls (Brittan-Powell et al. 2010). However, anoline lizards have a more extended high-frequency range, despite many species not being vocal (Brittan-Powell et al. 2010). Anatomically, lizards have auditory nerve fibre responses to sounds as low as 5 dB, much less than those generating behavioural responses (Manley 2000; Brittan-Powell et al. 2010).

To date, the effects of noise on lizards have been reported in very few species. Mining machinery noise at high frequencies (above 2 kHz) generates stress-related behaviours in the blue-tongued skink (*Tiliqua scincoides*), such as lateralisation of head movements and freezing (Mancera et al. 2017). Likewise, off-road vehicle noise (dune buggies) below 3 kHz induced hearing loss in the Mojave fringe-toed lizard (*Uma scoparia*) (Brattstrom and Bondello 1983).

Members of the order Crocodylia possess optimal hearing frequencies between 0.2 and 1 kHz (Dooling et al. 2000). Despite their presence in areas with anthropogenic influence and captive environments, there is no data addressing the effects of noise on these animals; nevertheless, it has been previously suggested that noise produced by motor boats may be a reason for reductions in crocodile populations in areas shared by human recreational activities (Mohammed 2017).

11.1.1.2 Characteristics of Noise in Captivity and Possible Noise Control Measures

Reptiles are regularly present in captive environments with acoustic stimuli that could be aversive to them. Noise in animal facilities comes from technical devices (air conditioning systems, fans), husbandry procedures (opening and closing doors, cleaning cages, human speech) and vocalisations of neighbouring animals and their own (for evidence in rats, see Castelhana-Carlos and Baumanns 2009). There is extensive research on the noise sources encountered in laboratory facilities, and these findings could be qualitatively related to the effects of auditory input in other captive environments where reptiles are found, such as zoos and aquaria, pet stores and people's homes. Captive environments where reptiles are on public view are likely to experience even higher noise levels than laboratories.

Ventilation systems, also present in many animal-holding areas, including laboratories, typically generate noise up to 55 dB at its highest intensity (Pfaff and Stecker 1976). Equipment associated with cleaning and husbandry activities produces noise with frequency spectrums between 10 and 100 kHz; the quietest sound being attributed to automatic flushing systems in cages (55 dB) and the loudest associated with a vacuum cleaner at 1 m distance (70 dB). Other sounds include cleaning activities, such as wiping glass walls, sweeping the floor or filling

metal containers with food, which also have a broad frequency spectrum (10 to 100 kHz) and amplitudes between 70 and 80 dB (Sales et al. 1999).

The variety of systems and materials used in captive environments generates a broad frequency spectrum of environmental noise. When sound levels were recorded in ten animal laboratory facilities for different rodent species, during working days, noise intensity reached a maximum of 90–100 dB in the frequency range of 0.01 Hz to 12.5 kHz and 70–85 dB in the range of 12.5–70 kHz, indicating that noise generated by animals was minimal and that most acoustic disturbance could be attributed to human activities (Milligan et al. 1993). Likewise, when ambient noise levels for three frequency spectrums were recorded in San Diego Zoo daily for 4 years, frequencies between 0.01 and 0.06 kHz were recorded at an amplitude of 52.3 to 75.4 dB, those between 0.12 and 0.5 kHz reached 45.5 to 71.5 dB and those between 1 and 16 kHz reached 33.1 to 65.7 dB (Owen et al. 2004).

Reptiles in pet stores will, additionally, be exposed to the noise produced by other animals. When the decibel levels of barks from 24 dog breeds were measured at 3 m from the source to microphone, barking amplitude reached 85–122 dB (Kay 1972; Van der Heiden 1992). Animals exposed to continuous sounds at moderate to high levels (80–100 dB) with unchanging intensity, such as in laboratories, may be at risk of hearing loss due to mechanical or metabolic impacts (Peterson 1980; Sales et al. 1999). Therefore, it is quite possible that reptiles exposed to continuous noise in captivity experience hearing loss if the amplitude is high enough, at frequencies between 0.4 and 5 kHz, which are within most reptile's hearing ranges. This observation, however, is not a final conclusion, because to date, hearing loss in captive or wild environments for reptiles has not been demonstrated. Research on this specific phenomenon should be a priority to reduce noise stress and improve reptile welfare.

In addition to continuous auditory input, environmental noise in animal facilities is associated with irregular pronounced peaks (Sales et al. 1999). For both human and non-human animals, impulsive sounds (sudden, brief sounds of high amplitude) are more damaging than continuous sounds at moderate high levels (Peterson 1980). Impulsive and unpredictable noise (i.e. that which is complex and non-linear) can rapidly affect animals; sounds of short duration (2–10 seconds) at high amplitude can produce deleterious effects, such as sound-induced convulsions in rodents (Gamble 1982). These effects are associated with General Adaptation Syndrome, that is, the nonspecific set of responses to stressors consisting of an alarm reaction, a stage of resistance, and a stage of exhaustion (Selye 1946; Baffy 2017). Captive reptiles can be exposed to impulsive sounds, such as a dog barking, during display in pet stores, zoos, laboratories and households, thus being at risk of developing diseases related to stress. It is worth noticing that, even though impulsive sounds are considered damaging, this does not mean that continuous noise is not deleterious (as explained earlier in this chapter), but rather that impulsive sounds could cause more immediate effects, especially when combined with a continuous noise background. In this regard, it has been shown that when many negative stimuli are combined, a stronger physiological response is generated, which can carry consequences such as the proliferation of inflammatory factors, which increase

sickness behaviours in acute illness (Deak 2007). Many anthropogenic noises are combinations of continuous and impulse sounds, such as mining noise (combination of machinery and sudden blasting) or traffic noise (constant motor noise and intermittent horns).

Given the characteristics of noise in captive environments, including the majority of these sounds being located in the lower parts of the frequency spectrum (Milligan et al. 1993), overlapping with the hearing range of most reptiles (Dooling et al. 2000), it is fair to assume that most reptiles, whether in zoological institutions, laboratories, pet stores or households, will be able to hear environmental noise. This is likely to produce behavioural and physiological effects similar to those encountered in animals experiencing anthropogenic noise in the wild. Therefore, maintaining quiet environments for reptiles in captivity is essential; however, to date, noise control protocols are not always publicly available, and if they are, they may not be followed (Warwick et al. 2018).

Despite a lack of guidelines, there are some basic practices that should be followed if the information available on the husbandry of other captive species is used. For example, Voipio et al. (2006) measured the noise inside rat cages in laboratory facilities whilst performing husbandry procedures in both a calm and hurried style. They found that hurried work amongst steel cages produced sound levels exceeding 90 dB (R, i.e. decibels weighted for rat hearing, 10–15 dB below human hearing). Unhurried calm work produced lower sound levels in many procedures (about 10–15 dB [R]). Likewise, working with polycarbonate cages instead of steel reduced noise by 10–19 dB (R) and pouring food in the feed hopper inside the cage was louder if measured directly in the cage than when measured in an adjacent cage by 17 dB (R). From this study, there were four recommendations that can be applied to the improvement of the acoustic environment of captive reptiles: 1. calm work is preferred to avoid excessive noise; 2. materials such as polycarbonate should be favoured above other materials that produce intense handling noise; 3. food and enrichment should be placed in reptiles' enclosures in the quietest way possible, and; 4. noise control measurements should be based on the hearing range of the specific reptile (turtle, crocodile, lizard, snake or tuatara).

Another potential noise control measure that needs to be explored is the use of other sounds to mask disturbing environmental noise for reptiles. For example, music (Adagio by Herbert Von Karajan below 40 dB, 5 hours daily for 8 days) has been shown to reduce metastaticity in cells of rats exposed to a fire alarm bell (1 to 3 hours, 60 times / 5 s at 100 dB), which was attributed to a reversal of the immune suppression produced by noise stress (Núñez et al. 2002). It is possible that using music at meaningful frequencies to mask irritating auditory input for reptiles could have similar effects on their immune system and increase their comfort, but research in this area would be necessary to make sure music is not a disturbance for reptiles and to determine in which circumstances the use of music would be appropriate. Another method to improve the reptile acoustic environment is the use of devices designed with consideration of their hearing abilities in mind; for example, Clough and Fasham (1975) designed a 'silent' fire alarm, taking into account the hearing range of rodents and humans. With the use of pure tones between 0.43 and 0.47 kHz

at 97 dB (C), they were able to produce sound below the optimal hearing of rodents yet sufficient for human purposes. A silent alarm for reptiles would be effective by generating sound impulses that avoid high intensities at frequencies between 0.1–5 kHz. Similarly, the use of low-frequency damping materials, such as soundproofing foam and clear plastic curtains in enclosures, is an option that could increase reptile welfare and health, justifying the cost. It is also worth mentioning that the use of these materials depends largely on the budget available in laboratory or zoological facilities, as well as on practical issues such as the difficulty that zoo visitors may have observing animals on display due to plastic barriers or the added difficulty that a curtain may add to access animals in laboratory settings. Research in this area is necessary to successfully apply and model these recommendations to specific contexts.

Temperature can influence reptile hearing and therefore welfare. Reptiles exposed to suboptimal temperatures have reduced hearing sensitivity (Dooling et al. 2000), making them potentially unresponsive to important acoustic cues, such as conspecific calls or sounds associated with live prey. Temperature is specifically important for pet reptiles; however, not all carers know the specific needs of their animals. In addition, laboratory and zoological facilities with poor budgets and/or information on reptile welfare would need more support to reach international animal care standards inclusive of the impact of noise on captive reptiles.

11.1.1.3 Sound and Vibrations

Although this chapter is partially focused on reptiles' sense of hearing, we consider that it is important to mention the significantly overlapped phenomenon of vibration. As mentioned by Hill (2008), vibrations can be airborne (sound waves are airborne vibrations), waterborne or substrate-borne because they all represent particle motion in a fluid or elastic body; however, although the perception of sound and other types of vibration can be simultaneous and inter-reliant, their perception is mediated by strikingly different mechanisms, making vibrations a topic of its own with different implications than those of sound. This section will briefly describe the terms 'airborne vibration' and 'substrate-born vibration' and their relationship with sound and hearing. It should be considered only a brief introduction to a much more complex topic, which needs to be explored thoroughly in the future.

The mechanical waves that create the hearing experience are known as airborne vibrations. When they stimulate hearing structures, they are processed by the nervous system as sound; however, when these mechanical waves are unable to stimulate hearing structures, they remain as airborne vibrations, which can still be perceived as a vibrotactile experience, but are not heard. In humans, sounds below 20 Hz are typically inaudible; however, they are still noticed when they pass through the human body (Alves-Pereira and Castelo Branco 2007). Likewise, reptiles perceive airborne vibrations, which may be used to search for prey, for example, by the royal ('ball') python (*Python regius*), the sand viper (*Cerastes vipera*) and the sandfish lizard (*Scincus scincus*) (Wever 1978; Hetherington 1989; Young and Morain 2002; Young 2003; Christensen et al. 2012). Airborne vibrations could potentially impact reptile welfare; because airborne vibrations are used to catch

prey, they could stimulate excessive foraging, which may be maladaptive and energy-wasting. Furthermore, in humans, infrasound can cause a series of symptoms classified as vibroacoustic disease (Alves-Pereira and Castelo Branco 2007) and it is possible that other animals experience similar effects when airborne vibrations are present. However, this remains unknown, because research in airborne vibrations and reptiles is scarce.

Airborne vibrations can also elicit substrate vibrations when the mechanical waves travelling through the air are induced in elastic solids (Hill 2009). Substrate vibrations are also produced by reptiles by vibrating their bodies, for example, on a leaf or soil (Barnett et al. 1999; Young 2003), that is, without interaction with airborne waves. Although substrate vibrations and airborne vibrations are intimately intertwined, substrate vibrations are a unique communication channel in its own right, with specific structures to produce and receive these stimuli that are present even before hearing structures; furthermore, substrate vibrations are perceived in the nervous system through different mechanisms unrelated to hearing (Hill 2008). Thus, substrate vibrations are a complex topic that deserves separate exploration; however, because they can be elicited by sound, it is important to acknowledge that their induction in walls, floors or any other contact surfaces in the reptile habitat can produce detrimental effects. In turtles (*Pelodiscus sinensis*) exposure to vibrations in their tank for 30 min at 2 h intervals over 28 days, produced elevated corticosterone and renal abnormalities, which consisted of damaged epithelium of podocytes (cells surrounding the inner layers of Bowman's capsule within the kidney, essential for blood filtration), as well as tissue damage, vacuolation and destruction of the renal tubules (Hur and Lee 2010). In addition to direct vibrational damage, some chameleons of the genus *Brookesia* are known to produce substrate vibrations as a stress response (Raxworthy 1991). Therefore, the vibrations induced on the floor or shelves where captive reptiles are housed, whether induced by sound or not, could greatly affect their welfare and special attention should be placed on keeping reptiles on non-damped, vibrating, surfaces. To date, there appears to be no research regarding the effects of externally induced substrate vibrations on reptile welfare. Studying this phenomenon separately to sound and other communication strategies is paramount to fully understand its role in the lives of reptiles.

11.1.2 Basic Characteristics of Light Perception: Special Characteristics

Reptiles, unlike humans, are highly perceptive to electromagnetic radiation. Whereas most mammals have two different types of cones (cells responding to different light wavelengths) and humans and primates three (trichromats), all reptiles are probably at least tetrachromats, because they possess a fourth cone sensitive to UV-A light (320–400 nm) (Bowmaker 1998; Brames 2007; see also Arena et al. 2023; Crowe-Riddell and Lillywhite 2023; Lillywhite 2023). Turtles may even be pentachromatic (Perlman et al. n.d.). The presence of these different cone types implies that colour vision is present in all reptiles. As well as UV-A, UV-B light (290–315 nm; not visually perceived) is received through the skin and is important

for the immune system and the synthesis of vitamin D₃, which can be essential for calcium metabolism. The transformation of previtamin D₃, which is produced in the skin on exposure to sunlight, to vitamin D₃ is temperature dependent. Vitamin D₃ produced in the skin is much longer-lasting in the body than dietary sources of vitamin D₃; therefore, UV light is important for reptiles (Watson and Mitchell 2014).

An important characteristic of reptile vision is the presence of coloured oil droplets, which selectively filter light and modify photoreceptor sensitivity (Douglas and Marshall 1999). These are located in the inner segments of the cone cells and selectively absorb light before it reaches the visual pigment housed in the cone outer segments (Goldsmith 1991). They are present in many diurnal lizards and turtles but not in snakes and crocodiles (Walls 1942). Oil droplets improve colour vision of diurnal animals by improving colour discrimination with increasing light, reducing chromatic aberration and glare, as well as serving as UV protection for the cone cells' photosensitive outer segments (Douglas and Marshall 1999; Vorobyev 2003).

Many lizard species (Order Squamata) and the New Zealand tuatara (Order Sphenodontia) possess a photoreceptor called the reptilian third eye or parietal eye, associated with the pineal gland (which is present in almost all vertebrates; for details in crocodiles, see, Firth et al. 2010) (Fig. 11.1). The parietal eye comprises

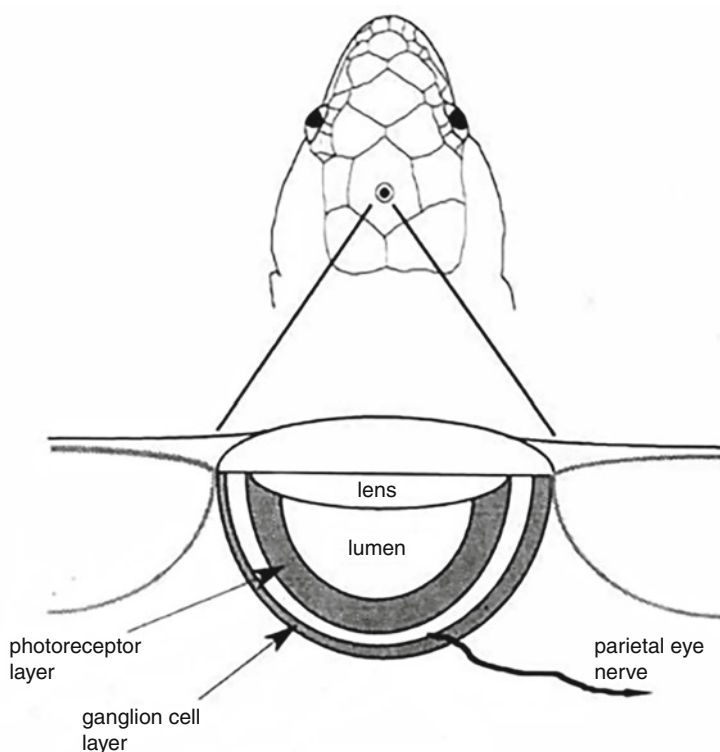


Fig. 11.1 Parietal or third eye of reptiles (from Solessio and Engbretson 1993)

a lens and retina, with photoreceptors and ganglion cells, leading to the parietal nerve, and is located in-between the parietal skull bones. It synthesises melatonin in the dark, but in lesser quantities than the pineal body. Parietal cells have high sensitivity to wavelengths of 650–700 nm. This third eye is used for thermoregulation and sun compass orientation. The parietal eye provides information on photoperiod, scotoperiod and blue light intensity, all of which can be used to regulate activity cycles and rhythms, including cues for reproduction (Bertolucci and Foa 2004; Brames 2007).

Many of the same photopigments used for colour vision in the eye are also present in the skin of reptiles. This feature is particularly important for animals that change their colouration by dispersion of pigments within the skin's chromatophores. Chromatophores have the capacity to absorb short wavelength by the surface yellow-coloured xanthophores, scatter light in the intermediate iridophores (which are silvery and iridescent) and absorb or reflect long wavelength light in the basal melanophores. By aggregating or dispersing these pigmented processes, reptiles can manipulate their skin colour to match that of their background (Kelley and Davis 2016).

The motile nature of chromatophores can affect rapid change in colour, whereas slower changes can be created by selective production of pigments. By this mechanism, the skin colouration can be directly attuned to the colouration of the background environment, thereby facilitating camouflage, thermoregulation and social signalling. The sensory mechanisms are light-sensitive pigments in the skin, because reptiles whose eyes have been covered still initiate colour changes to match their background (Kelley and Davis 2016).

11.1.2.1 Light Perception and Effects of Light Disturbance on Various Orders

In addition to the complex light utilisation and perception systems in reptiles, different orders possess additional characteristics that influence their behaviour in relation to the electromagnetic spectrum. For example, in the order Testudines (turtles and tortoises), painted turtles (*Chrysemys picta*) and red-eared turtles (*Trachemys scripta*) possess visual receptor cells that are sensitive to red light at high and blue at low intensities (Cooper and Greenberg 1992). This characteristic has also been reported for sea turtles, for whom light perception is crucial for survival, because females and hatchlings can become disorientated by the presence of lights on the seashore (Mohan-Gibbons and Norton 2010). Increased sensitivity and attraction to blue and green light have been observed in the green sea turtle (*Chelonia mydas*), showing a preference for short wavelengths that is related to the ability of hatchlings to reach the water in the dark (Carr and Osovsy 1967).

Similarly, hatchling loggerhead sea turtles (*Caretta caretta*) are attracted to short wavelength visible light sources, with an aversion to yellow light. This suggests that special lighting systems, such as low-pressure sodium vapour luminaires that emit only yellow light, could be used to prevent hatchlings from moving towards the dunes and orientate them towards the sea (Witherington and Bjorndal 1991). Recommendations are to keep light off the beach by repositioning or shielding

light sources, reducing luminance and minimising disruptive wavelengths by using sodium luminaires (Teikari 2007). Likewise, the use of red light whilst handling sea turtles and other nocturnal reptiles in zoo enclosures is a common practice to avoid light disturbance, because they are less attracted to wavelengths above 580 nm (Barschel et al. 2013). It has been suggested that turtles are also guided to water through their perception of polarised light (light waves in which the frequencies occur in a single plane). Although this remains to be further evaluated, it could be relevant for conservation, because polarised light generated by plastic bottles may represent a problem for turtles trying to catch prey, such as jellyfish and ctenophores, which also emit this kind of light (Yeomans 1995; Horváth et al. 2009).

In the order Squamata, artificial light sources can be an important factor affecting snake behaviour and survival. For example, the racer snake (*Alsophis portoricensis*) forages at night to catch a normally-diurnal anole attracted to artificial lighting (Perry et al. 2000; Henderson and Powell 2001); likewise, the normally-nocturnal house snake (*Boaedon capensis*) will forage under artificial light (Cunningham 2002). Although the presence of artificial light can increase predator success, laboratory experiments have found that altering lighting regimes can affect the interaction between temperature and hormones in reptiles (Firth et al. 1999). Thus, there is a potential welfare risk for diurnal snakes that extend their activities to later hours of the day due to artificial lighting in enclosures and for nocturnal snakes to reduce their prey success and threaten their survival when attracted to hazardous light sources.

Additionally, some snakes have the ability to perceive infrared light. Snakes from the groups Boidae and Viperidae use infrared sensors called pit organs. In the group Viperidae, only the pit viper (Crotalinae), not the common viper (Viperinae), these organs (Molenaar 1992). Although the pit organs are similar in these snake groups, important anatomical differences in this organ reflect different infrared sensitivity. For example, the ability of the western diamondback rattlesnake (*Crotalus atrox*) to detect infrared radiation is unmatched amongst snakes. The pit organs in these rattlesnakes are located between the eyes and nostrils of each side of their face, where hollow chambers accommodate the pit membrane that serves as an infrared antenna. The pit membrane is highly vascularised, rich in mitochondria and houses a high number of innervations of primary afferent nerve fibres of the somatosensory system. These fibres send infrared signals to the opticum tectum of the brain, where they converge with the information of other sensory systems. In contrast, non-venomous pythons have labial pit organs distributed over their snout and lack the complex architecture seen in vipers, making them 5 to 10 times less sensitive to infrared signals. The labial pit structures are similarly vascularised and innervated by nerve fibres, but at lower densities (Gracheva et al. 2010).

Pit organs help monitor infrared emissions in the environment and are essential when detecting and attacking prey, because they help assess features of objects and relative distances (Molenaar 1992). However, this ability can be hindered by the presence of artificial infrared sources. For example, western diamondback rattlesnakes detect rodent prey more effectively when the prey item is positioned in front of a cold background than a warm background (a disk warmed up with an artificial heater) (Theodoratus et al. 1997). Therefore, it is possible that artificial heat

sources, such as lights, machines and heaters could affect the survival of infrared-sensitive snakes by stimulating unnecessary and energy-consuming predatory behaviours in captive enclosures where food is readily available.

Some lizards possess special light perception features. For example, geckos and some other lizards have pinopsin, a non-visual photoreceptor pigment associated with the pineal gland, which is involved in the control of different circadian rhythms such as locomotor activity, temperature and behavioural thermoregulation (Bertolucci and Foa 2004). Geckos, unlike all other reptiles, lack rods (photoreceptor cells for low light intensity), but have very sensitive cones that are larger and more 'rod-like', thus providing night colour vision in dim light (Roth and Kelber 2004).

Lizards can be disturbed by artificial sources of light. For example, geckos are attracted to light traps designed to trap insects (Savage 2002). The gecko (*Sphaerodactylus macrolepis*) and nine species of lizard from the genus *Anolis* forage under artificial lighting (Henderson and Powell 2001). Although light pollution can have an initial beneficial effect on foraging success, any extension of the light cycle can affect their hormonal responses and have potential negative effects of disruption of orientation (Teikari 2007).

Unlike other reptiles, the order Crocodylia lacks a pineal complex, including the pineal gland. Their circadian rhythm is exercised through the secretion of extrapineal melatonin (the hormone secreted by the pineal that regulates the sleep-wake cycles), which is stimulated through environmental light (Sorenson 1894; Quay 1979; Roth et al. 1980; Firth et al. 2010). There is little information on the effects of light disturbance on crocodylians. Perry et al. (2008) argue that this lack of knowledge is attributable to their low abundance in urban areas (with the exception of Florida, USA, and Darwin, Australia) and the perception of these animals as human safety concerns; however, because most crocodylian species are threatened and their distributions are increasingly overlapping with urban areas, research on the effects of light pollution in this area is urgently needed.

11.1.2.2 Characteristics of Light in Captivity and Possible Light Control Measures

Because reptiles are highly receptive to light and depend, to a greater or lesser extent, on natural light for their survival, it is difficult to fully replicate their lighting needs in indoor enclosures. Those that naturally bask in sunlight need more light than those that naturally rest in the shade during the day (Baines 2019). Likewise, suitable brightness and contrast are needed for appropriate motion perception and foraging (Brames 2007), and to maintain an appropriate day/night lighting regime to avoid disruptions in the circadian rhythm. Circadian rhythms rely on glucocorticoid release to determine activity patterns in animals; peak glucocorticoid levels occur towards the end of the scotoperiod in diurnal animals, and in nocturnal animals, they occur towards the end of the photoperiod (Mormède et al. 2007). Simple tasks such as transferring reptiles to a new cage or cleaning their enclosure can cause arousal, disruption of glucocorticoid release, and circadian rhythm disturbances (Webb et al. 2010).

In reptiles, circadian rhythms are determined by light and, to a lesser extent, temperature (Oishi et al. 2004). Species such as the desert iguana (*Dipsosaurus dorsalis*) release corticosterone in response to circadian rhythms of light (Chan and Callard 1972). Therefore, in order to preserve appropriate activity levels and energetic balance in reptiles, the maintenance of appropriate light regimes is paramount to avoid welfare problems. Although not specifically studied in reptiles, for other animals, such as the brown kiwi (*Apteryx australis*), artificial light is reported to cause long-term desynchronisation of circadian rhythms and health problems (Berger 2011).

In terms of environmental perception, short electromagnetic waves are part of UV perceptive animals' colour space, which is necessary for optimal observation of their surroundings (e.g. in birds, Cuthill et al. 2000). Therefore, an appropriate UV light spectra and colour rendering of artificial light corrected for the reptile eye is necessary for conspecific, intraspecific and intersexual recognition (Brames 2007). In addition to its relevance for colour perception, UV lighting is vital for reptile welfare, with deficiencies or excesses of UV-B resulting in bone disorders in chameleons (Ferguson et al. 2010) and poor reproductive success in egg-laying vertebrates (Watson and Mitchell 2014). Regulation of UV-B intake is achievable through variation in basking times, which may respond to vitamin D level in the diet. Because there is little information on UV-B reception by reptiles in the wild, an adequate provision of a gradient of UV-B in captive enclosures should be used to allow reptiles to choose their required level (Baines et al. 2016; see also Arena and Warwick 2023).

In addition to the provision of a gradient, choosing the appropriate source of UV-B light is important. Incandescent bulbs provide mostly red and yellow light, lacking the short wavelength end of the spectrum (Adkins et al. 2003). Fluorescent tubes specially manufactured for reptiles can produce significant, but not dangerous amounts of UV-B light, and are increasingly recognised as sufficient to sustain healthy vitamin D levels in at least some lizards (Ullrey and Bernard 1999; Ferguson et al. 2002; Aucone et al. 2003). Mercury vapour and metal halide lamps emit significant infrared radiation, as well as UV and visible light (Baines et al. 2016), and they appear to be the best choice for reptiles from temperate, tropical and desert habitats, whereas fluorescent lights are recommended for montane species (Greene 2003).

Due to the plethora of light sources and the necessity for a UV gradient, four zones of UV-B exposure have been suggested, based on UV- index measurements that assign a UV-B requirement to 254 reptile species. These Ferguson Zones (Ferguson et al. 2014) allow any species to be assigned to one of the four zones based on the basking behaviour of the species. The use of this tool allows the creation of a suitable UV gradient in a captive environment, using the values provided in Table 11.1 as a guide. This gradient is meant to enable self-regulation of temperature in a range from zero (full shade) to the maximum indicated for that zone, which is the reptile's closest access point to the lamp (Baines et al. 2016).

In terms of infrared exposure, photothermal gradients that provide light and heat are the best choice for long-term care of captive reptiles (Regal 1980); reptiles can

Table 11.1 The Ferguson Zones, summarised from Ferguson et al. (2010)

	Characteristics	Zone range UVI	Maximum UVI
Zone 1	Crepuscular or shade dweller, thermal conformer	0–0.7	0.6–1.4
Zone 2	Partial sun/occasional basker, thermoregulator	0.7–1.0	1.1–3.0
Zone 3	Open or partial sun basker, thermoregulator	1.0–2.6	2.9–7.4
Zone 4	Mid-day sun basker, thermoregulator	2.6–3.5	4.5–9.5

experience negative effects on exposure to continuous high temperatures, because suppression of the immune system and gonadal damage (Dawson 1975; Pough 1991). Similar to UV-B light, heat provided by light should range from cool to warm enough for basking. The temperatures of lizards during activity are just a few degrees lower than those that are lethal; therefore, careful design of the thermal gradient is essential, because the ability to choose a thermal environment may provide for enhanced welfare. Infrared heat sources should be maintained in the enclosures with the use of a lid to avoid heat dispersion, as well as several sheltering places along the photothermal gradient to avoid forcing reptiles to choose between heat and security (Pough 1991; see also Arena and Warwick 2023).

Light levels will not only facilitate vision, calcium metabolism and circadian synchronisation in lizards, but also they impact directly on colouration of the animal, and hence its camouflage capabilities (Kelley and Davis 2016). Reptiles are frequently traded over long distances (Auliya et al. 2016), and during transport, which is often unregulated, it is common for them to be without any natural or artificial light. This issue probably contributes to physiological disturbances and related high mortality rates often associated with the transport of captive reptiles.

11.2 Animal Welfare Conclusions

Despite the lack of research related to the effects of noise and light on reptiles, the acoustic and light environments for these animals in captivity have characteristics that can potentially compromise their welfare. For example, unnatural variation in noise and light could encourage reptiles to engage in excessive foraging or aggression, both of which are energy consuming and likely to decrease success in captive and wild environments. Reptiles may also experience fear and stress due to unfamiliar noise or poor lighting, which, in turn, could chronically activate their flight or fight responses and compromise long-term physiological responses.

In relation to noise and stress, this occurs within a broad frequency spectrum that overlaps with reptile hearing. For light, disruption of circadian rhythms as well as inadequate UV-B exposure and infrared heat sources can be particularly deleterious. Inadequate sound and light conditions are known to affect reptiles in the wild, and this research can be used to assess the effects of these conditions on captive animals.

Given this evidence and considering sound and light perception capabilities by reptile order, it is possible to provide an acoustic environment where novel contingency measures such as sound masking, or devices to contain or avoid the generation of high amplitude noise within reptiles' hearing ranges are utilised. Similarly, preventing the incidence of non-auditory airborne and substrate vibrations is essential to maintain good reptile welfare, because these vibrations can generate inappropriate behaviours. With regard to electromagnetic waves, appropriate lighting for captive reptiles requires a well-designed gradient that considers the heat and lighting necessities of each species. This review has identified several deficiencies in the literature, and it is therefore important to increase our knowledge of the impact of noise and light on the behaviour and physiology of different reptile groups.

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Ethologically Informed Design and DEEP Ethology in Theory and Practice

12

Neil Greenberg

Abstract

The quality of our relationships with other species, as predators, prey, companions, and subjects of curiosity or research, profits from our being ethologically informed. This chapter explores several dimensions of these relationships along with comments on the importance of an ethological attitude and ethologically informed design in pursuit of a better understanding of how best to behave as responsible stewards and students of other species. Design, in the sense of a coherent program that guides our practice, involves identifying and defining the traits that appear important to us, as well as the ways in which we manipulate, observe, measure, and interpret them. Design both guides and is guided by the questions or problems we wish to address. To be ethologically informed, a design implicitly acknowledges four key biological perspectives, identified in the earliest conceptual beginnings of ethology. Each perspective reflects different temporal and spatial orientations and levels of organisation, but all are profoundly involved in the causation of behaviour; they are developmental, ecological, evolutionary, and physiological (DEEP). This integrative biology in concert with an ethological attitude, emphasising freedom from implicit bias, is a valuable approach to all forms of captive animal management as well as research design. Such an approach will reveal connections within and between our subjects and ourselves that are of both great intrinsic interest and generalisable utility in solving problems that we all share.

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Reptile · Ethology · Research design · Experimental design · Stress · Physiology · Welfare · Captive care · Animal models

12.1 Introduction

We are all, of course, deeply concerned with care and welfare of animals we live and work with, as well as those we wish to preserve, nurture, and study as subjects in scientific research. Whether behaviour is manifest in nature or the home or the zoo or laboratory, the welfare of our subjects is more than an ethical imperative, but one that also affects both the positive qualities of our experience: the effectiveness of veterinary care and the validity of research, particularly when the subjects are unfamiliar. The effect of studying unfamiliar subjects is twofold: we are drawn to find shared qualities such as details of physiology and behaviour but also the very alien nature of these fellow creatures challenges us to enlarge our understanding of the boundaries and possibilities of life itself.

Our concerns in this volume are mainly with health and welfare of animals subject to our control in captive circumstances ranging from private homes to zoos, from nature preserves to laboratories. It is our belief that as a general rule, our concerns are best served by eliminating or mitigating the distortion attributable to our intrusion into their lives, but this necessarily involves the best possible understanding of the undisturbed animal. The view adopted here is that this is best accomplished by adopting an ethological attitude and implementation of an ethologically informed design (EID)—a program to guide and support practice by means of the integrative perspectives of DEEP ethology. Hopefully, the result of this approach is an ethologically informed practice for any project that involves our influence on other species, from pets or companions, to subjects in education and conservation, veterinary science, and experimental research. In saying more about these ideas, I will build on and extend a previous version of this essay that emphasised ethologically informed design—an idealised concept that can inform real-world practice (Greenberg 1995).

As described below, these integrative perspectives can contribute significantly to our ability to predict behaviour attributable to circumstances ranging from the exigencies of nature to anthropogenic perturbations. In all cases, the quality of our stewardship will profit significantly from our knowledge of the ethology of the organisms in our care. Even in field research, our best approximation of a ‘natural experiment’ (one in which variables are in play spontaneously) will always have a measure of artificiality attributable to our presence. The best we can do is to mitigate confounding or misleading variables according to our awareness of them and the resources for alternatives.

This program challenges us to be mindful of the traits of interest and their place within the cascades of information that flow through multiple levels of organisation—from molecular to organismic and environmental—in animals that may be very different from ourselves. We must ask how similar or different these traits are from the countless reference traits we hold in mind or the recorded notes of our own reconnaissance and that of other scholars. We need to be mindful also that features distinguishing species—even individuals—are affected by our own experiences and perceptions and can thus never be fully extricated from each other. Traits are polygenic in that multiple paths of causation converge on their expression.

As I hope will be clear, among our most urgent concerns as stewards, scholars, and scientists is to see phenomena for what they truly are and not in terms of anything else. This is a concern of scientific practice in general (Shah et al. 2017) and resonates with and will build on some of the tenets of the philosophical tradition of phenomenology, a school of thought that in practice emphasises the avoidance of bias and preconception, the primacy of perception, and an emphasis on the life-worlds of individuals. By life-world, I mean the aggregate of congenital traits and previous experience that the individual brings to its current circumstances. Concern with bias recalls the now familiar sins of anthropomorphism, speciesism, and human exceptionalism, but those are just the most convenient of a litany of convenient examples. The constant interplay of subjective and objective perceptions and of deductive and inductive reasoning are essential elements in the ensemble of cognitive processes by which we function as organisms and as individuals. Among these cognitive processes, certain constellations may first appear as competing alternative ways of thinking (such as ‘art’ and ‘science’ or ‘theory’ and ‘practice’). However, their boundaries are inevitably lost in the minutiae revealed by close observation and their inevitable intertwining when applied to actually being in the world. So, whilst specific constellations cannot be expunged, we can be mindful of their seeming conflict at levels that will enable us to avoid error or harm.

Hopefully these ideas frame an approach to an understanding of other organisms sufficient to our task of assuring their welfare in all our possible interactions with them. This task begins by describing behaviour—either for its intrinsic interest or as a dependent variable in our pursuit of clues for a possible explanation of its causes and consequences. In either event, our best efforts will profit from an *ethological attitude* (Table 12.1), including an approach that integrates multiple streams of biological information or *DEEP ethology* (Table 12.2). Further, the complexity of the behavioural patterns and processes that are integrated in any phenomenon of interest and to which we must attend as part of our efforts at understanding requires an *ethologically informed design* (EID) (Table 12.3), all to be discussed below.

Table 12.1 Practice informed by the ethological attitude^a

• Prioritise the organism: Our direct perception of the animal we interact with is the centre of our concern. A sense of the whole animal and its welfare should precede any analysis of its parts or its place in the larger picture
• Define the behaviour: Utilise a shared vocabulary at all levels of complexity. Describe behaviour in as much detail as possible and from multiple perspectives such as those organised in DEEP ethology. Elements of definition involve <ul style="list-style-type: none">– Direct Description: Avoid inferences about behaviour at one level based on expectations from other levels, whilst being mindful that some phenomena are barely or only subliminally presented or perceived– Indirect description: Reliance on technological prostheses to extend our senses must be approached with care and supported by independent corroboration utilising alternate techniques
• Cultivate a Janusian perspective: Aim at simultaneously adopting both past/future and analytical/synthetic perspectives. Consider top-down and bottom-up perspectives. Balance generalities and specifics
• Be aware of and eschew congenital and acquired bias <ul style="list-style-type: none">– Consider the respective <i>umwelten</i> of ourselves and of others: This will emerge out of the attention to all four perspectives in DEEP ethology– Employ epoché: A process at the core of the phenomenological method that allows for the bracketing—Setting aside but not denying—the distracting influence of preconceptions and assumptions

^aThe ‘ethological attitude’ is informed by a ‘phenomenological attitude’, close to heart of the qualitative data gathering and the interpretative procedures of generations of philosophers, theoreticians, and practitioners of the phenomenological method

Table 12.2 DEEP ethology^a

Development	Ecology	Evolution	Physiology
Definition Change within individuals from conception to demise involves the progressive expression of genetic potential as enabled or suppressed in specific environments. As well as the programmed disintegration and renewal of cells and tissues Developmental change involves neural, physiological, and behavioural plasticity, enabling adaptation to environmental change	Definition The abiotic contexts of behaviour including climate and geology and the biotic contexts of behaviour including predators, prey, and conspecifics (including networks of reciprocal interactions of organisms with each other and their environments) • Environmental change confronts selection pressures with which organisms must cope to maintain stability	Definition Change across generations and the study of probable ancestors and likely descendants ‘Ultimate’ causes and consequence of behaviour involve biological variations that are naturally selected and determine the nature of future generations	Definition How animals function and manifest cascades of ‘proximate’ biological causes and consequences resulting in the expression of any behavioural trait Physiological change integrates multiple levels of organisation in coping with selection pressures to maintain the stability of the organism (homeostasis)

(continued)

Table 12.2 (continued)

Development	Ecology	Evolution	Physiology
Keywords: Ontogeny, experience, genetics, epigenesis	Keywords: Biotic (predators, prey, conspecifics), abiotic (geology, climate), and umwelt (environment as perceived by animal)	Keywords: Genes, memes, adaptation, direct and indirect fitness, natural selection, traits, selection pressure	Keywords: Homeostasis, nervous system and endocrine system, stress
Kinds of questions When did the behaviour appear? How does the predictable change in a developing organism interact with the unpredictable change in its environment? Does the likelihood of a specific behavioural pattern change throughout one's life? Would a specific experience affect the organism in different ways at different ages? Why?	Kinds of questions What resources are available to enable an animal to meet its needs? Is the likelihood of a specific behavioural pattern different in different (physical or social) contexts? What aspect of the environment enables or impairs specific experience and adaptive change? Why? Given a specific ecology, what are the costs and benefits of a particular trait?	Kinds of questions Are comparable patterns seen in kin or other progenitors? What are the ultimate causes and consequences of the likelihood of a specific behavioural pattern? How is it adaptive? How does it cope with selection pressure? How do specific traits affect direct or indirect fitness?	Kinds of questions What are the proximate causes and consequences of the likelihood of a specific behavioural pattern? How is a current experience integrated with past (and possible anticipated) experiences? What is the path information takes considering 'top-down' and 'bottom-up' information transfer? How does error-detection help the organism navigate its umwelt?

^aThe DEEP view of behaviour begins with an inventory of elements of behaviour and an ethogram, the patterns these elements manifest. Elements of behaviour may range from very modest (eye blink, tail twitch); patterns are exemplified by assemblies of coordinated behaviour such as courtship or predation. This approach is also a formula for interdisciplinary collaboration and creative interactions between the disciplines. There is an inevitable, perhaps necessary and useful tension between the relative importance of generalities and specifics

Table 12.3 Ethologically informed design (EID)^a

1. Describe and define the behaviour of primary concern relative to the problem to be solved or the question asked in terms of
(a) Units of behaviour ('behaviour inventory')
(b) Patterns of behaviour ('ethogram')
2. Assess DEEP ethology by asking key questions about the behaviour of interest from each of the DEEP perspectives as described in Table 12.2
(a) Development (When is the behavioural trait of interest first seen? How has it manifested over time?)
(b) Ecology (In what environment(s) is the behavioural trait of interest seen?)
(i) Biotic (conspecifics, predators, prey, symbionts)
(ii) Abiotic (climate, geology)
(c) Evolution. When is the trait of interest first manifest in. . .
(i) Ancestral history
(ii) Siblings or contemporary kin
(iii) Descendants
(d) Physiology (What processes act to maintain homeostasis? What are the internal and external expressions of those processes? How are they coordinated?)
3. Identify and prioritise the biological needs of your subject(s) (a biological version of Maslow's (1943) hierarchy of motivational needs) How does behaviour of interest serve
(a) Physiology (homeostasis, health)?
(b) Safety (from environmental extremes, predators, and competitive conspecifics)?
(c) Sociality (nurture, courtship, reproduction)?
(d) Individuality (uniqueness, traits of possible interest to reproductive partners)?
(e) Self-actualisation (maximising direct fitness (survival and prosperity of progeny) and/or indirect fitness (propagation of genes and traits shared with more-or-less closely related kin)?

^aEthologically Informed Design enables practitioners in research, husbandry, and veterinary practice to more fully contextualise and thereby minimise sources of confound or confusion in planning, executing, and interpreting their actions with respect to the animals for which they are responsible. The questions of a unit or pattern of behaviour suggested by the categories above will help identify the gaps in understanding the causes and consequences of behaviour that could impair our efforts to secure the optimal welfare of an animal in any management situation

12.2 Ethological Attitude

As a matter of everyday routine, most of us maintain a 'natural attitude', grounded in our subjective experiences of an objective world and even of ourselves. We act to navigate our world based on our experiences and the expectations they engender. Experiences that fail to meet any part of the test of expectation create a stressful dissonance that we avoid with all the cognitive resources available—both nonconscious and elaborately calculated—hence the great difficulty in eschewal of implicit bias that is at the heart of the ethological attitude.

The ethological attitude, most simply put, involves our best effort at bias-free observing, documenting, and analysing a unit of behaviour or a pattern of units in the context of an *integrative* biological approach to its causes and consequences (DEEP

ethology, described below). In this context, for example, physiology and ecology are understood to co-constitute the research experience. The integrative approach requires that we take every effort to interpret the causes and consequences of phenomena in both bottom-up and top-down terms. These resonate with analytical and integrative approaches that are often viewed as alternatives with a long history of antipathy, but that are, in fact, intertwined: the ethological attitude views specific acts of behaviour in the context of their participation in larger patterns as well as being the outcome of interactions at successive subordinate levels. The effort (if not success) in perceiving these perspectives simultaneously is often called Janusian, referring to Janus, a Roman god of doorways and dualities, discussed below.

The eschewal of the biases that subvert valid understanding is a crucial element of the ethological attitude. This sounds simple, but biases exist at many levels of organisation of which conscious attention is only the most obvious, but they can be particularly difficult to identify and cope with when they have roots deeply conserved in our evolutionary biology and ingrained throughout our social and cultural development. Biases may be implicit as well as explicit and not the least of these is human exceptionalism—the venerable and persistent view that there is a profound discontinuity between ourselves and the rest of the natural world. Of course, there are discontinuities between species—indeed between all categories—but the paths that lead to them are (or should be) subject to scientific scrutiny. However, this scrutiny must be bi-directional, or we are handicapped by apparently conflicted alternatives. Awareness of these (if not their suppression) can be difficult, and we are likely best served, as Kuhn (1959) would put it (speaking of divergent and convergent thinking), by cultivating the ability to tolerate tensions ‘that can become almost unbearable but are one of the prime prerequisites for the very best sort of scientific research’. The single mind looking in two directions, the ‘Janus face of science’ (Burghardt 2013) has been identified as contributing significantly to a wide range of creative activities (Koestler 1978; Rothenberg 1979), but crucially for us, the Janusian perspective of simultaneously considering causes and consequences—looking up and down the apparent chain of events at appropriate levels of organisation—is a key element of the ethological attitude. In my own research, the Janusian perspective was first apparent in simultaneously considering the reciprocity of top-down and bottom-up neurological causes and social behavioural consequences of specific units of behaviour.

Lizards, as I knew them in the laboratory of my research professor at the outset of my graduate career, were quite unlike what I had expected based on seeing them in the field. An interest in this dissonance and an emerging enthusiasm for ethology in my university’s interdisciplinary atmosphere at the time provided the motivation and opportunity to study them in unique ways. Observations of ‘laboratory lizards’ in a naturalistic laboratory environment revealed an unexpected diversity of behavioural patterns that were difficult to study in nature. Combined with remote sensing of body temperatures, this approach also answered questions about behavioural thermoregulation. This led to a ‘conversion experience’, consolidated in my dissertation and my first few research publications.

We can fairly say that the ethological attitude is also the basis for *ethologically informed design and practice*. It includes explicit strategies to be deployed whenever we undertake organised efforts to better understand, remediate, repair, or otherwise secure the wellness of animals we encounter and for which we have responsibility. Such an approach has the added advantage of minimising our effects on an animal's experience when we intrude into their lives to conduct experimental research or prepare or modify their environment when in captivity or determine causes for a health problem. Indeed, distorted experimental findings in particular have a way of cascading through the community of researchers and subsequent experiments in a pernicious and wasteful way.

The ethological attitude is also informed by comparable principles developed in phenomenology, the philosophy that undertakes to include subjective experience in the perception of phenomena. Phenomenology as presented and developed as opposed to traditional philosophy in the last half-century has had considerable success but has regrettably neglected relationships with non-human animals. Important exceptions to that neglect are driven in part by the self-created existential crises for ourselves and nature in general and may enable healthier relationships, catalyse more productive understandings, and hopefully mitigate the environmental difficulties in which we are embroiled; see, for example, *Phenomenology and the Non-Human Animal: At the Limits of Experience*, where Painter and Lotz (2007) point out the harmful ideology of human exceptionalism and the need for mindful ethics in dealing with non-humans. The seminal philosopher of phenomenology, Edmund Husserl, believed that the attempt to separate observations from contaminating ideology is crucial and involves considerable personal effort, the outcome of which would result in the adoption of the deceptively simple 'phenomenological attitude' (see Greenberg et al. 2019). Nothing less than this is required to invoke an ethological attitude, distinctive by its eschewal of bias—most conspicuously human exceptionalism—and acknowledging and suspending other more subtle, but comparably misleading, assumptions about the natural world and its constituent processes, not least of which is its conformation to traditional, often arbitrary ideals. Thus, in ethology as in phenomenology, observers or researchers avoid idealisations or generalisations about their subjects and rather emphasise real animals in their real worlds. Here, the important concept of *epoché*—with its rigorous eschewal of bias—is applied. The concept is central to phenomenology but is, in the view of the physicist Piet Hut (2001), common among creative scientists. A related core element of phenomenology is 'bracketing'—a much more general setting aside of the burdens of acquired hypotheses and theory, of bias and expectations, in order to enjoy a greater clarity of perception that will enable us to conceptualise major revisions of received theories. Further, practitioners can better focus on securing remediation, recovery, and future welfare of specific subjects.

In an earlier report (Greenberg 1995), I made much of the pernicious effects of neglecting independent natural variables associated with the life history of the animal subject in any situation involving their care and welfare, not least in scientific inquiry. However, this neglect is sometimes strategically calculated when an

ethological inquiry evokes ‘investigative optimising’ as researchers seek to balance urgency of question, available resources, efficiency, and effectiveness in the conduct of their work and the analysis of their findings. For example, zoological facilities are particularly eager for captive reproduction of their animals, but the expense and effort needed to cope with the many—often very sensitive—elements of reproductive behaviour require balancing their mandate to educate the public with that of conservation.

Questions asked at different levels such as the proximate (e.g. physiological) and ultimate (e.g. evolutionary) causes and consequences of a specific unit or pattern of behaviour are characteristically answered by different modes of analysis, but when question, process, and mode of analysis are not carefully matched, much sterile controversy may be generated (Sherman 1988). This is often attributable to the conflating or misattributing of levels of organisation. The familiarity of lists of levels such as cells to tissues to organs can obscure the fact that to specialists, functions at each level can often be subdivided (as particularly prominent in the brain, Freeman 1995; Goebel 2014). Within a more proximate domain, levels from gene transcription to cellular activity have been sketched out for the stress response at levels that precede levels subject to specific adaptive contexts (Kassahn et al. 2009). A multitude of natural variables are much too infrequently considered conjointly because research methods and historical traditions have served to isolate them. Whilst isolation and narrow focus can be an important component of the analytic part of creative inquiry, it cannot be allowed to exclude the integrative part and dominate the discourse.

Lizards were at the heart of a sustained research effort I undertook at the National Institute of Mental Health where I sought to introduce ethological attitudes in a traditional behavioural neurophysiology laboratory. The expertise of my neurophysiology colleagues in concert with ethological methods led to some otherwise unattainable insights about the neurological correlates of species-typical display behaviour (e.g. Greenberg 1977a, b, 1978). This work encouraged support for a major interdisciplinary conference in which specialists in the micro-minutiae of neurology spoke freely with field biologists (Greenberg and MacLean 1978).

I turn now to the integrative vision of biology applied to behaviour that inspired the earliest ethologists and that is still central to effective and productive animal care.

12.3 Deep Ethology

The expression of behaviour at any given moment occurs at the intersection of four key processes or factors, each reflecting a different level of organisation through which biologically significant information flows in the causation of behaviour: developmental, ecological, evolutionary, and physiological (DEEP) (Greenberg et al. 2019). This task begins by describing behaviour—either for its intrinsic interest as a trait or as a variable in our pursuit of the causes and consequences of some phenomenon of interest. Descriptions done well become a shared vocabulary for research and its application in diverse domains. Descriptions of behavioural patterns

and their relationships are often listed in ‘behaviour inventories’ and ‘ethograms’ (exemplified in Greenberg 1977a, b).

Description, once available, enables ethologists to consider causes and consequences of behaviour and can advance most productively by conceptualising a unit or pattern of behaviour as emergent at the intersection of the four DEEP domains that correspond to the aims identified in the earliest conceptual beginnings of ethology by Tinbergen (1951) and continue to guide ethological thinking.

A fifth aim, termed ‘private experience’ has been ventured by Burghardt (1997). This was influenced by Jakob von Uexküll who embedded the ‘inner world of the subject’ into his functional circle that emphasises the animal’s perceptual and phenomenal worlds (Burghardt 2020). A means of accomplishing this aim is to apply a ‘critical anthropomorphism’, in which our human-derived hypotheses are informed by what we scientifically know about the species’ natural history, ecology, physiology, perceptual and cognitive abilities, as well as the prior experiences of the individual animals themselves.

More recently, the idea of a ‘fifth aim’ was also advanced at the 50th International Congress of the International Society for Applied Ethology (ISAE), held in Edinburgh, Scotland in 2016 (Siegforda et al. 2018). This most recent effort seemed unaware of the more theoretically informed proposals a generation earlier (Burghardt 1991, 1997) and was inspired by advances in detecting and analysing the shared physiology as well as the apparently homologous emotions of many animals. This approach reflects the belief that a sense of shared neurocognitive architecture (see Font et al. 2023) as well as outward appearances of emotion imparts greater confidence in such an interpretation (see de Waal 2011; de Waal and Preston 2017).

Whilst we might conceptualise every act or pattern of behaviour as occurring in terms of the four perspectives of DEEP ethology, we must also remain mindful that each perspective has its own tradition and culture. Each observes behaviour at a different level of organisation, including raw perception (Brewer 2015), and each asks different questions, employs different standards of evidence, and may reach different judgements as to what constitutes a satisfying story. Thus, these disciplines individually as well as in various combinations entail more-or-less cognitive bias. The following paragraphs summarise the character of each discipline as commonly conceptualised by biologists, its assumptions, keywords, and kinds of questions that might be addressed. This is the approach used in Greenberg et al. (2019) to help naturalise phenomenology for researchers employing qualitative research methods. These sibling disciplines are perhaps familiar to most biologists, but I will try to emphasise those aspects that are highly suited to make connections with other domains. They are identified with examples of questions they address in Table 12.2.

12.3.1 Development

Development involves all the processes that unfold within an individual organism from conception to demise, including the continuing disintegration and renewal of cells and tissues. Understanding the developmental trajectories of animals is

essential to any long-term relationship with them. These processes involve the cascades of information encoded in the genes inherited from the previous generation(s) as well as those attributable to individual experiences within one's lifespan. Activation of specific genes and the programs of change they instantiate are more-or-less tolerant of environmental influence (the 'open' or 'closed' genetic programs of Mayr 1974). For example, programmed developmental changes in diet or temperament or environmental needs must be understood for any companion animal, conservation, or research program. Further, the pleiotropic nature of genes should be appreciated: each gene may influence many traits in addition to the ones that dominate our interest because of their importance in meeting biological needs.

Developmental experiences such as isolation, agonistic trauma, dietary deficiencies, or deprivation of key stimuli during sensitive periods can all have persevering effects (see Burghardt and Layne 1995; Burghardt and Layne-Colon 2023; Mendyk and Augustine 2023). At present, studies involving other taxa offer some insight into possible welfare issues in reptiles. For example, in the laboratory, a well-meaning ethologist saw to it that newly hatched birds in the nest were well fed, only to see their parents reject them. Later, it was learned that in nature, hatchlings that do not beg for food are often discarded by their parents, presumably because they are sick or dead (Eibl-Eibesfeldt 1970). Acoustic qualities of various habitats such as forest, edge, or grassland are known to affect bird song and other sounds, critical in many species for successful reproduction (e.g. Morton 1975). Such selection is likely also when attributable to anthropogenic, urban sounds (e.g. Luther and Baptista 2010). The effects of history on an animal need not, of course, be so dramatic or limited to a particular context. In a study of several vertebrate taxa including reptiles, it was found that handling animals each day negatively affected weights of reproductive organs and fat stores (Meier et al. 1973). The degree of the effect depended on the regularity and time of handling relative to photoperiod and was presumably a result of transient mild stress. The likely effects of even mild stress on metabolism reminds us that it is reasonable to expect significant spontaneous variability in non-domesticated species. Animals in the wild are certainly subject to occasional stress, and behavioural and physiological responses to stressors are so intimately involved with each other (see Hennessy and Levine 1979; Moore and Jessop 2003; Martinez-Silvestre 2014; Gangloff and Greenberg 2023) that there may be many ways that such episodes may even be necessary for the proper maturation of coping mechanisms.

Animals in relationships with humans learn a diversity of behavioural patterns that reflect their experience and efforts to cope. The biological and circumstantial 'constraints on learning' (Shettlesworth 1972) underscores the diversity of species and circumstances: for example, reptiles vary in the sensitivity of specific sensory modalities and the salience of any stimulus may vary with the animal's evolved competencies as well as transient motivational state (see Crowe-Riddell and Lillywhite 2023). Learning is always keyed to experience in context and will be commented further in the following paragraphs on ecology (see also Font et al. 2023).

12.3.2 Ecology

It has become a truism that the behavioural patterns seen in animals are profoundly affected by the context in which they occur. The environment includes the temporal and spatial physical and biotic contexts in which organisms must survive and thrive. It is also the source of all perceptions that organisms use to create their reality that is the basis for adaptive behaviour, their *umwelt*, von Uexküll's (1909) invaluable term, that emphasises each species uniquely perceived construct of 'nature for themselves according to their special needs'. In recent years, the concept of 'embodiment' (especially developed in phenomenology) has brought to the foreground the extent to which mental processes go beyond mere sensing of an organism's physiological state to an 'intertwining' of mental and physiological processes such that study of the causation of behaviour must look beyond the nervous system. This concept began with innovative ways of thinking about emotion in humans (e.g. James 1884) but has come to attract significant attention in phenomenology (e.g. Johnson 2007). This phenomenal way of thinking emphasises the unity of mind and body in fruitfully integrative ways such that when Janus faces in both analytical and integrative directions, the questions that emerge can be more informed and incisive.

Ultimately, our understanding of animal welfare hinges on our understanding of animal needs, but how can these needs be known? Further, the perceptual world of an organism is necessarily experienced in a uniquely self-centred way that affects the meaning of experiences. Thus, even in identical environments, different individuals can perceive, integrate, and act in unique ways. The ethological attitude would include consideration of each animal's individual *umwelt*, an effort that necessarily involves, as mentioned above, an acute awareness of one's personal biases as well as the disposition to characterise one animal in terms of a conspecific that may have a different developmental history.

At every level of organisation, every distinguishable element of life—from the multiplicity of organelles within a cell through the outermost boundaries of an organism—is embraced—embedded—in protean concentric spheres of the matrix of the world. In our concern for the behaviour of animals we relate to, this idea echoes principles that have entered contemporary phenomenology as 'embodied cognition' and 'socio-cultural embeddedness' and builds on the understanding that all cognitive processes involve proprioceptive, interoceptive, and exteroceptive input (Lakoff and Johnson 1999; Johnson 2007), as well as the influence of their place in the biotic world of conspecifics, predators, and prey. Output, then, may be manifest as behaviour when the need to cope with change exceeds automatic physiological responses as, for example, when one changes behaviour as a result of experience—that is, learning.

The overlap between development and ecology is particularly evident in learning, and reptile learning provides some of the most striking examples of context-dependent behaviour. The well-known difficulty in training many reptile species has engendered a sense of their relative inability to learn (see Burghardt 1977). However, some lizards manifest a surprising capacity to learn in response to

ecologically relevant stimuli (Brattstrom 1978; Font et al. 2023). They are, in Seligman's (1970) term, 'prepared' to make certain associations much more easily than others. Suboski (1992) suggests that the assumption that learning in reptiles is 'impoverished' is attributable in part to an inappropriate model of the learning process that neglects the importance of action-specific releasing stimuli. As Burghardt (1977) pointed out, expressions of behavioural plasticity such as learning are subject to gross misrepresentations by researchers if considered apart from ethological variables such as physiology or ecology. For example, in a field study of the curly tail lizard (*Leiocephalus schreibersi*), Marcellini and Jenssen (1991) observed that one-trial acquisition of novel predator (human) avoidance behaviour was manifested by 80% of the animals tested. Interestingly, long flight distances developed more rapidly among females than males, suggestive of possible endocrine corollaries.

Many reptiles habituate to human observers and appear to behave naturally, that is in a manner comparable to that of reptiles covertly observed (e.g. agamas [*Amphibolurus* sp.], wall lizards [*Podarcis muralis*], side-blotched lizards [*Uta stansburiana*], and some *Anolis* spp., see Sugerman 1990), but some species appear resistant to habituation (Sugerman and Hacker 1980). In the presence of an observer, captive collared lizards (*Crotaphytus collaris*) will markedly reduce activity levels (Sugerman and Hacker 1980), but the obtrusiveness of the observer is important. Even in the relatively insensitive anoles (Sugerman 1990), an observer will increase the duration of tonic immobility (Edson and Gallup 1972; see Gallup 1974 for review), but probably in response to eye contact (Gallup 1973). Further, the duration of the immobility manifested by anole lizards (*A. carolinensis*) in response to apparent predation (human handling) is significantly diminished in subsequent trials (McNight et al. 1978; and see Hennig 1979).

Whilst the ecological variables of predator–prey dynamics, geology, climate, and physical habitat are important in many obvious ways, the subtlety of some of their interactions can be surprising: for example, slight differences in temperature can elicit alternative defensive responses to prospective predators (humans) in the anole lizard (*Anolis lineatopus*) (Rand 1964). Approach distances (how near a potential predator may approach before triggering an escape response) are generally reduced at lower body temperatures (Rociia and Bergallo 1990). The adaptive rationale was that neuromuscular responses were impaired at lower temperatures. Two other anoles (*A. cristatellus* and *A. stratulus*) were observed to have significantly different approach distances in comparable thermal environments that appeared most likely correlated with the degree of crypsis they manifested: the more cryptic anole (*A. stratulus*) had a shorter approach distance (Heatwole 1968). In anoles (*Anolis carolinensis*), the presumably defensive strategy of immobility when a prospective predator approaches is of significantly longer duration when foliage is nearby than when it is absent, but only in the early days of captivity (Hennig 1979). The transfer of animals from the field to the home, zoo, or laboratory is likely to result in altered behaviour, but we cannot know without preliminary field work if the variations in behaviour are within the range spontaneously manifested by the animal in nature. This idea of a range of tolerance resonates with what in stress research is referred to

as adaptive scope, the range in which a stressor is accommodated without the necessity to move to a higher level of organisation (Greenberg 2002a; Gangloff and Greenberg 2023).

12.3.3 Evolution

Evolutionary biology is concerned with the change in traits and organisms and societies across generations, from ancestors to the present moment, and forward to direct and indirect descendants. Traits are understood to have their present form because of their preservation through the processes of natural selection of variations that are found adaptive—that is, able to compensate for environmental forces (often called ‘selection pressure’) that affect their ability to meet needs. *Adaptation* is at the centre of concern. There are several definitions of adaptation, and all are unified by the idea of compensation for change, either short-term changes at the developmental level (such as a stimulus or life experience) or long-term changes when natural selection preserves them in subsequent generations (such as coping with changing climate) (Rappaport 1971). For example, even gut microbiota diversity is known to be affected by climate warming (Bestion et al. 2017). In a recent report, anoles (*Anolis sagrei*) were observed in experimentally established colonies on small islands with and without predators (Lapiedra et al. 2018). The researchers found that both behaviour and morphology were rapidly changed simultaneously and independently and that differences in survival between males and females was likely attributable to differences in habitat use between the sexes.

A poignant exercise of Janusian thinking evoked by the evolutionary perspective is the ‘reverse engineering’ or deconstruction of the path taken by ancestors whilst simultaneously speculating on the advantage the trait may convey to descendants. There is a certain resilience in many evolved traits such that organisms need not be perfect (‘ideal’), but only ‘good enough’ to be better than competitors. This is another example of ethologists, like phenomenologists, prioritising real individuals over ideal ones. At best, the ideal individual is a reference point which enables us to approximate the future change and variation. Beyond merely providing data, however, efforts to understand the source of this resilience in both epigenetically evoked alternative paths and the adaptive scope between levels of organisation through which information moves are in themselves illuminating.

12.3.4 Physiology

Physiology, the fourth domain of DEEP, describes the proximate processes by means of which internal and external changes are undertaken. This domain includes the sensory detection of environmental and internal information from the body, its integration in conjunction with everything else the organism experiences (or may have experienced in the past) as well as expectations for outcomes, and then the selection (or suppression) of appropriate actions.

The processes within and between organ systems, including the many functionally specialised components of the nervous system, are dynamic and in continual pursuit of balance (homeostasis). However, such a state (known in human biology as ‘organ cross-talk’) is subject to constant ecological and developmental change and thus can at best be only temporarily attained within a range of tolerance such that animals may appear outwardly stable. Because these processes are tightly integrated with memory as well as anticipated outcomes, various levels of error detection are an integral component. Most of an organism’s actions are directly or indirectly necessary to provide life-essential factors. Whether congenital or acquired, many such actions may be collateral or incidental to their main function. The microevolutionary process of ritualisation characterises many adaptive behavioural traits as having been transformed by natural selection from wholly unrelated functions (Hinde 1970). Many of these actions originate in homeostatic reflexes of the sympathetic nervous system as ways to cope with stressors. Together with the structures they utilise, ritualised behaviour often contributes to confusion when we try to tease out causal relationships. Ritualisation begins because the processes evoked are available for natural selection in serving other, often unrelated functions. Interpretations of ritualised behaviour is also complicated by the fact that these traits evolved in environments very unlike anything we might recognise today. As a result, there is often a mismatch between past utility and contemporary function.

Many of the physiological processes with which we are concerned as proximate influences on overt behaviour are elaborated expressions of the routine maintenance of the organism in the course of moment-to-moment circumstances and the ebb and flow of diurnal, seasonal, and developmental needs. Beyond routine, the physiological processes are often recognised as stress, that, as commented earlier (and see Gangloff and Greenberg 2023), is evoked by a real or perceived challenge to our ability to meet our real or perceived needs. The physiology of stress and its capacity to balance or reconfigure the cognitive processes associated with motivation can be discussed in conjunction with a biological interpretation of Maslovian motivational needs that are based in homeostasis and have biological fitness as an ultimate outcome (see below).

12.4 Ethologically Informed Practice

Applying the ethological attitude to the four domains of DEEP ethology with respect to the behaviour of animals affected by our relationship with them provides the best vantage point to assure their welfare. Ethologically informed design (EID) is an idealised application of ethological principles that must be adapted to specific projects, particularly where research findings can inform cascades of subsequent work (Greenberg 1995). In practice, the ethological attitude is brought to bear on a broad spectrum of concerns for stewardship, husbandry, welfare, and research. A thoughtful application of this attitude will alert us to dimensions of practice that are unsuspected or even counterintuitive. For example, learning that is manifest by animals with which we may interact is often subject to unsuspected and uniquely

species-specific traits generally involving experiences of specific kinds of stimuli in specific contexts (Seligman's 'preparedness', mentioned above), or specific qualities of stimuli (such as Gibson's 'affordances' 1979), elements of the stimulus to which an animal is particularly responsive.

The questions associated with each domain of DEEP ethology (see Table 12.2) provide a scaffold—the beginning of a framework for characterising the causes and consequences of animal behaviour. Treating this issue as a pre-clinical or pre-treatment checklist may inform the practitioner or researcher in assessing how prepared they are to provide for the corresponding biological needs of the animals for which they have taken responsibility (see also Jessop et al. 2023). In the network of causes and consequences in which a behavioural pattern is manifest, any change in structure or process will ripple through the system with variable effect. An assumption in ethologically informed design (EID, Table 12.3) is that the system as it exists in nature possesses structures and mechanisms that are capable of buffering or otherwise coping with change as may have affected the organism's fitness in ancestral environments. In modern or artificial environments, on the other hand, coping can become dysfunctional and our observations misleading.

This buffering is an expression of 'adaptive scope' mentioned above, the amount of tolerance for stress within any of the many levels of organisation within an organism before another, 'higher' level—typically more accessible to observation—needs to be invoked (see Gangloff and Greenberg 2023). This tolerance often proceeds unbeknownst to caregivers or researchers. The level at which an effect of stress may be apparent to the researcher may not be the level at which it would be best addressed as a responsible keeper or clinician.

12.5 Validity

Considering the potential distortions imposed on a captive animal's development, relations with its environment, expressions of biological fitness, and physiological processes such as stress and reproduction, an EID informs the procedures used in animal care. Such ethologically informed practice will have more consistent and reliable outcomes across a broader spectrum of applications. At best it alerts the practitioner to the diversity of possible responses and instils respect for the uniqueness of species and even individuals. Validity is not the same as reliability in which outcomes can be replicated frequently, but do not necessarily speak to the real animal in its real world.

It is easy to speak of anthropogenic distortions imposed by the way that we care for captive animals, but in some respects, the research environment is arguably the most challenging of circumstances. Here, formal concerns regarding the validity of information that we deploy or acquire are important and deserve comment. The deployment of our idealised design in practice requires an important distinction to be made between 'internal' and 'external' validity: the first is highly reliable in a narrow context (e.g. an individual animal in a specific context); and the second, somewhat generalisable to other individuals, species or taxa, or even the same individual in a

different context. Because research often relies on specific animal models, generalisability of the information it provides is a fundamental concern of science in everyday practice. Researchers in medicine and drug development have learned—sometimes painfully—that findings in a model species do not always map on to humans (Pound and Ritsket-Hoitinga 2018); they are at best a start.

The proximate and ultimate causes and consequences manifest in DEEP ethology are concerns that help keep the researcher and the practitioner at an appropriate level of organisation for the questions being asked or problems to be solved. The immediate or physiological causes and consequences of behaviour are often termed ‘proximate’ to distinguish them and their levels of organisation from evolutionary or ‘ultimate’ causes—the presumably naturally selected adaptive background to the proximate cause.

The immediacy of concern is the area where these terms are relevant: mitigation of pain, restoration of health, or successful reproduction and maximising biological fitness. The welfare of animals utilised in research is typically characterised in terms of apparently dysfunctional behaviour or expressions of distress or pain either in the course of captive maintenance or through a scientific procedure (reviewed by Morton et al. 1990). For example, hierarchically organised ‘pain scales’ have been suggested (Orlans 1990), but as Bateson (1991a) points out, both the evolution and the functions of a subjective sense of pain are obscure. To assess animal well-being, both physiological and behavioural measures have been suggested and an enlightening debate has been engendered about their respective complexities and relative merits (summarised in part by Barnett and Hemsworth 1990). Novak and Suomi (1988) identified four different approaches to defining psychological well-being: physical health, behavioural repertoire, reaction to stress, and responsiveness to environmental events. Similarly, the importance of integrating local resources and the history and behaviour of specific organisms in the development of a maintenance or treatment plan cannot be neglected (e.g. Rose and O’Brian 2020).

However, some of these approaches, as many authors point out, lead to contrary conclusions about how best to manage captive animals, even within a specific approach such as reaction to stress. Within an individual or small population, the consequences of sustained stress changes from positive to negative as physiological stress levels increase (see the Yerkes-Dodson ‘inverted-U phenomenon’, the ‘stress-response curve’, Gangloff and Greenberg 2023). In addition, the great variability in the expression of distress between taxa makes generalisations overly dependent on extrapolation from more familiar to less familiar models. For example, when a presumed stressful stimulus (a live snake) is presented to squirrel monkeys, they will appear highly agitated and apparently stressed, but there is not necessarily an elevation in the stress hormone, cortisol, over what would result from mere novelty (Vogt et al. 1981). The emotional aftermath of a presumably stressful situation suggests that there may be a discontinuity between what we may perceive as a reflexive response and its affective component (Prinz 2003).

Behavioural and physiological perspectives have suggested various ‘objective’ criteria for welfare as well as some sterile controversy, but the ethological appreciation for the complexities of adaptive change may help resolve differences. For

example, well-meaning efforts to maximise an animal's welfare by minimising an 'objective' measure of stress such as elevated circulating levels of adrenal hormone may deprive animals of opportunities to exercise and develop responses needed to deal with the normal variability in their environments. Whilst not all needs are of comparable importance to welfare (Greenberg 1992), we could argue that the 'ultimate biological need' of any animal is the realisation of its maximum biological potential—its inclusive fitness, even where this involves a non-reproductive state. Long-term expressions of stress in animals that may appear healthy and stable may become manifest in phenomena such as retarded development and impaired reproduction (Tokarz and Summers 2011), and behavioural dysfunctions (see Christian 1980), as well as more subtle phenomena such as accelerated ageing and impaired immunocompetence (see Johnson et al. 1992; Gangloff and Greenberg 2023).

12.6 Laboratory and Field

For animal welfare in any context, not least the exquisitely sensitive context of experimentation, the scrutiny of presumably relevant variables whilst all other possible influences on dependent variables are held constant can lead to heroic efforts for control, if not uniformity, of all potential variables. However, the complexity of an animal's interdependence with its natural habitat may dictate that meaningful study is possible only in nature or if necessary in a simulated habitat (Warwick and Steedman 2023)—even if this trade-off entails the sacrifice of fine control of potentially relevant variables. An extreme example of faulty design was identified by Warwick (1990) who observed that restrictive environments that do not allow sufficient exercise may lead thereby to an array of behavioural and physical problems.

It has long been appreciated that many debilitating dysfunctions in zoological parks are attributable to an incomplete accommodation for the needs of captive animals (e.g. Hediger 1950, 1955). The concerns of zoological parks have undergone a marked transformation; modern zoos manifest much more interest in subtleties of welfare and behaviour, particularly when they impact the reproductive effectiveness of endangered species (see Eisner 1991). Special scrutiny has been afforded some of these problems in recent years with respect to environmental 'enrichment'. For example, Mahoney (1992) espouses a systematic investigation of the sensory capacities of captive animals and encourages accommodation of specific needs and aversions (see also Mendyk and Augustine 2023; Warwick and Steedman 2023).

In many contexts, we, as stewards of welfare of the animals under our influence, are satisfied when practices apparently meet basic biological needs, including reproduction. In the more narrowly 'problem-focused' context of the clinic and the research laboratory, we must be able to contrast the specific problem with normalcy revealed by field studies. Ethologists typically do this by means of an inventory of units of behaviour and an ethogram of how these units may be organised in patterns of behaviour (Greenberg 1978). If sufficiently complete, these approaches will show

the full range of traits that have evolved to cope with, even rare, challenges (Wingfield et al. 1998).

Frequently, even subtle aspects of an artificial setting may affect behaviour in ways that underscore the importance of previously unnoticed or under-appreciated environmental influences on behaviour in nature. For example, wavelength and intensity of ambient light may affect agonistic behaviour of some lizards (Moehn 1974; Mancera and Phillips 2023), environmental scale may affect timing of activity patterns of captive anoles (DeLong et al. 1986), interaction of light and temperature affects reproductive activity in male anoles (Licht 1967), humidity may affect reproductive activity in female anoles (Summers 1988; and see Stamps 1976), and mild stressors may affect some but not all of forms of tongue-flicking manifested by lizards—presumably modifying their awareness of certain environmental cues, but also expressing non-specific arousal (Greenberg 1993).

Misleading observations in any context may occur due to unknown changes introduced into an animal's environment that may evoke a differential representation of behaviour in an individual. Such observer effects are familiar to herpetologists who have found that target animals were affected by stimuli ranging from observer-associated clothing (e.g. Putam et al. 2017) to chemical or auditory stimuli or apparatus. These factors are often aversive but (rarely) might be attractive, presumably evoking curiosity (Rand et al. 1975). Frequently, only a subset of a population, such as social subordinates or a sex or age class, may be amenable to observation, and then perhaps only in specific parts of their environments such as an ecotonal boundary or within proximity to a refuge (see Zani et al. 2009).

Insight into behavioural flexibility in the field can inform caregivers in captive situations. For example, different patterns of natural selection for risk-taking behaviour were observed in anoles (*Anolis sagrei*) in populations coping with the presence of natural predators (Lapiedra et al. 2018). With respect to differential responses to human intrusion, adult iguanas (*Iguana* sp.) may change their home ranges or sleeping areas in apparent response to perturbations such as observing at night with a spotlight or the activity of constructing a blind 80 m away during the day; hatchlings may not disperse but appear to increase the height of their sleeping perches where tall vegetation was available (Rodda et al. 1988). An artefact of observation of *Anolis* lizards in a naturalistic captive environment using video surveillance apparently evoked a mechanised version of the observer effect by reducing the amount of spontaneous activity recorded. When the dark round eye-shape of the lens was disguised by attaching an irregularly shaped camouflage painted piece of foam, activity levels were restored to levels seen in field observations (personal observation).

When it is necessary to sustain animals in captivity, we may minimise the distortions of circumstance by using field observations as a reference point: to the extent possible, we can quantify temporal and spatial aspects of key life-history variables such as activity patterns, feeding habits, social activities, or the proportions of various daily activities. Once documented in the field, one may then observe the spontaneous expression of the same variables in an empirically derived simulation of the natural environment in the laboratory or zoo.

12.7 Observation and Context

Our knowledge of nature is grounded in observation. However, our senses are notoriously vulnerable to congenital as well as acquired biases, and not everything we might wish to know is comparably amenable to observation, requiring us to resort to artificial (and thus more-or-less trustworthy) extensions of our senses. The ‘logic of the lamppost’ describes the disposition to look for answers where the illumination for one’s search is brightest. Suffering from either insufficient light or inadequate vision, many possible answers remain hidden in the deep shadows. Unfortunately, the experiments of nature—spontaneously occurring combinations of variables that we suspect may illuminate a particular problem—are rare. In research we must, as J.S. Mill (1882) put it, resort to ‘artificial’ experiments of our own devising in order to add to nature’s experiments. Because the essence of an experiment is the selection and selective control of relevant variables, it is fair to say of science, as Langer (1957) famously said of art, that all useful representations are abstract. The premises of experimental observations—indeed all observations of other species with which we would productively interact—leads us to minimise sources of variation such as age, experience, and context and thus to emphasise reliability in, for example, animal models for research, from medical models to husbandry, productivity, and even companionship. Therefore, we must turn our attention briefly to models utilised for herpetological investigations.

12.8 Animal Models

Reptiles have been identified as useful animal models in research with implications for human well-being (e.g. Greenberg et al. 1989; Greenberg 1992; Lovern et al. 2004). Applications have been identified in development of behaviour (Burghardt 1978), brain research (Greenberg and MacLean 1978; Greenberg 2002a; Nomura et al. 2013), stress physiology (see Gangloff and Greenberg 2023), genetics (Tollis et al. 2014), and reproductive biology (Crews 1980; Lovern et al. 2004; Wade 2012), among many other specific research domains. Sanger and Kircher (2017) identified the anole lizard (*Anolis* sp.) as a uniquely valuable model and reviewed the scholarly resources for integrative studies of ecology, evolution, development, and genetics.

Animal models—like all models—are selective representations of phenomena of interest; they often obtain their status as a model because of circumstances of convenience. Whilst this approach enables some of the most integrative and comprehensive overviews, it may also limit external validity. Accordingly, although valuable reference points for the practitioner, they must be used with caution. Concurrently, animal models have led us into new areas such as emotion and cognition that may further diminish confidence in human exceptionalism (Siegforda et al. 2018; see also Font et al. 2023). Recent research, in Toadvine’s (2007) view, suggests that ‘the cognitive gap between humans and other animals is much narrower than has formerly been supposed, with the growing consensus that our differences are a matter of degree rather than kind’.

This factor, and growing prestige for the idea of continuity of traits, has instilled in many a deep sense of respect for the lives of research subjects (see Preston and de Waal 2002; de Waal 2019 for reviews). At the same time, uniqueness, indeed the exceptionalism of other species, is revealed by a deep familiarity with them, and arguably, every species may be found to be exceptional. Although we cannot know the inner life of any organism that manifests behaviour resembling our own, we can no longer assume that they do not have comparable experiences. In the spirit of Hobbes (1651/1982), when we observe animals in a context that would for us evoke joy or grief, we are inclined to ‘... thereby read and know what are their thoughts and passions ... upon the like occasions’.

Therefore, once our eschewal of bias allows us to observe behaviour that resembles grief or joy or jealousy or love, we can employ our Janusian perspective and look for correspondences of causation with the most intensively studied organism—ourselves. We can ask about the critical stimuli evoking these affect-laden patterns. For example, in recent decades, the public imagination has been stimulated by so-called odd couples (Nature 2012), extraordinary relationships between taxa that are rarely if ever in direct contact with each other (e.g. Romm 2015). Relationships other than those seen spontaneously in nature are often inadvertent experiments that can illuminate cognitive competencies that humans share with other species that structure social relationships. I turn now to several themes—‘case studies’—in reptile research that in aggregate, inform our understanding of important variables in reptile management.

12.9 Case Studies

There are several domains of reptile research that can inform practitioners by virtue of the reciprocal illumination that is provided by the integration of findings analysed at different levels. Such case studies represent points of articulation between commonly isolated disciplinary domains (Bateson 1991b) and various species. These examples represent aggregates of good faith attempts to understand organisms from multiple perspectives by means of implicit application of the ethological perspective, including DEEP ethology, and by employing ethologically informed design when possible. Such overviews tell the best story they can with the best—most valid—information available, and although patched together using information derived from various species, they provide a template against which new instances of application can be assessed; in other words, these case studies may be valuable in general, but often unreliable in their particulars.

In the following few paragraphs, I wish to briefly outline a few such areas in which theoretically fertile overviews are growing rapidly. The ethological attitude in action reveals, for example, dismissing the fallacy of reptiles for their ‘lack of complex social behaviour, emotions, cognition, and phenomena such as play, social learning, and deception’ (Doody et al. 2021; Gillingham and Clark 2023; Doody 2023; Font et al. 2023). Whilst evincing enthusiasm for integrative science, we should not infer disdain for analysis. Indeed, the relative intensity and focus provided by analysis offers solid

grounding for integrative views that are brought to bear on understanding life at the level of organisation such as we, as organisms and communities, find ourselves. Such analyses also have the further virtue of illustrating how analysis and synthesis are mutually constitutive processes (see Beaney 2014).

12.9.1 Thermoregulation

Thermoregulation is among the most studied of the physiological variables affecting reptile behaviour and is valuable for us to consider because it occurs across all levels of organisation and in reptiles and is readily expressed in behaviour. Since the work of Cowles and Bogert (1944 and see Bogert 1959), few researchers would neglect the need for reptiles to regulate their body temperatures by behavioural selection of microhabitats of varying thermal qualities (see Heath 1965; Lillywhite 2023; Crowe-Riddell and Lillywhite 2023; Gillingham and Clark 2023; Arena and Warwick 2023). Because the means by which a ‘preferred body temperature’ is attained in a specific reptile or at a specific developmental time is very variable (e.g. ‘shivering’ or positioning to maximise absorption of solar radiation) and extensively studied in many contexts, the practitioner must extrapolate from well-studied examples that resemble the animal of interest at the moment before making assumptions about its welfare. Between its central importance to physiological functioning and its amenability to documentation, investigations of the various thermal strategies of reptiles provide many points of articulation between different levels of organisation and analysis. Ethologically integrative views of reptilian thermoregulation have focused on interlocking variables ranging from morphology (Pough 1980) to mental capacities (Avery 1976; Regal 1980) and have helped dispel the ‘endothermcentric’ prejudice that birds and mammals represent the evolutionary benchmarks for success (Greenberg 1976; Pough 1980).

The richness of research into behavioural thermoregulation also provides us with examples of how compromised validity at one level can ramify through a cascade of subsequent research. For example, in adult male anoles (*Anolis carolinensis*), an appropriate body temperature is important to the responses of lizard adrenal to ACTH (Licht and Bradshaw 1969), and thus the entire ensemble of chronic stress effects on physiology and behaviour. The attainment of a specific body temperature is known to affect the production and action of androgens (Pearson et al. 1976) and spermatogenesis in *Anolis carolinensis* (Licht 1971), as well as the hormonal state and reproductive status of other species (Hutchison et al. 1966; Licht 1971; Garrick 1974; Schwarzkopf and Shine 1991; Daut and Andrews 1993). Other physiological variables that involve thermoregulation and are also likely to affect behaviour include diet, digestive state, and dehydration (Larson 1961; Regal 1966, 1980; Harwood 1979), and even response to infection and disease (see Regal 1980; Warwick 1991). Thermal influences on muscle physiology (Licht 1964a, b) might underlie the selection of specific defensive strategies at different temperatures (Rand 1964 on *Anolis*, and see Hertz et al. 1982 on *Agama* and for a brief review), although

‘escape burst speed’ and stamina documented in six genera of lizard by Bennett (1980) appear relatively independent of ambient temperature.

Progressive environmental effects on thermoregulation are most familiar in the developmental phenomena of acclimation and acclimatisation. These processes, indicative of an organism’s attempt to maintain homeostasis by compensating for an environmental change, exemplifies the complexity of generalising laboratory research to observations in the field. When, in the laboratory, all conditions are held constant except for a single variable of interest (such as ambient temperature), the animal’s compensating adjustments are termed acclimation. In the more complex situation in the field (such as seasonal change), adaptive adjustments are termed acclimatisation (Prosser 1986). However, in either event, different species can be expected to compensate at different rates (Art and Claussen 1982) and in different ways. Evolutionary background is brought to the fore when species such as the periodically winter-active anole (*A. carolinensis*) apparently uses partial acclimation to cold as an overwintering strategy whilst the sympatric race-runner lizard (*Cnemidophorus sexlineatus*) hibernates rather than acclimates (Ragland et al. 1981). In the laboratory, following acclimation to an elevated temperature, the anole (*Anolis carolinensis*) appears to be more heat-tolerant than those maintained at lower temperatures, but the temperature animals will spontaneously select (their ‘mean preferred temperature’) is unaffected (Licht 1968).

Animals studied after acclimation in the laboratory are often assumed to be comparable to those acclimatised to the more complex environmental stimuli in the field, but this assumption may be unwarranted. Gatten et al. (1988), for example, observed oxygen consumption and lactate concentration at rest and during induced exercise at 20 °C in two populations of green anoles, (*Anolis carolinensis*): one acclimatised to various seasonal changes in the field and one acclimated to warm or cold conditions in the laboratory. In this study, resting oxygen consumption was unaffected by acclimation to warm or cold laboratory conditions, but did vary seasonally in the field animals. However, oxygen consumption during exercise showed significant differences between warm and cold acclimated lizards in the laboratory but was not affected by seasonal changes. Turtles are known to manifest an increase in their tolerance to abrupt temperature changes in response to increasing photoperiod and largely independent of seasonal temperature acclimation (Hutchison and Kosh 1965).

12.9.2 Stress

Welfare of an animal may seem necessarily compromised by stress, but this is often an unwarranted assumption. Without a test for circulating hormone levels [itself usually a stressor and often a poor indicator (Moore and Jessop 2003; Martinez-Silvestre 2014; Gangloff and Greenberg 2023)], the practitioner will have to rely on manifest behaviour—or (very fortunately) in some species, body colour (see about *Anolis carolinensis*, below). The stress response is an ensemble of coordinated autonomic and endocrine activities that in varying proportion are essential parts of

other systems (see Axelrod and Reisine 1984; Johnson et al. 1992; Gangloff and Greenberg 2023) that serve both somatic and neurobehavioural (psychoactive) functions such as thermoregulation, aggression, and reproduction (Greenberg and Wingfield 1987) and can represent seasonal or developmental changes such as sexual maturation, social subordination, and reproductive competence (reviewed by Cooper and Greenberg 1992).

The stress response is energetically demanding and, if a limiting constituent such as one of the key enzymes or hormones is exhausted, could lead to death. Nevertheless, many species readily endure or even pursue highly stressful experiences when certain rewards (e.g. the higher need of successful reproduction) are at stake. For example, one of the key indications of stress is an increased level of circulating adrenal corticosteroid, but at least in some taxa, this hormone can manifest bimodal effects, stimulating feeding, exploration, or other activities at low levels whilst *decreasing* both feeding and activity when elevated (reviewed by Leshner 1978). This phenomenon is effectively described by the U-shaped ‘stress-response curve’ illustrating the adaptive response to increasing stress hormones up to a point, and then decreasing with additional stimulation (Chrousos and Gold 1992), what Zelena (2015) calls ‘The Janus Face of Stress on Reproduction’ (and see Gangloff and Greenberg 2023). This situation appears manifest in anoles (*Anolis carolinensis*) in which body colour associated with extreme stress (green with a dark eyespot) is seen briefly during male-male aggression but is also evident in wounded or aged animals as they decline and approach their demise. In the field, zoo, or clinic, such signs are often observed although cause and effect are unusually difficult to discern, and the phenomenon is by far more studied in humans (e.g. Borjigin et al. 2013).

A fundamental preliminary to all other biological needs is physiological homeostasis: the maintenance of an internal state that is stable within the range of variation an animal can experience before energetically demanding and potentially dysfunctional compensating responses are triggered. Within this range, sometimes termed ‘adaptive scope’ (see Greenberg 2002b; Gangloff and Greenberg 2023), animals can compensate with little or no energetic expenditure; beyond this range, a comprehensive physiological stress response is engaged that involves an ensemble of coordinated physiological and behavioural responses (Crews 1980; Crews and Garrick 1980; Greenberg 1990; Guillelte et al. 1995). Clearly, failure to provide for one stress-sensitive variable can affect others because the stress response ramifies throughout the organism. In the absence of explicit information about the capacity of an organism to cope with a specific variable, we are obliged to limit potential challenges to a range within which it is known to be able to cope. Examples would be the altered yet stable endocrine profile of subordinate anoles (*Anolis carolinensis*) (Greenberg and Lumsden 1990) or lizards subjected to frequent handling (Meier et al. 1973).

In practice, both short- and long-term changes in the physical appearance of many species are prominent phenomena that inform the practitioner regarding welfare. Much of appearance such as weight and muscle tone can be an expression of sustained stress possibly indicating an underlying pathology. However, rapid, relatively brief, or seasonal episodes are also important in considering animal

management and treatment, and a steward might be easily misled if natural stress dynamics were taken as indicative of disorder.

Body colouration of the green anole (*Anolis carolinensis*) is, for the wellness-concerned steward, an outward expression of usually hidden physiological phenomena. In this anole, only circulating hormones affect chromatophores: green is the basic colour of an unperturbed animal, whereas light brown indicates successful coping with modest disturbances, green complemented with a dark eye spot can represent a surge of stress hormones, and a blotchy green and brown colour is manifest in animals in extreme distress. Only a few animals are known to so readily provide a visualisation of their inner state, but observing the phenomenon in real time provides a penetrating sense of the labile dynamics of acute and chronic stress, including its expression in social interactions, as it likely occurs in many other species.

12.9.3 Social Dominance

Whether in nature or captivity, reptilian sociality may be relevant to welfare and dependent on ecological or artificial resources (see Brattstrom 1974; Gillingham and Clark 2023; Doody 2023). Many reptiles are seen in aggregations when resources are sufficient such that competition for them would waste energy, but in many species, competitive and social dominance relationships can change as resources change. Males of the black iguana (*Ctenosaura similis*) will compete for exclusive territories unless a sudden abundance of prey occurs at which times they appear mutually tolerant enough to aggregate (Evans 1951). Blue spiny lizards (*Sceloporus cyanogenys*) will compete for first daylight for warmth and for hibernacula in the evenings (Greenberg 1978). The behaviour of anole (*Anolis carolinensis*) males maintained in vivaria can be affected by each other's presence, particularly after a loser of a competitive interaction is unable to escape the presence of the winner, something unlikely to occur in nature (Jenssen et al. 1995).

In some species, a continuum of degrees of territoriality can be seen in captivity and in the field (Hunsaker and Burrage 1969). At least a few species of lizard also shift their social organisation from territorial to social dominance hierarchy in response to environmental characteristics such as available space (Evans 1951 for black iguanas [*Ctenosaura pectinate*]; Norris 1953 for desert iguanas [*Dipsosaurus dorsalis*]). Field data on social dominance in the well-studied anole (*Anolis carolinensis*) (Jenssen et al. 1995) indicates seasonal dependence, but in the laboratory simulating breeding season conditions, dominance relationships are established that are rapidly suggestive of a conservative behavioural pattern (Greenberg et al. 1984). Social dominance, in the conventional sense of one animal manifesting a priority of access to a limited resource over another, is seen in winners of aggressive interactions between males cohabiting a single enclosure. In this species, winners continue to perch at the highest site available and court females, expressing little more than occasional interest in the cohabiting loser. However, the loser changes markedly: he becomes darker in body colour, selects lower perch sites, is less active,

and does not court—he has become a social subordinate. Such pairs often share food and water and maintain stable relationships for extended periods, suggesting a pattern well fixed in their behavioural repertoire. Laboratory observations, no matter how consistent, can do no more than suggest ecological hypotheses about the possible advantages accruing from the changes in subordinates: depending on the species, adopting protective microhabitats, lower posture and activity levels, colours that could be cryptic or resemble non-provocative individuals such as juveniles or females.

The significance of understanding social relationships in husbandry settings is that the interacting dynamics of stress and reproductive physiology are both cause and consequence. Endocrine dynamics of stress interact with those of reproduction (courtship, mating, parental behaviour; see, for example, Greenberg and Wingfield 1987; Tokarz and Summers 2011). Natural elevation of testosterone, for example, can lead to aggressive interactions after which circulating levels are briefly elevated and then sustained in winners but reduced in losers amongst anoles (*Anolis carolinensis*) (Greenberg and Crews 1990). In at least captive settings, the behavioural consequences of reduced androgen in subordinates may be protective in that they will avoid the potentially harmful responses of their unavoidable dominant companion (Greenberg et al. 1995). Association of the stress response with social dominance (as indicated by the model anole lizard [*Anolis carolinensis*], Greenberg 2002b; Summers 2002) is now a familiar idea. However, there is a diversity of relationships between the central nervous system, autonomic, and endocrine causes and consequences of social dominance or subordination (Greenberg 1983) that prevent easy generalisation.

Can we say anything as yet about the physiological substrate of altered social behaviour? Whilst the ecological aspects of the phenomenon in the laboratory are as yet elusive, the control and consistency of the laboratory facilitate investigations of the neurobiology and behavioural endocrinology. Development, ecology, and physiology clearly converge in investigations of forebrain sites apparently responsible for integration of stimuli leading to the expression of specific social displays (reviewed in Greenberg 1983, 1990), and brainstem nuclei controlling a key effector of the dewlap displays (Font et al. 1986; Font 1991).

Body colour, mentioned above in discussing stress, is in many species a nexus of interest, manifesting both short-term and long-term physiological phenomena associated with autonomic reflexes and stress at levels of organisation from homeostasis to communication (Cooper and Greenberg 1992). For example, the darker body colour of anoles (*Anolis carolinensis*) when losing a fight can provide a key to endocrine variables associated with social subordination and submissiveness. This phenomenon, well known in the laboratory (Greenberg and Noble 1944) is also seen in the field (Medvin 1990) and presents provocative possibilities because the hormones that affect the chromatophores are also associated with the physiological stress response and, at least in other taxa, have appeared to act to suppress aggressiveness and facilitate the expression of social submissiveness (Leshner 1978). In the limited space in which captive reptiles are typically maintained where winners and losers of staged dominance contests remain in each other view,

changes indicate increased melanotropin (animals remain dark) and reduced testosterone (animals will not court females), but when the dominant is removed, the formerly suppressed individual recovers green colour and motivation to court over a period of up to 3 days (Greenberg unpublished observations); interestingly, these defeated males (with presumably low testosterone) are at first aggressive to females introduced to test courtship, but over 3 days (with presumably higher testosterone) court in normal fashion.

12.9.4 Reproduction

Beyond mere individual survival, successful reproduction is the highest expression of the biological potential of individual animals—at least in evolutionary terms of direct and even indirect fitness. Whilst reproduction may be of great concern to stewards of animal welfare in zoos and conservation parks, many species can tolerate otherwise dangerous levels of stress to reproduce and to protect their progeny (see, for example, MacLeod et al. 2019; Gangloff and Greenberg 2023). Because of the conservatism and complexity of reproductive processes, reproductive success is often regarded as an indication of well-being, and the environment in which this occurs may be regarded as at least adequate. However, physiological stress is a relatively extreme expression of an animal's unmet needs. In reproductive behaviour, environmental influences can be subtle and counterintuitive (e.g. see Whittier and Crews 1987). Further, specific kinds of stressors can evoke physiological and behavioural change important in synchronising or activating important elements of reproduction.

Failure of captive or managed animals to produce successful progeny can, therefore, be regarded as a failure of adequate ethological insight. For example, whilst adult *Anolis* spp. can be successfully maintained and will reproduce in the laboratory (Greenberg and Hake 1990), rearing of progeny is notoriously difficult. Methods of facilitating reproduction in captive reptiles have thus rightly emphasised the convergence of external climatic, physical, and social stimuli on the internal processes leading to courtship, copulation, pregnancy, and parental behavioural patterns such as nest-site preparation, oviposition or parturition, and in some cases even brooding (see Carpenter 1980; Crews and Garrick 1980).

Coordinated field and laboratory studies are effective ways of isolating the often subtly interdependent aspects of the complex reproductive process in ways important to practice. In particular, reptiles that are subject to arbitrary maintenance regimens and for whom different experiences such as predator or prey or even illumination levels can frustrate efforts to provide for their welfare and ensure prospects for successful reproduction. For example, whilst some opportunities for thermoregulatory basking would certainly be provided by most ethologically informed reptile keepers, only recently have clues been forthcoming about the means by which the physiology of brooding females of various viviparous species affects thermal preferences in order to accelerate embryogenesis and decrease gestation time. The altered basking patterns of gravid females of several viviparous

species was reviewed by Shine (1980), who noted that whilst there are several reproductive advantages, there are also distinct costs. In the laboratory and in the field, gravid female viviparous skinks (*Eulamprus tympanum*) will attain body temperatures comparable to those of males and non-gravid females, but will increase the duration of daily basking time. Also, in the laboratory, it was learned that the increased basking time results in accelerated gestation (Schwarzkopf and Shine 1991).

12.10 Mitigation of Distress

Whilst we must anticipate that captivity distorts behaviour, the nature of that distortion may not be obvious if there are no ethological reference studies. The capacity of many species to compensate for inadequate resources to meet biological needs can obscure diminished competences until they are manifest in a conspicuous way such as failure to thrive or reproduce or expression of other stress-related signs, common in zoos and other captive breeding contexts. The laboratory context in which efforts are taken to minimise potentially confounding independent variables is particularly vulnerable to unknown distortions. However, beyond the practical compromises that may distort findings, research designs often utilise procedures that knowingly cause ‘unavoidable’ distress. The most extreme procedures involve surgery and sacrifice. Practitioner stewards must, like the reptile itself in nature, seek an optimal compromise. Such a circumstance is considered below.

Two reviews of the use of hypothermia and freezing as means of anaesthesia and euthanasia for amphibians and reptiles (Shine et al. 2015; Lillywhite et al. 2017) underscore that our intuition might fail us when we judge other species by our own experience. For example, Langkilde and Shine (2006) present data indicating that hypothermia could be less stressful than a commonly recommended alternative. These authors also observed in their review that ‘stress’ and ‘distress’ are commonly conflated and that many authors use emotionally biased language in their narratives.

A perennial concern in both clinic and laboratory is cooling reptiles for experimental procedures. This is identified and briefly reviewed by Gangloff and Greenberg (2023) and Arena and Warwick (2023) where, work is cited that supports the idea that small ectotherms probably do not experience pain when subjected to cooling anaesthesia or euthanasia (Shine et al. 2015; Keifer and Zheng 2017). Until such time as sufficient data is collected to develop such a design, Warwick et al. (2018) recommend we hold off, and primary scientific advisory bodies continue to recommend against induced hypothermia in most situations (AVMA 2013; OIE 2019). Surely animal size, life history, and experience are significant and given the great physical and physiological diversity of Reptilia, ethologically informed design is crucial to avoid or mitigate the stress of unavoidable procedures. In fact, evidence of having such a design should be clearly evident in any proposed appeal for research support.

12.11 Animal Welfare Conclusions

Concerns of researchers and practitioners for the welfare of their animal subjects have grown greatly in recent years. Sometimes we do this as a matter of compassion and responsible stewardship, other times out of a concern for validity of research findings. Integrative thinking as exemplified in DEEP ethology will help minimise the neglect of variables outside one's traditional disciplinary experience.

Welfare is usually perceived as the circumstances that enable specific animals to meet their biological (including psychological) needs in specific contexts. This includes sanctuaries, farms, zoos, households, or research laboratories. These efforts should be pursued even in the light of bias attributable to the narrower needs of their human caretaker. What constitutes 'welfare' can be quite variable depending on context. Nevertheless, all animals have comparable basic needs such as those characterised by Maslow (1943) in his famous hierarchy of motivational needs. We can translate this original scheme into one emphasising biology: physiology (homeostasis, health), safety, sociality, individuality, and self-actualisation (reproduction, maximising direct or indirect biological fitness) (see Table 12.3).

Ethologically informed design considers natural history from multiple perspectives: including DEEP ethology (Table 12.2), in concert with a hierarchical view of the animal's needs (Table 12.3). Taken together, such consideration of description and function will enable care-givers to provide effective husbandry. But, in the culture of animal welfare-concerned traditions, several other design models have emerged. These include, for example, the 'five domains' model (nutrition, environment, health, behaviour, affective experience; see Mellor and Beausoleil 2015). However, methods of assessment for affective experience are likely to be variable in different reptile taxa and are in need of closer, species-specific, study. This need was emphasised by Benn et al. (2019) who looked at and evaluated the utility of both resource-based and animal-based factors and applied a proposed inventory of criteria to a specific endangered skink. Consistent with the comparative perspective of ethologically informed design, Benn et al. observed that environmental enrichment for captive reptiles might promote 'positive welfare states' in different ways for different species.

Before we undertake any intrusion into the life of another species, we must be thoughtful about our motivation. Where we have justified such an intrusion, the ethological attitude (Table 12.1) will hopefully improve welfare. To this end, I suggest the use of flexible checklists in which the elements of DEEP ethology—the variables relevant to development, ecology, evolution, and physiology (Table 12.2)—are easily documented and organised in a format convenient to interspecies comparison in as much detail as possible for a given taxon. Continuing developments in data management and access have the potential to make such an enterprise available. This approach resembles a kind of behaviour taxonomy—individualised for species—extended into the DEEP domains. For example, such lists could include, in the spirit of Warwick et al. (1992), species-typical behavioural patterns (see also Carpenter 1977; Greene 1988) and detailed inventories of social variables (McBride 1976). Animal care and welfare concerns could then be better

grounded in what is known about a particular species or the next most closely related species, or even species known to occupy comparable ecological niches. I think we can be hopeful that current rapidly emerging computer resources can facilitate development of such a resource.

Given the accelerating pace of environmental degradation, we cannot move quickly enough to secure the welfare of animals subject to the impact of human activities. We must also be unrelenting in our efforts to facilitate the activities of researchers and ensure the utility of their labours. These closely related, often mutually dependent concerns can be united and significantly enhanced by efforts to approximate the ethological attitude (Table 12.1) and the ideal of an ethologically informed design (EID, Table 12.3). Taken together, these efforts may significantly enhance our aspirations for responsible research and conscientious animal care and husbandry.

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Spatial and Thermal Factors

13

Phillip C. Arena and Clifford Warwick

Abstract

An understanding of spatial and thermal factors, two fundamentally intertwined elements, is essential to the health and welfare of captive reptiles; carers cannot address one without consideration of its influence on the other. This chapter highlights the need to recognise the many shortcomings of past practices, and urges individuals charged with keeping reptiles to become familiar and competent with new understandings revealed by research into the complex interplay of spatial and thermal factors. Essential to this issue is recognition that a ‘one-size-fits-all’ approach is never a good option. However, despite advances in our understanding of the spatio-thermal requirements of both wild and captive reptiles, there remains opportunity for abuse, exemplified by the highly restrictive rack system for housing snakes. In terms of spatio-thermal requirements, the modern, progressive reptile carer must become familiar, not only with species-specific requirements, but also the needs of individuals, taking into account the impact of seasonal and behavioural factors.

Keywords

Space · Temperature · Spatio-thermal · Home range · Enrichment · Rack system · Sociality · Behaviour · Body size · Overcrowding · Ectothermy · Hyperbasking · Welfare

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13.1 Introduction

The nature of captivity places constraints on organisms. These constraints can be multiform as the captive animal is no longer free to perform the same range of activities and behaviours that it can within the significantly less constrained environments experienced through living in the wild. These activities and behaviours include feeding, interactions with conspecifics, courtship, predator avoidance, wandering, hunting prey and, more specifically in the case of reptiles, thermoregulation. In captivity, all these expressions of a reptile's normal biology must be performed within the conditional limits as established by an artificially designed environment. In other words, every environmental need of the enclosed reptile must be met by the captor and, thus, the onus is on the captor to be familiar with all the species-specific requirements of the species held captive. This consideration is particularly notable in the case of zoos where the opportunity to educate exists and where some visitors not only appreciate a well-informed exhibition, but also the opportunity to ask questions of a keeper (Tribe and Booth 2003; Packer and Ballantyne 2010; Saunders 2013; Woods 1998; Yilmaz et al. 2017). In the case of reptiles and any other groups of animals that are similarly confined, species-specific knowledge may be lacking, thus knowing what is normal or abnormal can itself be a challenge. Also, fundamentally, conditions of captivity are such that expression of a normal or natural repertoire of behaviours probably becomes impossible; captive environments simply lack both the space and the stimuli present in nature (Burghardt 2013). There is a myriad of requirements that must be provided within any 'cage', but an enclosure ultimately serves to confine and in broad terms, this means a restriction of spatial requirements (Gillingham 1995; Greenberg 1995; Warwick and Steedman 1995; Gillingham and Clark 2023; Warwick 2023; Mendyk and Augustine 2023; Warwick and Steedman 2023).

As ectotherms, reptiles will orientate their bodies or move around the spatial environment to optimise the use of a heterothermic environment and thus achieve their thermal requirements (Lillywhite 2023). Thermal environmental variation itself requires space; one cannot have much temperature variation in a small area or in an area that lacks topography. Accordingly, spatial and thermal factors are, for the most part, inextricably linked to the needs of reptiles to fulfil their activity (and inactivity) demands so that they may select body temperatures that enable expression of a 'normal' repertoire of behaviours (Gillingham 1995). The present chapter explores spatio-thermal considerations of reptiles, highlighting both the importance of providing or failure in providing adequate space and temperatures for captive individuals.

13.2 Historical Approaches

Historically, determination of spatial needs and associated cage sizes largely was based on the requirements of the most recognised repositories of exotic species—zoological gardens. It was believed that the most effective way to maintain an 'intimate' relationship between the visitor and the animal being exhibited was to

limit cage size and simulate key aspects of natural habitat (Bacon and Hallett 1981). Thus, the development of early animal exhibits incorporated major input from graphic designers in order to present an illusion of space and to satisfy the exhibitory plans of the institution, as well as the convenience of the keeper. Some of these early displays may have appeared grandiose, but in fact still provided relatively small areas for the animals they contained. Nevertheless, such ‘diorama’ displays were quite successful and became the standard approach in the design of enclosures at many zoological (and museum) exhibiting worldwide (Bacon and Hallett 1981; Inasley 2007; Holmes 2009; Carter et al. 2015; Reiss 2015).

In those zoos, the size of enclosures provided to the exhibited species was also determined or influenced by the need to prevent injury or death in wild animals that were intent on escaping (Hediger 1950). For example, ungulate mammals would frequently charge against cage boundaries with dire consequences and, according to Hediger (1950), ‘*A practical step to avoid this is to keep such animals in cages so small that they are quite unable to develop sufficient dynamic energy for fatal fractures.*’ The approach was employed for varying periods that were considered long enough to enable the animals to ‘adapt’ to imposed physical boundaries. Following this period of adjustment, the animal could be moved to a more spacious enclosure. However, reptiles have a long history of confinement in enclosures (vivaria) that severely limit normal behaviours from the moment they are wild-captured or captive-born (see Gillingham 1995). In regard to zoological exhibitions, an early aim was to house the greatest diversity of reptile species possible, largely in an effort to highlight variation in the animal kingdom (Benbow 2000, 2004). There was certainly little notion of the role future zoos would play in conservation and nature education (Hoage and Deiss 1996; Reid and Moore 2014; Minter et al. 2018). Zoo cage size continued to be restrictive—reptile houses or exhibits would have deviated substantially from the norm were they to contain just a few individuals in a few extensive enclosures. That said, spatial conditions and related environmental thermal variation for privately held reptiles typically will be inferior to that of the professional zoo. Arguably, throughout the history of reptile-keeping, evidence-based welfare requirements have characteristically been secondary to practical housing and spatio-thermal considerations—a situation exemplified by the inappropriate housing commonly provided for snakes (Warwick et al. 2019; see also Mendyk and Warwick 2023).

However, today, more is known of the spatio-thermal requirements of reptiles. As Warwick (1995) noted in the first edition of this volume, satisfying the spatial requirements of reptiles involves more than just increasing the physical dimensions of an enclosure. In the 25 years since this statement, additional research has explored the complex interplay between spatial requirements and various aspects of a reptile’s life history such as behaviour (including social interactions and play) and thermal requirements (e.g. Huey 1991; Lillywhite and Gatten 1995; Burghardt 2013; Noble et al. 2014; Rose et al. 2017; Lillywhite 2023; Gillingham and Clark 2023).

13.3 Space Utilisation, Exploration, and Enrichment

Utilisation of space by reptiles is variable according to habits, ecological niche, and biological need. Food search, prey biology, reproductive drive, reproductive status, genetic transient behaviour, social pressure, climate, season, habitat state, environmental neophilia (enthusiasm for novelty), and other factors influence when and how much an animal needs or 'wants' to move around (Warwick 1990a, b; Kerr and Bull 2006; Warwick et al. 2013; Arena et al. 2014; Cunningham et al. 2016). In contrast to mobile activities are 'immobile' activities such as, rest, sleep, brooding, hiding from predators, sit-and-wait ambush tactics, aestivation, brumation, hibernation, injury- or disease-related energy conservation, and other factors (Huey 1982; Warwick and Steedman 1995; Hayes et al. 1998; Barten 2006; Funk 2006; Rossi 2006; Brasfield et al. 2008; Fleming and Skurski 2014; Wilkinson 2015). These activity profiles may not be reliably determined or set other than by the animal itself; thus, as expected, a human keeper can only make assessments and assumptions regarding how much space an animal needs or when it needs it based on their level of knowledge and understanding. Of course, such a situation is true of every captive animal scenario. However, one must also consider that the effects of spatially related stresses are regularly observed in captive reptiles, should one be sufficiently minded and informed to look for them (Warwick et al. 2013; Warwick 2023).

In general, very few studies have investigated the influence of captivity on any group of vertebrates, particularly in terms of behaviour, and it is only largely within the past decade or so that more detailed attention has been applied to examining the impact of captivity on the behaviour of, for example, mammals, when Ross et al. (2009) investigated the limitations imposed by captivity on the behaviour of gorillas (*Troglodytes* sp.) and chimpanzees (*Pan* sp.). This study focused on the way a captive animal utilised its spatial environment, and how such investigations can facilitate assessment of welfare. Similarly, a study of space utilisation by African wild dogs (*Lycaon pictus*) determined that an understanding of how captive animals use space can reduce the occurrence of stereotypic behaviour in captivity (Hunter et al. 2014). These studies are based on the premise that in order to most effectively address the impact of captivity on the welfare of individuals, one must first examine how the occupant utilises the space of its enclosure. This concept of effective usability was explored further by Browning and Maple (2019) who developed an approach ('metric') for assessing the quality of zoo animal (pygmy marmoset, *Cebuella pygmaea*) enclosures in three dimensions. Again, emphasis was placed on providing enough space to enable the occupant to have a high degree of choice in its proximity to conspecifics and resources such as furnishings—preferences that may be quite variable (Browning and Maple 2019). A study of habitat selection in the Panamanian grass anole (*Anolis auratus*) demonstrated the value of conspecific association in habitat selection whereby anoles of one species chose to associate with others of the same species rather than individuals of a related species. This behaviour highlighted the value of conspecifics as 'cues' in the selection of suitable habitat (Kiestler 1979).

Recent years have seen an increase in the number of investigations of the way reptiles utilise their spatial environment in captivity, and how this can be altered through provision of adequate space, increased opportunities for exploration, and other forms of enrichment (e.g. Case et al. 2005; Bashaw et al. 2016; Spain et al. 2020). In terms of enrichment in captivity, this can be defined as providing opportunities for an animal to express its natural behaviour in a naturalistic environment (Claxton 2011). Enrichment may include alterations to enclosure design and various stimuli, and presentation of novel objects (Brent and Belik 1997; Wells 2009). In order to quantify the impact of enrichment and consequently, the welfare of the captive animal, the presence (and absence) of specific behaviours is often used. However, again, in reptiles, until recently, this area had been rarely explored (see Warwick et al. 2013). Paucity of reptile-related research, with particular emphasis on the lack of enriched stimulating and novel environments was recognised by Burghardt (2013), who described such conditions as ‘controlled deprivation’ (Burghardt 1996; see also Mendyk and Augustine 2023). However, few recent studies, have noted that species-specific enrichment requirements of some reptiles may vary considerably (Rosier and Langkilde 2011). For example, Wheler and Fa (1995) investigated enclosure utilisation by Round Island day geckos (*Phelsuma guentheri*) and found that individual lizards utilised the environment in their enclosures in specific ways, preferring cage furnishings and hides and avoiding vertical glass walls. Lizard preference for specific areas within their enclosures was also influenced by the size of individuals (Wheler and Fa 1995). A study of captive corn snakes (*Pantherophis guttatus*) and chuckwalla (*Sauromalus ater*) determined that structural and thermal heterogeneity was vital if the captive individual was to express a normal range of behaviours (Rose et al. 2014).

Elements of enrichment can range from variable substrates to opportunities to explore, climb, and play (see Mendelson III et al. 2019; Mendyk and Augustine 2023; Warwick and Steedman 2023). Enclosure enrichment led to an improvement in the welfare (expression of positive behavioural indicators) among leopard geckoes (*Eublepharis macularius*) (Bashaw et al. 2016). Interestingly, in this study, greater levels of engagement were elicited with forms of enrichment that were linked to normal biological requirements (such as ‘thermal’ and ‘feeding’ enrichment), rather than to forms of enrichment based on novelty such as toys. This implied that the animals prioritised their behaviours, preferring forms of enrichment that addressed their physiological and behavioural needs (Bashaw et al. 2016). In a study of play, thick-toed geckos (*Chondrodactylus turneri*) were observed to engage in variable manipulation of objects in a weightless environment (Barabanov et al. 2015). Spatial memory and learning were recorded in the side-blotched lizard (*Uta stansburiana*) (LaDage et al. 2012) and the eastern water skink (*Eulamprus quoyii*) (Qui et al. 2018), whilst complex cognitive capabilities such as problem-solving were demonstrated in the anole (*Anolis evermanni*) (Leal and Powell 2012) implying that squamates have the capability to use spatial memory when performing everyday tasks such as defending territories and food acquisition. Studies such as these are beginning to highlight the complexity of reptilian behaviour and decision-making, and thus provide insight into their response to captivity and, by extrapolation, the

need for greater investigation and understanding of the spatial requirements of captive animals. However, again, few such investigations exist although significant approaches to enrichment in reptile enclosures may be more prevalent than reported in the scientific literature (Eagan 2019). In addition, due to the paucity of data for reptiles, the mammalian response to captivity continues to inform (see Wolfensohn et al. 2018) and be applied to the reptilian condition despite largely different sets of physiological, behavioural, and spatial needs. At a minimum, what such research shows is that the welfare of captive reptiles extends beyond providing 'adequate' space to infer the furnishing of space that promotes opportunities for interaction and exploration.

The greater the knowledge base regarding the welfare of reptiles in captivity, the more obvious it becomes that spatio-thermal requirements are not being adequately met. Stress responses are often expressed as abnormal behaviours such as hypoactivity, hyperactivity, and interactions with transparent boundaries (Warwick 1995; Warwick et al. 2013; Rose et al. 2017; Gangloff and Greenberg 2023; Warwick 2023; Arena et al. 2023). Key investigations to propose the use of behavioural responses to assess the welfare of captive reptiles listed over 30 behaviour-related signs of stress, over half of which were attributed to deficient and inappropriate environments, highlighting the potential impact of restricted spatio-thermal environments (Warwick 1990a, 1995; Warwick et al. 2013).

13.3.1 Home Ranges

It is virtually impossible to provide an enclosure that replicates an animal's natural habitat (Zwart 2001; Mendyk and Augustine 2023) or fully satisfies the innate (hard-wired) psychological and behavioural requirements of a wild animal, but if captivity is to be considered acceptable, then the appropriate size of an enclosure is one where the desire or tendency to escape no longer exists (Warwick 1995, 2023). In reality, this may never be attainable because captivity in and of itself (as stated earlier) implies confinement and restriction. Furthermore, many species regularly include naturally long-distance wanderers and others include individual population transients whose home ranges may vary by size, habitat, sex, and reproductive status (such as males wandering in search of females) and energy requirements (Kiestner et al. 1982; Rose 1982; Perry and Garland 2002; Sillero and Gonçalves-Seco 2014). Here, 'home range' refers to the area through which an animal moves in order to satisfy its normal requirements such as acquiring food, mates, and shelter (Powell and Mitchell 2012). Even strategic sedentary sit and wait or ambush species, such as alligator snapping turtles (*Macrochelys temminckii*) and viperid snakes that employ caudal-luring (e.g. *Cerastes vipera*) are known to occupy large home ranges (Riedle et al. 2006; Subach et al. 2009). Furthermore, seasonal wandering and significant home range extension occur in many species in the search for mammalian prey or mates (Gardiner et al. 2013; Mata-Silva et al. 2018), whilst proximity to den sites is a crucial factor influencing home ranges and the distances that northern latitude snakes will travel (Edkins et al. 2018; Shonfield et al. 2019).

Under natural conditions, reptiles occupy space in terms of regularly traversed home ranges. These are areas that an animal regularly roams in order to fulfil its requirements for foraging, hunting, reproduction, basking, and other behaviours. In the case of arboreal, semi-aquatic, aquatic, or fossorial species that climb, swim, or burrow, respectively, such environments can be measured in three fuller dimensions. Contrary to statements such as ‘herpetofauna’ do not move frequently (Row and Blouin-Demers 2006), field studies indicate that reptile home ranges are commonly extensive, and many animals regularly travel large distances (e.g. up to several kilometres) in search of prey, mates, and shelter (Baeckens et al. 2017). Furthermore, even these estimates of home range size are quite miniscule compared to the transoceanic migratory behaviour of, for example, loggerhead sea turtles (*Caretta caretta*) (Polovina et al. 2004; Boyle et al. 2009) and male estuarine crocodiles (*Crocodylus porosus*), which are known to travel many kilometres in a single day (Campbell et al. 2013). Table 13.1 provides examples of home range estimates for reptiles from representative orders as determined by minimum convex polygon method in relation to average snout to vent length.

As indicated in Table 13.1, the home ranges of even comparatively small reptiles vastly extend beyond the dimensions of enclosures typically used to house them and even though more modern institutions may provide enclosures that far exceed previously acceptable norms, spatial provisions in such institutions commonly equate to a fraction of natural home ranges. Merely providing basic presumed environmental, physiological, behavioural, and psychological elements within an enclosure does not negate innate, hard-wired, drivers for greater space (Warwick 1990a, 1995; Warwick et al. 2013; Warwick 2023).

A common view among reptile keepers is that because an animal’s essential needs are met (as perceived by its caregiver), then this reduces or eliminates requirements for them to engage in an array of normal behaviours common to their wild counterparts. This perspective, at its roots and within a spatio-thermal context, follows the thinking that an animal in nature essentially roams large areas because ‘it has to’ in order to secure what it needs. Some studies have shown that spatial need is influenced by habitat quality—what the environment provides (Christian and Waldschmidt 1984; Perry and Garland 2002; Verwaijen and Van Damme 2008; Stellatelli et al. 2016; Patterson 2018); thus, home ranges may be larger within poorer habitats (Perry and Garland 2002). Theoretically, this argument suggests that if captivity has provided all relevant requirements, corresponding drive states become redundant, and the animal does not need and does not ‘miss’ the natural world.

If correct, an animal contained within a high-quality enclosure—i.e. one that is abundant in terms of, for example, provisions regarding thermal range, food, water, habitat diversity, opportunities for key normal positive behaviours, social conspecifics where relevant, and general enrichment, ought not attempt to escape nor even harbour a drive to do so. However, if this were true, then there would be absolutely no need to utilise restrictive boundaries in an artificial environment, because the occupant would simply have no interest in exploring beyond the immediate provisions. This perception is essentially discounted by numerous observational and other evaluations concluding that, for example, many animals with

Table 13.1 Examples of home range estimates for reptiles from representative orders as determined by minimum convex polygon method in relation to average snout to vent length (SVL)

Order	Common name	Scientific name	SVL (average)	Home range estimate	Source
<i>Testudines</i>	Green turtle	<i>Chelonia mydas</i>	90 cm	1662 ha	Seminoff et al. (2002)
	Red-eared slider	<i>Trachemys scripta</i>	21 cm	23.35 ha	Slavenko et al. (2016)
	Gopher tortoise	<i>Gopherus polyphemus</i>	28 cm	3.2 ha (m) ^a 1.24 ha (f) ^a	Castellon et al. (2018)
<i>Crocodylia</i>	Nile crocodile	<i>Crocodylus niloticus</i>	410 cm	2200.7 ha (m)	Calverley and Downs (2015)
	Estuarine crocodile	<i>Crocodylus porosus</i>	700 cm	^b 23.9 ha (m) 5.9 ha (f)	Brien et al. (2008)
<i>Lacertilia</i>	Round Island day gecko	<i>Phelsuma guentheri</i>	12 cm	73 m ² (m) 31 m ² (f)	Gerner (2008)
	Australian sleepy lizard	<i>Tiliqua rugosa</i>	35 cm	4 ha	Bull and Freake (1999)
	Black-headed monitor	<i>Varanus tristis</i>	70 cm	40.3 ha (m) 3.7 ha (f)	Thompson et al. (1999)
	Komodo dragon	<i>Varanus komodoensis</i>	300 cm	278–530 ha	Ciofi et al. (2007)
<i>Serpentes</i>	Stephens' banded snake	<i>Hoplocephalus stephensii</i>	100 cm	20.2 ha (m) 5.4 ha (f)	Fitzgerald et al. (2002)
	Milk snake	<i>Lampropeltis triangulum</i>	150 cm	24 ha	Row and Blouin-Demers (2006)
	Eastern indigo snake	<i>Drymarchon couperi</i>	220 cm	201.7 (m) 75.6 (f)	Breining et al. (2011)
	South western carpet python	<i>Morelia spilota imbricata</i>	230 cm	17.6 ha	Pearson et al. (2005)

m male, *f* female

^aData for scrub habitat

^bData for late dry/mid-wet season

naturally large home ranges are less able to adapt to zoo environments, resulting in compromised welfare, often expressed as stereotyped behaviours such as pacing (Clubb and Mason 2003).

As indicated earlier, almost all captive scenarios, from reptiles kept as pets in private homes to those in the highest-quality zoological facilities, typically rely on barriers to forcibly confine animals to the human perceived 'all-providing' conditions. Therefore, a simple test could be applied to ascertain the degree of acceptability of enclosures to reptiles, which would be to remove all limiting barriers from captive situations—open the cages 24/7. Of course, opening such barriers would likely result in most, if not all, of the occupants exiting the areas. Accordingly, there is more to the issue of spatio-environmental needs than meets the eye of the

caregiver's belief that basic provisions negate need for space. Indeed, as previously stated, it is a common phenomenon among animals that activity patterns and home range use are significantly influenced by hard-wired drive states (whether for additional space, novel territory, reproduction, and other factors), as well as the biological need to control their own space (Dawkins 1990; Broom 1991; Owen et al. 2005; Ross 2006; Morgan and Tromborg 2007; Alligood and Leighty 2015; Kroshko et al. 2016; see also Warwick 2023), and these influences are not eliminated by 'abundant' captive provisions.

The evidence regarding home ranges stands contrary to the over-simplified assumptions by many (in particular hobbyist) herpetologists who wrongly claim (and frequently report in online reptile-keeping forums) that reptiles are stressed or 'agoraphobic' in open spaces on the basis that they may seek shelter or cover (see Mendyk and Warwick 2023). Indeed, the belief that agoraphobia (which is a human anxiety disorder) exists in reptiles is used as frequent justification for overly and severely restrictive enclosures (Warwick et al. 2013). Few studies have examined the impact of confinement on the welfare of reptiles. However, one such investigation of ball pythons (*Python regius*) found a significant rise in plasma corticosterone (i.e. a stress response) when animals were confined to a narrow container (a PVC—polyvinyl chloride) tube that prevented the snake from turning around) (Kreger and Mench 1993). Similarly, reptiles that are restrained in collection bags show increases in corticosterone levels (Tyrell 1998; Mathies et al. 2001). Although these are extreme examples of reduced space, they demonstrate that an elevated stress response is likely if a confined reptile (or likely, any other animal) is restricted to the extent that it is unable to express normal behaviours and exercise control over its environment.

In snakes, vindication for the approach of adopting highly restrictive enclosures is partly fueled by a long held erroneous belief that snakes do not need to stretch out, making them the only captive vertebrates denied by flawed information the ability to straighten their bodies at will (Warwick et al. 2019; Mendyk and Warwick 2023). Moreover, snakes regularly adopt near rectilinear postures during daily activity and this need to fully stretch should be a prime consideration in both the design and enrichment of enclosures (Warwick 1995; Warwick et al. 2018a, 2019). In the case of semi-arboreal and arboreal species, this requirement applies to both horizontal and vertical dimensions. The need to wander, explore, and problem solve are no longer traits of endothermic vertebrates alone (see Warwick 2023). It would perhaps be more honest of reptile keepers to acknowledge that typical vivaria are designed for human convenience rather than for the welfare of their charges.

13.3.2 Rack Systems

Considerations (and the lack thereof) regarding the spatio-thermal requirements of reptiles are arguably exemplified in reference to the rack systems used to house large numbers of reptiles (commonly snakes) within a limited area (Warwick et al. 2019; Cadenas and Martínez-Silvestre 2020). Rack systems, which effectively disregard basic principles of reptile biology and responsible husbandry, typically involve

individual drawers or tubs, each commonly containing an individual snake. In many cases, a single rack of uniformly sized containers will house snakes of different sizes, indicative of the application of a naïve standardisation of care in regard to species-specific or indeed ontogenetic variation in needs.

The extreme spatial restriction of rack systems results in a myriad of basic husbandry deficiencies. Opportunities for important and effective thermal selection by individuals according to variable physiological need simply do not exist. Instead, occupants are subjected to a largely uniform temperature that is governed and influenced by the physical design of the system, the position of the tub, and the estimates of the manager (Davis 2008). In many cases, the complete rack system is maintained at or close to the ambient temperature of the room with little variation; and both tropical and temperate species may be housed in the same room and subject to the same thermal regime (Davis 2008). Constant temperatures across all enclosures within a single facility or room are not only poor practice, but may result in stress with both short- and long-term welfare issues (Warwick et al. 2018a; Gillingham and Clark 2023). Although localised heating in the form of heat pads, tapes, wires, or probes may be installed, spatial restriction simply does not provide the animals with opportunities to willfully and diversely thermoregulate in order to match normal physiological variation or requirements (Arena and Warwick 1995; Gillingham 1995; Mendyk 2018).

Regardless of how heat is provided for the rack system, the result is thermal entrapment, which likely serves to compromise physiological processes within the individual. A recent study concerning the spatial requirements of snakes itemised 24 signs of captivity-stress (including interactions with transparent boundaries, open mouth breathing and co-occupant aggression), and 22 signs of clinical illness (including rostral abrasions, dystocia, and ventral contact dermatitis) associated with snakes confined to small environments (Warwick et al. 2019).

13.3.3 Space Utilisation: Sociality and Size

For many vertebrates (including fishes) the carrying capacity (stocking density) of the enclosure is often determined by its size or volume. However, as we have discussed, the physical dimensions of an enclosure do not necessarily imply holistic utilisation of every surface or furnishing by the occupant. In addition to satisfying the various aspects of a reptile's biology, meeting the spatial requirements of captive reptiles demands an understanding that these requirements may change as investigations reveal more of the complex nature of reptilian life histories. One such factor is sociality and the housing of individuals with conspecifics (see Doody 2023).

Members of the genus *Egernia* (Family, Scincidae) include highly social species of lizards that regularly form aggregations such as family groups (Duffield and Bull 2002; Chapple 2003; Masters and Shine 2003; Gardner et al. 2007). In some species such as Cunningham's skink (*Egernia cunninghami*), which occupies rocky habitat, family groups are common and individual lizards will selectively choose

specific sites where they defaecate (Chapple 2003). These latrines are not utilised for any other purpose, but specifically as sites for ‘scat piles’, which may act as spatial boundaries or social markers. For example, the pygmy blue-tongued skink (*Tiliqua adelaidensis*) also uses scat placement as a form of chemosensory marker or social signal (Bull et al. 1999, 2000; Fenner and Bull 2010) whilst scat placement by the related Australian sleepy lizard (*Tiliqua rugosa*) appears to have little social value (Fenner et al. 2015). In captivity, although the skink (*E. cunninghami*) may be kept in groups in order to emulate their natural social aggregations, whenever enclosure dimensions are provided, they are rarely of a dimension sufficient for latrines. For example, guidelines provided by Walker (2016) suggested that four adult skinks (*E. cunninghami*) can be maintained in an indoor enclosure with a floor area of approximately 1 m²; dramatically little space for a reptile that regularly utilises rocky outcrops and crevices and with recorded movements of individuals in the wild of up to approximately 70 m (Barwick 1965; Stow et al. 2001).

As such, severe spatial constraints may result in a form of social dissonance where animals are unable to interpret chemosensory cues or are not provided with enough room to exercise appropriate behavioural responses. Bernheim et al. (2020) found that restrictive captive conditions had a negative impact on reproductive behaviours of spur-thighed tortoises (*Testudo graeca*), proposing that female tortoises failed to emit the chemical cues necessary for initiation of precopulatory behaviour in males. At the very least, a more spacious, semi-natural enclosure was necessary for normal reproductive behaviour in this species (Bernheim et al. 2020). Furthermore, Mancera et al. (2017) showed that blue-tongued skinks (*Tiliqua scincoides*) would try to escape environmental stressors such as noise and cold and, again, smaller enclosures would restrict expression of appropriate stress avoidance behaviour.

It would be erroneous to assume that smaller species and individuals do not always require as much space as larger occupants (Warwick 1995). Smaller individuals may be regularly more active during hunting because of their highly mobile invertebrate prey as well as the exploratory behaviour necessary to locate them; also, smaller individuals feed more frequently and engage in greater predator avoidance and conspecific interactions (see Warwick 1995, 2023). Accordingly, the spatial needs of smaller species and individuals may be underestimated.

It is possible that larger species and individuals must overcome constraints of body size (such as frictional forces) when they are required to hunt or escape. Indeed, it may be energetically costly to accelerate a larger body mass (Higham 2019). However, one must be cautious when attempting to apply generalisations regarding the influence of size on the physiological performance and spatial demands across and within taxonomic groups. For example, within the genus *Varanus* (family Varanidae) (that includes species that vary in size of almost four orders of magnitude), larger species tend to be foragers whilst smaller species tend to adopt a sit-and-wait feeding strategy (Clemente 2006; Clemente et al. 2009). Heavier individuals were also found to have the fastest speed and acceleration although both factors were related to the topography with faster species occurring within open habitat. The form

of substrate may also have an influence on performance. For example, Glasheen and McMahon (1996) found that smaller individual basilisks (*Basiliscus basiliscus*) were able to generate greater relative forces that enable them to more effectively run across water than larger conspecifics. In a similar fashion, hatchling green iguanas (*Iguana iguana*) have been observed to ‘run bipedally’ across water, whereas adults swim (Burghardt et al. 1977). Similar reasoning applies when a lizard is moving quickly across a surface such as soft sand—larger individuals cannot generate the force required to oppose the greater gravitational forces and move themselves efficiently over these surfaces. However, again, within the varanids, substrate type was shown to have no effect on either speed or acceleration (Clemente 2006).

Accordingly, the impact of body size on spatially associated behaviour may be quite complex and is also influenced by foraging mode; for example, a sit and wait predator may not have to move far to acquire prey. Thus, in principle, some sit and wait predators can afford appropriate increases in body size and reproductive state (in most cases, pregnant or gravid females are less active than non-gravid individuals; see Schuett et al. 2013). Therefore, appropriate and adequate space may in fact, be of proportionately greater importance for smaller species and individuals if they are to be permitted to express a ‘normal’ repertoire of locomotor behaviours.

13.3.4 Overcrowding

Overcrowding may manifest overtly or covertly. Overt overcrowding relates to the plain physically excessive numbers of animals in a given space (Warwick et al. 2013, 2018a; Arena et al. 2014). Overt overcrowding is relatively easy to identify and may result in, for example, crushing injuries, asphyxiation, co-occupant aggression, and competition for food and basking sites. Covert (or crypto) overcrowding may not be as apparent and relates to the inability of all animals in an enclosure to access any one of its features at any one time (Warwick et al. 2013, 2018a; Arena et al. 2014). For example, larger, less populated, enclosures may not appear overcrowded, but may not allow free access for all occupants to use a water container or basking site at one time (i.e. too few or disproportionately small provisions for the number of animals); causing an enclosure to be covertly overcrowded. Both overt and covert overcrowding are often seen at intensive farming facilities of sea turtles (Arena et al. 2014) and most likely to occur in the freshwater turtle farming schemes of China where large quantities of turtles are raised in a multibillion dollar industry, supplying food, medicinal products, and the pet trade (Haitao et al. 2008) and crocodiles (Tosun 2013), when the carrying capacity of an enclosure results in reptiles scrambling or perching on top of each other to access a radiant heat source in order to satisfy thermoregulatory requirements. However, the problem is also observed in zoos (see Almazan et al. 2005), laboratories, the pet trade, and private homes where multiple animals share single poorly conceived environments. As a final point here, when housing more than a single animal, keepers must be familiar with life history traits of captive species, in particular, with managing sex ratios.

Male reptiles, for example, copperhead snakes (*Agkistrodon contortrix*) in the wild may seasonally engage in agonistic rivalry behaviours towards other males (Schuett 1996; see also Doody 2023), and should not be housed together in captivity (Whiting and Miles 2019). This principle also applies to females that may display aggression towards other females (Oonincx and van Leeuwen 2017; Whiting and Miles 2019).

13.3.5 How Much Space Is Enough Space?

It is probable that captive reptiles do not and cannot have enough space to meet their inherently natural and normal needs. Although space is often emphasised as a requirement (e.g. in the housing of tortoises (*Gopherus* spp., *Testudo* spp., *Agronemys* spp., *Centrochelys* spp. and box turtles *Terrapene* spp.)—see Boyer and Boyer 2019), spatial considerations for housing reptiles (particularly indoors) are likely to be governed by keeper convenience rather than species-specific behaviour. Reptiles are commonly maintained in overly restrictive permanent enclosures, but many species are often sold as novelty items along with small housing kits that, whilst satisfying market appeal, impose a severely restrictive environment for the occupant (Warwick et al. 2018b). Of course, there are situations when a small enclosure may be acceptable and indeed, unavoidable. This includes short-term confinement of reptiles, such as for essential clinical, quarantine, or transportation purposes (Warwick 1990a, b; Warwick and Steedman 1995; Warwick et al. 2019), assuming such confinement is for the benefit of the animal. Minimally, space should provide opportunities for expression of an appropriate range of normal behaviours; access to an adequate range of thermal zones; ability to fully extend bodies and travel in any dimension; ability to accelerate, decelerate, and stop without injuriously impacting boundaries; ability to make rapid descents without injury and conditions where spatially related physical injuries and diseases or psycho-behavioural stress signs are absent.

Where appropriate, enrichment and hiding sites should be provided so that an alarmed or otherwise stressed animal may take refuge without the need to resort to uncontrolled flight. An observational study of the spatial requirements of 65 species of snakes found 31 species regularly stretched to full length and adopted rectilinear or near rectilinear postures (Warwick et al. 2019). Thus, snakes, which have long been wrongly assigned especially diminutive enclosures, should, as an absolute minimum, be able to fully extend their bodies within an enclosure when they choose to do so.

Warwick et al. (2018a) proposed a method of determining absolute minimal spatial provision for captive animal (including reptile) enclosure sizes in commercial situations. This process involves visualising the animal in a coiled or rolled ‘ball like’ state and multiplying this estimated dimension by a factor of 10. For arboreal or semi-arboreal species, this same principle would apply to the vertical enclosure dimension. For small species or individuals, a proposed minimum primary dimension was 100 cm with all other dimensions no less than 40% of this (Warwick et al. 2018a). However, this algorithm is intended to indicate absolute minimum enclosure

dimension primarily for commercial establishments in order to improve commonly overly minimalistic approaches utilised by those sectors. It should not be confused with aspirational and progressive approaches to accommodation including requirements previously discussed in this chapter.

Providing meaningful space infers more than marginally expanding small quarters; it implies allowing substantial room, in association with naturalistic (or natural) conditions, so that in most cases, the desire or attempt to escape is not created. The spatial requirements of some reptiles (for example, those that exhibit migratory tendencies) may never be fulfilled, even with areas measured in hectares or kilometres. Nevertheless, if allowing sufficient room to cater for animal well-being seems impossible, then it is their very presence in captivity that requires review.

13.4 Thermal Considerations

It could be argued that no organism is entirely independent of ambient temperatures, and as stated earlier in this chapter, for ectotherms, ambient temperature and individual thermoregulation are key factors defining and governing the lives of reptiles (Fernandez et al. 2011; de Andrade 2016; Nowakowski et al. 2018; Taylor et al. 2020). Accordingly, the need for reptiles to express thermal choices is fundamental to their health and welfare (Heatwole and Taylor 1987; Arena and Warwick 1995; Lillywhite and Gatten 1995; Lillywhite 2023). For the majority of reptiles, temperature is regulated primarily through behavioural means, such as shuttling between warmer and cooler areas and to a minor extent, through physiological processes (Sears et al. 2016).

Within this general scheme of ectothermy, most reptiles may be classified as either heliotherms (their prime source of heat being derived from sun-basking) or thigmotherms (their prime source of heat is derived from direct conduction with warm surfaces) (Carter et al. 2012; Garcia-Porta et al. 2019; Lillywhite 2023). However, reptiles, at least diurnal species, likely utilise a combination of these approaches to satisfy their thermoregulatory requirements (Fei et al. 2012), selecting a range of temperatures at any point in their activity cycles in response to specific needs whether on land or, in the case of aquatic and semi-aquatic species, in water. For example, some species of freshwater turtles are able to maintain relatively stable body temperatures via semi-aquatic basking (exposing the carapace to the air whilst submerged) or by aquatic basking (altering their position in response to the vertical temperature stratification within water bodies) (Chessman 2019).

In a similar fashion, sea snakes thermoregulate by 'tracking' appropriate temperatures within the water column, whilst the latter, when on land, utilise strategies such as basking and kleptothermy (stealing heat) by sharing burrows with seabirds (Brischoux et al. 2009; Heatwole et al. 2012). The latter behaviour has also been recorded for the tuatara (*Sphenodon punctatus*) (Corkery et al. 2018). In terms of habitat selection, a study of the thermoregulatory behaviour of three species of sympatric Mediterranean lizards (*Podarcis* spp.) found that individuals

were able to maintain their preferred body temperatures within narrow limits by moving between microhabitats (patches) of variable thermal quality (Sagonas et al. 2017). Sears et al. (2016) also highlighted the importance of the spatial distribution of ‘thermal microclimates’ in the regulation of body temperature in spiny-tailed lizards (*Sceloporus jarrovi*).

Key to determinations of this thermal heterogeneity has been the use of physical models in establishing operative temperatures—the temperature to which a non-metabolising object would equilibrate in a particular environment (Bakken and Gates 1975). To determine operative body temperature, various physical models are used to approximate the size, shape, and reflectivity of live animals (Shine and Kearney 2001; Seebacher et al. 2003; Tracy et al. 2007). These predictions take into account heat exchange involving radiation, conduction, and convection (Shine and Kearney 2001).

In captivity, spatial limitations certainly act to reduce this thermal ‘landscape’ and thus compromise the ability to effectively thermoregulate. As mentioned earlier, the spatial and thermal environments are inextricably linked, and one cannot have much temperature variation if there is little space and reduced structural heterogeneity. In nature, the thermal requirements of a basking reptile in the wild (e.g. heliothermic lizard) are achieved through a combination of modes of heat transfer, all of which would be influenced, not only by the nature and temperature of the primary heat source, but also by the physical nature of the surrounding environment, which acts to provide secondary sources of heat (Angilletta 2009; Kearney et al. 2009; Battles and Kolbe 2018; Battles et al. 2018).

13.4.1 Thermal Gradients and Zones

Contrary to popular claims or aspirations (as evident through current practices in reptile-keeping and fueled by arbitrary husbandry practices; see Mendyk and Warwick 2023; Warwick et al. 2017), it is practically impossible in most captive situations to provide thermal heterogeneity that even approximately matches natural thermal conditions, especially within small enclosures. Even where larger environments are involved, misinterpretation or misjudgement of space versus thermal heterogeneity often arises from presumptions that total linear length (extreme point-to-point within an enclosure) temperature variation provides meaningful variation, whereas total variation in some larger enclosures may register temperature differences of, for example, 15 °C (which may theoretically suit some species), actual usable thermal options (the important feature of gradation) may be diminutive or practically non-existent. Thermal gradation zones (i.e. thermally distinct and behaviourally relevant useable areas of space) infer that each zone is of adequate size to enable one or all of the occupants, at any single time of their choosing, to occupy that zone. Each zone must, therefore, offer a temperature relative to the next higher or lower temperature zone. Thus, a gradient variation of 15 °C may actually include micro-zones of incremental changes that singly are too small to physically accommodate an individual for optimal thermoregulation.

Accordingly, multi-zone thermal environments provide for animals to occupy an entire region of an enclosure that offers important thermal variation, and all zones ought to be of sufficient size and enrichment complexity to accommodate normal behaviour, indeed to encourage normal behaviour. This zonal gradation requires significant space—for example, as proposed here, five thermal gradation zones may require at least five square metres of ground area, which may provide essential thermal conditions for smaller individuals less than 1 m in length (as determined by the range of desired temperatures and intensity/form of the heat source).

Numerous studies have demonstrated the complexity of temperature selection in reptiles. For example, ring-necked snakes (*Diadophis punctatus*) will select temperatures 3 °C higher than their usual preferred temperature when they share sites in aggregations of conspecifics, whereas solitary snakes prefer sites where the temperature is similar to their usual preferred body temperature (Cox et al. 2018). Some species of python are able to metabolically raise their body temperature during incubation of eggs (facultative thermogenesis) (Harlow and Grigg 1984; Stahlschmidt et al. 2011; Brashears and DeNardo 2015), and other reptiles, for example, leatherback turtles (*Dermochelys coriacea*) (Bostrom et al. 2010) and tegu lizards (*Salvator merianae*) (Tattersall et al. 2016), possess limited but distinct endothermal capacity. Also, reproductive state can influence thermal preferences in reptiles, and reproductive success can be dependent on temperature. For example, oviparous species such as the spiny lizard (*Tropidurus spinulosus*) will select higher temperatures when gravid (López et al. 2018). The intensity of courtship in male red-sided garter snakes (*Thamnophis sirtalis parietalis*) has been shown to be directly related to the length of cold temperature dormancy periods (Krohmer 2004).

Finally, it is well known that temperature has a profound effect on reptilian digestion (Plasman et al. 2019) and reptiles will select higher body temperatures when fed than when unfed (Regal 1966; Lang 1979; Sievert 1989). Studies such as these have clear implications for captive animals and require due to consideration of whether animals are housed individually or with conspecifics in addition to the provision of appropriate retreats, refugia, and basking sites (these may include appropriate semi-aquatic sites and sandbanks in the case of turtles and crocodiles).

Despite recognition of the importance of temperature as a key factor governing the lives of reptiles, in captivity, major transgressions of this basic principle occur, leading to failure to identify suboptimal or even detrimental conditions. For example, one phenomenon seen in captive reptiles involves ‘hyperbasking’, which is a state where individual reptiles spend excessive portions of their daily activity budgets basking (Warwick 1995; Warwick et al. 2013). Essentially, hyperbasking typically occurs in several situations, the most common being when a heat source does not provide sufficient heat for an animal to elevate its body temperature to a desired level (Warwick et al. 2013; Benn et al. 2019). Another scenario concerns large individuals in environments where heat sources do not adequately radiate over the animal’s body. In nature, radiant sources (such as the sun) are general and thus can, where required, heat the whole animal. In captivity, heat sources (such as lamps) often can warm only part of an (especially large) animal causing it to prolong basking in an endeavour to elevate the temperature of its entire body. However,

not uncommonly in nature, reptiles will partially expose themselves to sunlight, i.e. not their entire bodies (Heath 1964; Seebacher 1999; Gibson et al. 2015; Black et al. 2019).

The logical conclusion from this behaviour is that thermal zones in captive situations should include both areas where the animal can exposure its entire body to heat resources within the thermal zone as well as areas where heat within the zone is more patchy—a ‘thermal mosaic’, enabling selective heating of particular areas of the body. A further scenario is when an entire thermal zone represents the only acceptable (even if suboptimal) environmental temperature in an enclosure, thus the animal occupies that zone for prolonged periods (Warwick 1990a, 1995). Reptiles may also manifest behavioural fever (elevation of body temperature due to stress or disease) (Kluger 1979; Frye 1991; Cabanac and Gosselin 1993; Cabanac and Bernieri 2000; Warwick et al. 2013; Rakus et al. 2017).

‘Hyperbasking’ may also occur where an animal unsuccessfully attempts to achieve a higher target temperature, which could incur important reductions in immune competence and homeostasis. Hyperbasking is extremely common in poor conditions of captivity, and seems largely unrecognised by keepers. Many may take for granted seeing reptiles basking for long periods—perhaps on the false presumption that such behaviour is always normal or healthy. However, hyperbasking is now recognised as abnormal and a form of maladaptation, rather than normal thermoregulatory behaviour (Warwick et al. 2013; Mendyk 2018; Warwick 2023). Accordingly, all forms of hyperbasking may be considered as negative thermoregulatory compensation behaviours (Warwick et al. 2013; Warwick 2023).

Thermal needs not only vary in response to physiological requirements (e.g. post feeding), but also seasonally. Here, knowledge of behaviour in the wild becomes crucial to understanding the requirements of reptiles in captivity. Many reptiles will experience seasonal periods of reduced activity, in response to fewer natural resources and metabolic conservatism or as part of their reproductive strategy (e.g. post mating, when there is no longer a need to seek out potential mates) (Bull et al. 1991; Christian et al. 1999; Seebacher 2005; Berg et al. 2017). At these times, provision must be made to enable the captive individual to meet its thermoregulatory requirements. Therefore, adequate space is needed so that thermal inputs can be adjusted—there must be enough room provided to enable the individual to escape heat if required, and this may include the provision of sufficient and appropriate substrate to enable an animal to bury itself or seek other suitable seclusion.

13.4.2 Subtle Thermal Changes May Be Critical

It is widely accepted that subtle differences in thermal conditions can influence a variety of physiological and developmental phenomena in reptiles. For example, immune competence is closely linked to temperature and physiological state, which can result in protective behavioural fever (e.g. Kluger 1979; Frye 1991) or alternatively, disease-associated voluntary hypothermia (Warwick 1991). Also, in species that exhibit temperature-dependent sex-determination, ambient temperature

variation of a few degrees can have a pivotal influence on the sex of offspring (Mitchell and Janzen 2010, 2019; Singh et al. 2020). Therefore, thermal environments require gross and subtle variations in order to provide reptiles with essential temperatures for normal life. Furthermore, the conceptual landscape and horizon for these gross and subtle variations are extensive and arguably ought to include relevance to species-specificity, season, physiological state, size, stressors, and diet—each of which requires multiple considerations. These issues highlight the need for a detailed understanding of spatio-thermal requirements of reptiles and for the necessary provision of a wide range of temperatures and multiple thermal zones extending beyond the commonly narrow limits based on presumed preferred body temperatures.

13.5 Animal Welfare Conclusions

Despite growing interest in the welfare of captive reptiles, spatial and thermal considerations for these animals continue to fail to meet biological norms. Whilst there may appear to be progressive provision of recommended standards and guidelines for husbandry, in practical terms, much of this information is not evidence-based, and cannot satisfy all spatio-thermal criteria. Relevantly, when one drills-down into the rationale and ‘evidence-base’ for both claims and common practices that promote or result in reptiles being confined to their typical spatially minimal vivaria, one quickly discovers a paradigm devoid of scientific merit.

Furthermore, regardless of increasing understanding of spatio-thermal requirements for reptiles, the multimodal influence of space and temperature (and indeed, water—Kearney et al. 2018), and the value of enrichment in improving the welfare of captive reptiles (Londoño et al. 2018), there remains an ongoing tendency among some to disregard important welfare biology—perhaps exemplified by the impoverished constraints of the snake rack system (see Warwick et al. 2019; Cadenas and Martínez-Silvestre 2020). In whatever form, smaller spaces offer fewer opportunities to provide the habitat variation and essential features important to overall health and welfare, and likely directly impose specific stressors (Martínez-Silvestre 2014). Thus, a paradigm shift towards consistently providing larger environments should be a benchmark of best practice. Larger, well-designed enclosures with known thermal gradient mosaics may also offer greater opportunities for understanding species-specific spatio-thermal requirements. For an ectothermic vertebrate, spatial provisions and the physical nature of an enclosure must aspire to allow the animal to manifest its daily and seasonal cycles of preferred body temperatures across a diversity of relevant contexts.

Reptiles may be nocturnal, diurnal, or crepuscular; tropical or temperate; fossorial or arboreal; terrestrial, semi-aquatic, or aquatic with preference for habitats from the topographically very barren to structurally complex with an abundance of retreats. Meeting the spatio-thermal requirements for this highly variable class of animals is particularly difficult given that the biological needs of a large number of species from this group remain poorly understood or investigated (Oonincx and van

Leeuwen 2017). Without this knowledge, it is impossible to confidently provide for spatio-thermal issues in the context of the health and welfare of captive reptiles. However, home range studies demonstrate that reptiles are considerably, often dramatically, more active than frequently presupposed, and there are no good reasons to believe that the wide spaces of nature are not relevant to captive reptile welfare. Furthermore, even with the promise of enrichment, natural behavioural responses cannot be expressed if spatio-thermal requirements are not adequately addressed, and moreover we can be confident that there are many more important spatio-thermal needs than we currently understand.

Regardless of normal sedentary or nomadic traits, animals in nature move around expansive habitats in search and location of appealing environments, and this activity may be regular. Within captivity, the environment is typically predetermined and set, not by climate or natural features, but by characteristics perceived relevant by human custodians. Realistically, the chances are remote that conditions being imposed would match the gross and subtle influences driven by nature. As a result, captive reptiles are forcibly confined and restricted to environments that they would unlikely freely select.

Captivity may be most aptly considered as a situation where animals are effectively trapped, rather than accommodated. Options for an individual animal to select its normal preferences for self-maintenance and well-being are largely removed by its presence in captivity. As captives isolated from normal contextualised regulatory activities, reptiles are fundamentally dependent on the knowledge and practices of their keepers. Accordingly, keepers have an overriding obligation to address all of their charge's positive needs regardless of inconvenience to the manager or to refrain from holding reptiles in captivity.

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Nutritional Considerations

14

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Abstract

Appropriate nutritional husbandry for captive reptiles is inherently challenging. The health and welfare of all reptiles, like any other animals, is linked to the role of nutrition, which should be regarded as a continuum, beginning with selection or gathering of food sources and ending with elimination of waste products. Reptiles have evolved to represent all known foraging strategies, and the various alimentary tract morphologies exemplify this complexity. Many reptiles have long life spans and, possibly more so than other taxa, can be outwardly very forgiving of short-term nutritional mismanagement resulting in compromised long-term health. Because nutrition is complex and does not happen in a vacuum, often the impacts of correct and incorrect provisions get lost in a myriad of variables that contribute positively and negatively to the overall health of captive reptiles. Quality of diet and appropriate mode of presentation are essential to health, and natural foods are preferable. This chapter will provide detail about how reptiles acquire and process food items and to what end (what are the target nutrient levels met by a reasonable, appropriate diet). Furthermore, this chapter

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presents some of the challenging factors associated with nutritional husbandry of reptiles in a managed setting—provision of appropriate moisture and/or UV light, selection of specific diet ingredients, and what do we still need to learn.

Keywords

Apprehension · Digestion · Assimilation · Elimination · Diet · Nutrition principles · Target nutrients · Light · Health · Disease · Injury · Stress · Treatment

14.1 Introduction

When considering the health and welfare of any animal, the role of nutrition—with all of its obvious, and more subtle ramifications—must be examined. Nutrition should be regarded as a continuum, beginning with selection or gathering of food (including water) sources, initial processing, digestion, assimilation of nutritive and water constituents and, finally, elimination of waste products including non-nutritive fibre, particularly indigestible bones, foreign matter accidentally ingested, microorganisms, mucus, and senescent epithelial cells lining the alimentary tract. The immediate needs of the animal such as orderly growth and maintenance of cardiopulmonary, digestive, immune, haematopoietic, endocrine, reproductive, and nervous system functions are but some of the vital processes that rely on an adequate intake and processing of metabolites. Furthermore, it has been found that human moods and other neurological functioning are directly affected by diet (McMillan et al. 2011; Chaput 2014; Strasser and Fuchs 2015). Thus, even the psychological ‘health’ of a creature in captivity may be linked to the food that it is fed and the manner in which it is presented. Because moisture is intimately related to food processing, digestion, assimilation, faecal and urinary waste elimination, water consumption and its provision in a suitable manner must also be regarded. Also, the condition of the food-gathering structures often determines the ability of an individual to bite and/or reduce the size of its fare, swallow a bolus of food, and commence the initial and later processes of food digestion.

Therefore, with such considerations in mind, it should not be surprising that appropriate nutritional husbandry for captive reptiles is inherently challenging. For mammals, well-studied domestic animal models exist, and there are ample opportunities for liberal application of lessons learned from one species to another; however, for the vast majority of reptiles, this is not the case. Reptiles have evolved to represent all known foraging strategies, and the various alimentary tract morphologies exemplify this complexity. Furthermore, commonly accepted energy metabolism calculations for mammals have little application across this group of vertebrates (see Lillywhite 2023).

Many reptiles have long life spans and, possibly more so than other taxa, can be outwardly very forgiving of short-term nutritional mismanagement resulting in compromised long-term health. Because nutrition is complex and does not happen in a vacuum, often the impacts of correct and incorrect provisions get lost in a myriad of variables that contribute positively and negatively to the overall health of captive

reptiles. Many herpetoculturists have successfully maintained and even reproduced a wide variety of reptiles with a 'less-than-scientific' approach to nutritional management. Diet ingredients, amounts, physical form, provision timing, delivery methods, environmental conditions, and other nuances are all adjusted according to years, if not decades, of trial and error experiences. Where beneficial to animals, such individuals and groups should be commended for these efforts. Conversely, herpetoculturists also have used these same approaches to impose deleterious diets yielding catastrophic results.

Beyond this, a lack of documentation and reasonable application of the scientific method have, in some cases, confounded our ability to effectively learn the most from 'errors' and solve pressing nutritional issues across a wide variety of reptile species. For the long-term health and welfare of captive reptiles, it is imperative that we apply scientific methodology, critically examine successes and failures, and learn from these practices and techniques to ultimately improve the nutritional care of reptiles. Without a consistent, critical approach to nutrition management, we are destined to repeat the same mistakes from generation to generation (of both herpetoculturists and animals), as evidenced by repeated incidence of the same metabolic disorders (e.g. metabolic bone disease, obesity, steatitis, gout) over the last 50 years (and likely the next 50).

Appropriate diets can be created for many species, whether reptile or otherwise, following a consistent, standard template to evaluate existing information and relevant experience. In some cases, there is a paucity of data on which to function (from specific nutrition and nutrient metabolism details to basic natural history). Following a consistent approach helps to identify data deficiencies and limitations to what and how we apply the information available. The information to consider includes, but is not limited to: foraging strategy and digestive structure (food identification and acquisition, what an animal is likely to consume, how it consumes it, and how it digests the food into nutrients once it is consumed), physiological state of the animal (e.g. growth, maintenance, reproduction), development and application of target nutrient values (what are the levels/amounts of nutrients an animal needs to survive, grow, reproduce), consideration of the food items available on an annual or seasonal basis and their nutrient profiles, and any noteworthy species- and/or taxa-specific needs. Beyond this, the basic natural history of a species needs to be considered to provide the context within which to apply the nutrition-specific information available.

Diet formulation involves an evolutionary process of nutritional physiology and nutrient biochemistry, and the nuances of captive husbandry need to be considered in order to tailor the diet to the individual animal situation (e.g. temperature, humidity, light cycle, type and quality of light exposure, space, activity level). Developing appropriate diets for reptiles is a dynamic and complex task that begins before an animal or species is brought into managed care and continues throughout its life. Constant evaluation and re-evaluation of the myriad of variables that contribute to the physiology of the animal (e.g. diet and nutrients available, environmental factors) is imperative to maintain appropriate nutrition and welfare of these animals throughout their lives.

Gross overt and subtle covert aspects of a reptile's environment, biology, and habit can be considered relevant to nutrition. At the gross overt level, because most reptiles are functionally hetero- or ectothermic, their deep-core body temperatures and, thus, their metabolism are determined largely by external heat sources; therefore, the effects of inappropriate ambient temperature, as well as improper photoperiod and relative humidity, are often intimately associated with the overall nutrition and health of these animals (see Lillywhite 2023). At the subtle covert level, there are few completely carnivorous or herbivorous reptiles, because they can ingest and sometimes benefit from the gut contents of their prey; the practice of 'gut-loading' small invertebrates such as crickets and locusts, takes advantage of this paradigm. One of the few reptiles that usually subsists on a strictly animal protein diet is the egg-eating snake (*Dasypeltis* sp.); however, when eggs are not available, this snake may hunt for and eat small rodents and birds and, therefore, consumes their gut contents, which may contain plant materials.

Many solitary or non-colonial animals display some degree of social dominance and territoriality when kept together, and the behaviour of these creatures can impact their appetite and access to food (see Doody 2023; Mendyk and Augustine 2023). Even when a splendid menu is offered to a group of reptiles, if one or more dominant individuals bully or keep lower ranked individuals from a favoured feeding site or a water source, the latter animals will be harassed and are likely to languish and die (Warwick 1990; Warwick et al. 2013). Thus, the effects of interactive social stress and other forces on nutrition must also be considered. Conversely, social housing may have psychological and physiological benefits that are absent when animals are completely isolated to avoid food competition (see Burghardt and Layne-Colon 2023). Many captive reptiles die because they refuse to feed, even when the most tempting items are offered. It is crucial to understand the natural history of captive animals. For example, it is a normal behaviour for some snakes, especially African royal ('ball') pythons (*Python regius*), to exhibit anorexia during the approximately six months of heat and drought each year (Donoghue and McKeown 1999; Rizzo 2014). Even when they are maintained in comfortable temperatures and humidity, and provided with favoured food items, it is not unusual for these snakes (especially wild-caught individuals) to refuse to feed. The deleterious consequences of human interference or disturbance (conditioned by the very nature of captivity) can also severely affect the appetite and, therefore, health of captive animals. Improper dietary supplementation with vitamins and minerals can lead directly or indirectly to iatrogenic or artificial diet-related imbalances and other nutritional disorders.

There is much reported in the literature, both peer-reviewed and popular, about nutritional husbandry of reptiles. Some of this information is rooted in practical years of experience and backed by detailed and rigorous testing through science, whilst much is not. This chapter will provide additional detail about how reptiles acquire and process food items and to what end (what are the target nutrient levels met by a reasonable, appropriate diet). Each topic will be discussed utilising a 'holistic' approach that considers the entire animal and the conditions of its captivity that may impinge on its overall health—and survival. Further, this chapter will consider some of the challenging factors associated with nutritional husbandry of

reptiles in a managed setting, including the provision of appropriate moisture and/or UV light, selection of specific diet ingredients, various miscellaneous factors, and what do we still need to learn. Also, some clinical implications, recommendations, and treatment of conditions linked to compromised nutrition are mentioned where appropriate, bearing in mind that this volume is not a veterinary manual.

14.2 Selection of Food

A thorough understanding of a species' natural history and food preference is essential when providing captive diets, as diets need to be both accepted and nutritionally sound (Frye 1991a, b, 1994). However, providing managed animals with nutritionally appropriate diets can be challenging, particularly for reptiles, as their nutritional needs are poorly understood. Furthermore, food selection is an important aspect of a species' natural history that can affect the interest and acceptance of food in captivity. Availability of food as it relates to natural history is an important aspect of husbandry as well and should be taken into consideration when providing diets to captive specimens (Kawata 2008). Ideally, the nutrient composition of diet items should reasonably mimic the nutrient composition of their 'natural' diet items (i.e.—the goal is to match the nutrient profile, not necessarily the botanical or physical form, even though physical form can be vitally important). This 'dietary mimic' element can be difficult to ascertain, because field studies are lacking and, when available, usually do not provide the documentation needed to determine nutrient content. Beyond this, many studies are focused on single season or location preferences rather than long-term observations that can capture seasonal preferences through annual cycles and/or items sought out during specific physiological states (e.g. healing, reproduction). Furthermore, the nutritional composition of commercially produced diet items may not necessarily be comparable to their wild counterparts (Dierenfeld et al. 2009). For example, fruits (and some vegetables) cultivated for human consumption tend to be high in sugar and low in fibre (e.g. apples, bananas). Such a nutrient profile is inappropriate for most reptiles, as the 'fruit' they would encounter if, free-ranging, would be considerably higher in fibre (possibly also secondary plant compounds) and much lower in sugar (sugar to fibre ratios >2:1 in Table 14.1).

Table 14.1 Examples of comparative sugar to fibre ratios in produce commonly used in reptile diets (based on the United States Department of Agriculture Nutrient Data Laboratory 2018)

Sugar: Fibre Ratio		
>2:1	2:1–1:1	<1:1
Grapes	Carrots	Green beans
Bananas	Rutabaga	Cauliflower
Pears	Green and red peppers	Turnip, dandelion greens
Apples	Winter squash	Endive
Oranges	Leeks	Red and green leaf lettuce
Papaya	Iceberg lettuce	Kale

Some reptiles are highly selective in their choice of food; others are much less so. In some cases, free-ranging reptiles may select a particular type or class of food that contains a specific nutritional element that the animal needs at that specific moment. However, in managed care many of these mechanisms do not exist because the animal has been removed from cues with which it has evolved. Some free-ranging terrestrial tortoises are attracted to carrion, dried skeletal remains, and even, as previously noted, faeces of other animals. Visual, chemical, thermal, and even auditory cues are utilised by reptiles when selecting prey and these factors should be considered in a managed setting to promote natural behaviours as well as the acceptance of nutritionally appropriate prey. Motion is perceived acutely by many reptiles, and many chelonians—particularly terrestrial tortoises—are able to discriminate bright colours; red, orange, yellow, and green are attractive to most of these animals. Thus, it is likely that many chelonians, most lizards and snakes, crocodylians and probably the tuatara (*Sphenodon punctatus*) are, to a large extent, sight feeders.

Egg-eating snakes readily accept freshly laid eggs gathered from a nest but will reject cleaned eggs purchased from a grocery store. Some large carrion-eating varanid and teiid lizards, crocodylians, and a few aquatic turtles may refuse to eat freshly killed food objects, preferring to wait until decomposition occurs (Auffenberg 1981; Sprackland 1990; Sazima and Angelo 2013). It is a common practice to warm quick-frozen rodents and chicks in a microwave oven just before presenting them to some carnivorous reptiles, but this is not recommended due to the potential for undetected hot spots that can occur within the food item, potentially damaging delicate oropharyngeal, oesophageal, and gastric tissues as the prey item is ingested.

Few reptiles are attracted by auditory cues, but some possess one or more highly specialised non-visual, non-auditory sense organs. The facial pit organs of the pit vipers and the labial pits of some boid snakes are examples of non-visual organs for the perception of both prey and potential predators. The vomeronasal (Jacobson's) organ is well developed in snakes and most lizards, and chemical or organoleptic (scent/taste) cues are utilised extensively by these squamates, some chelonians, and most crocodylians. Highly specialised touch receptors have been found subjacent to the anteriolateral aspects of some tiny worm snakes (Frye unpublished data).

Frugivorous (fruit-eating) skinks and geckos are attracted to sweet and nectar-rich fruits because of these lizards' ability to sense fragrant foods. Similarly, many tortoises are attracted to flavourful fruits and vegetables. Therefore, pleasant tasting nectars and purees can be used as carrier media for vitamins and minerals that can be added to their diet to provide important supplementary micronutrients.

A thorough knowledge of which animals prefer what specific dietary items is essential to provide a diet that is both attractive and accepted by captive reptiles and, at the same time, one that is nutritionally sound (Frye 1991a, b, 1994). Moreover, the physical size, the nutritional density or quality, and the quantity of the preferred dietary items must be matched to the requirements of each individual reptile. For example, very large boid snakes find it nearly impossible to catch a small mouse and a very tiny kingsnake is far too small to subdue and swallow a large mouse, lizard, or snake.

Placing excess rodents, meal beetle larvae, crickets, or other insects into a cage that houses lethargic lizards often results in the rodents or insects attacking, injuring, and sometimes killing the reptiles in a quest for moisture or sustenance. Feeding living rodents should be limited to only when living prey is accepted by a captive reptile—after several attempts to feed killed prey have proven fruitless. Also, feeding in excess of what an animal can be reasonably expected to consume at one meal may result in obesity, food spoilage, promotion of fungal and bacterial growth, and attraction of invertebrate vermin and/or disease to the uneaten portions or items.

Animal prey should also be free from infectious disease or evidence of gross pathology and, if possible, should be tested periodically for the presence of bacterial infection and parasitic infestation. Fresh and frozen fish should be of the highest quality to avoid fish-related diseases and nutritional disorders such as hypovitaminosis B, which is associated with the presence of the lytic enzyme thiaminase commonly present in improperly handled or stale fish and some shellfish. The flesh of some fish, especially herring, tends to contain significant levels of this thiamine-lytic enzyme. To avoid inducing steatitis, the inflammatory disorder that affects body fat, it is crucial to limit the feeding of fat-laden fish. Both conditions can often be avoided by feeding live fish to piscivorous (fish-eating) reptiles.

The quality of the diet is essential to the animal's health. Vegetables and fruit should be fresh and free from fungal infection, spoilage, or other signs of decay. Produce that is long passed its recommended consumption date and spoiled is likely to be unappealing to animals and lacking in nutrition. Dietary items that consist largely of indigestible non-nutritive fibre must be consumed in large quantity in order for them to yield sufficient digestible nutrients. In some cases, this is necessary based on the natural history, foraging strategy, and alimentary morphology and function of the species in question (i.e.—giant tortoises). However, some plants have been associated with the induction of goitres due to their thiocyanate and isothiocyanate content and these should not be fed excessively. These vegetables include cabbage and many of its relatives in the family Brassicaceae (Cruciferae): broccoli, Brussels sprouts, cauliflower, kale, kohlrabi, mustard, rutabagas, turnips, and others. Collard greens, a member of this richly diverse family, are much less likely to induce hypothyroidism; this vegetable is highly nutritious and avidly eaten by many folivorous (leaf-eating) reptiles, particularly iguanas (*Iguana* sp.). Also, collard greens possess a calcium:phosphorus ratio that is well within the desired range (at least 2:1); that is, it contains much more calcium than phosphorus. Soy beans also contain goitre-inducing substances. The foliage and blossoms of many common plant species are nutritionally sound (e.g. dandelions, nasturtiums, mulberry leaves), but should be evaluated for appropriateness and safety on a case by case basis.

Generally, a variety of vegetables or other plant fodders should be fed to herbivores; this will help to avoid nutritional deficiencies and the development of undesirable habitual dietary preferences. It is relatively common for some reptiles to develop strong preferences for specific diet items and refuse to accept other more nutritionally sound food items. The reasons for these partialities are manifold and include lack of choice in the captive diet, attractive taste, or visual appeal and, in

some instances, the water content or chemical composition of one or more particular dietary constituents. One should bear in mind that food preferences vary with the individual animal.

Other challenges to providing an appropriate diet to reptiles include procurement of prey or other food items, disease risk, and cost. Consistently attaining certain types of prey from commercial sources can be challenging and collecting these items from the wild requires significant time and resources. Additionally, compatibility of predator and prey (even if considered 'native') should be carefully evaluated (example: reports of fatalities in bearded dragons (*Pogona vitticeps*) species after firefly ingestion; Fitzgerald and Newquist 2008). Alternatively, developing and maintaining breeding colonies of prey species can provide a consistent food source, but establishing these colonies can be resource heavy depending on the invertebrates cultured. Live prey can also pose a disease risk when being brought into an animal facility that is not necessarily mitigated by obtaining prey from commercial sources, because some of these companies may collect animals from the wild and do not conduct routine disease screening. Routine faecal parasite screening on captive reptiles can help detect and control parasite loads, as some diet items harbour different life stages of parasites. Offering live prey (invertebrate or vertebrate) should be evaluated on a case by case basis, given the risk of injury to the species consuming the prey and the welfare of the prey species being consumed.

Maintaining colonies of small rodents, crickets, and other invertebrates such as roaches, mealworms, and fruit flies can be time intensive, but provides a reliable source of food to a captive reptile collection. Other prey species that are not so easily propagated including fishes, crayfish, larger birds, and mammals can be purchased, although it is important to remember that the nutritional quality of the prey is dependent on its diet and care. Finding reliable and trust-worthy suppliers who will inform people of their procedures for colony care (e.g. husbandry practices, euthanasia), is extremely important. Conducting occasional nutritional analysis of prey items is recommended to ensure that the nutrient analysis of the prey is appropriate, consistent, and 'known'. Whether an invertebrate or vertebrate prey item, hay or plant material, or a commercially manufactured feed or supplement, knowing the nutrient content is the most basic piece of information nutritionists, veterinarians, and animal managers need to begin the process of providing an appropriate diet for reptiles.

Available options for feeder invertebrates in managed settings are limited and much work has provided reasonable nutrient profiles for most commonly available invertebrate prey species (Bernard et al. 1997; Oonincx and Dierenfeld 2012; Finke 2013; Oonincx et al. 2015). Studies have found that commercially-sourced invertebrates are poor dietary sources of several nutrients, most noteworthy, vitamin A and calcium (Allen and Oftedal 1989, 1994; Mader 2006; Oonincx and Dierenfeld 2012; Finke 2013; Latney et al. 2017). In order to use these invertebrates in captive reptile diets, their nutrient content must be adjusted to better meet the target nutrient needs of the animal(s) in question (Table 14.2). Two methods that are commonly used to adjust the nutrient content of feeder invertebrates include dusting (Trusk and Crissey 1987; Finke 2003; Attard 2013) and gut loading prior to feeding to animals

Table 14.2 Proposed target ('safety net') nutrient values for reptiles, based on foraging strategy

Nutrient	Herbivorous ^a	Omnivorous ^b	Carnivorous ^c
Protein, %	5.99–26.0	10.0–27.8	20.0–50.0
Fat, %	2.0–8.5	5.0–8.5	9.0–15.0
Linoleic acid, %	–	1.1–2.0	0.5–1.0
Acid detergent fibre, %	10.0–18.0	–	–
Vitamin A, IU/g	0.5–5.0	0.5–13.9	3.55–10.0
Vitamin D, IU/g	0.37–0.68	0.55–2.5	0.25–1.0
Vitamin E, mg/kg	34.0–150.0	30.0–100.0	38–273
Vitamin K, mg/kg	0.2–2.0	1.0	1.0
Thiamin, mg/kg	1.38–6.94	1.0–3.0	1.0–5.6
Riboflavin, mg/kg	0.94–10.5	2.2–10.5	1.6–4.25
Niacin, mg/kg	15.0–180.0	15.0–25.0	10.0–42.5
Pyridoxine, mg/kg	1.5–6.0	1.5–4.0	1.6–4.0
Vitamin B ₁₂ , mg/kg	0.025–0.035	0.01–0.035	0.02–0.032
Folacin, mg/kg	0.18–0.80	0.18–4.0	0.20–0.80
Pantothenic acid, mg/kg	15.0–25.0	12.0–15.0	6.0–10.0
Choline, mg/kg	1200–1700	750–1700	1250–2550
Calcium, % ^d	0.22–1.2	0.30–1.2	0.30–1.08
Phosphorus, % ^d	0.16–1.0	0.30–1.0	0.30–0.90
Magnesium, %	0.03–0.17	0.04–0.08	0.04–0.06
Potassium, %	0.12–0.60	0.4–0.44	0.40–0.60
Sodium, %	0.04–0.46	0.04–0.22	0.068–0.20
Iron, mg/kg	23.4–100.0	30.0–100.0	60.0–80.0
Zinc, mg/kg	18.7–100.0	20.0–100.0	50.0–75.0
Copper, mg/kg	4.7–13.9	6.0–20.0	5.0–8.8
Manganese, mg/kg	2.5–7.0	5.0–20.0	4.8–7.2
Iodine, mg/kg	0.17–0.90	0.35–0.90	0.30–2.2
Selenium, mg/kg	0.05–0.35	0.11–0.35	0.10–0.40

^aNRC (1977, 2007), Allen and Oftedal (2003)^bNRC (2003, 2006)^cNRC (1982, 2006), Allen and Oftedal (1994)^dRegardless of absolute amounts, a minimum Ca:P ratio of 1:1 is recommended

(Bernard et al. 1997; Hunt et al. 2001; Finke 2003). These adjustments can help prevent or even rebound reptiles from common nutritional disorders.

Gut loading insects prior to feeding has been proven to increase their inherently poor calcium content. However, invertebrates that have been fed mouldy poultry or other cereal-containing meals may include sufficient aflatoxins to induce acute and chronic aflatoxicosis and thus severe liver disease, particularly toxic hepatitis, in the insectivorous reptiles that consume them. A better alternative is to gut-load the invertebrates with a flavoured calcium source, which these insects will readily ingest, or consider the use of invertebrate prey with a more adequate calcium composition (i.e.—black soldier fly larvae, *Hermetia illucens*).

When using supplements, the nutrient content of the proposed supplement should always be known prior to its implementation. Ideally, single-ingredient supplements are used only on an as-needed basis to address specific, identified shortfalls in the diet as formulated, consumed, or digested. Neither the guaranteed analysis nor any manufacturer provided information should be considered reasonable substitutes for known nutrient content of any supplement or commercially manufactured feed. Minimum and maximum values provide very little insight into actual nutrient content of a particular supplement and given the sometimes-precise nutrient tolerances of the animals being fed, well-meaning supplement use can lead to unintentional deleterious consequences, such as cholecalciferol toxicity (Crissey et al. 2001; Fitzgerald and Newquist 2008). The general inability to determine the amount to offer (due to variable consumption and challenges with measurement) means supplement use should always be approached with caution.

Vitamin D, when fed excessively, can induce severe pathological mineralisation in normally non-calcified soft tissues such as the smooth muscle that is present in the alimentary, respiratory, cardiovascular, and urogenital systems. Moreover, an intimate relationship exists between excessive amounts of vitamin A combined with deficient amounts of vitamin D; it appears that excessive preformed vitamin A can initiate some of the physiological and anatomical sequelae usually characteristic of vitamin D deficiency (ingestion of excessive vitamin D and calcium also must be avoided). The precise mechanism of this competitive interrelationship is currently being studied and the view has emerged that vitamin A should be supplied by feeding natural sources of beta carotene. The vitamin A precursor, beta carotene, is usually well accepted and is substantially less toxic than the bioactive retinol (or retinyl ester) vitamin A; beta carotene can be furnished safely in the diet by providing a selection of orange, yellow, and green leafy vegetables. Hypovitaminosis-A is often a consequence of feeding a carotene-deficient diet to aquatic chelonians. Under natural (non-captive) conditions, aquatic turtles and terrapins consume algae and other aquatic plant material, and, of course, the gut contents of their prey. Without appropriate supplementation, dietary imbalance, particularly associated with Vitamin D can result in the development of osseous lesions and osteofibrosis (Figs. 14.1, 14.2, 14.3, 14.4 and 14.5).

14.3 Acquisition of Food

With the exception of chelonians, nearly all reptiles possess teeth for grasping, tearing, or crushing (Stevens and Hume 1995). The mouth of the reptile is the primary way that food is apprehended, regardless of foraging strategy. This apprehension can be aided by appendages (e.g. digits, claws), or by the action of the entire body (i.e.—constriction in some species of snakes). Mouths serve as the conduit for food between the outside world and the rest of alimentary tract within the animal and can be specialised for aiding procurement. With cranially kinetic skulls that enable a wide gape, some reptiles also benefit from having a specialised gular apparatus, supported by dedicated hyoid components that allow for swallowing of large food items (O'Malley 2005).

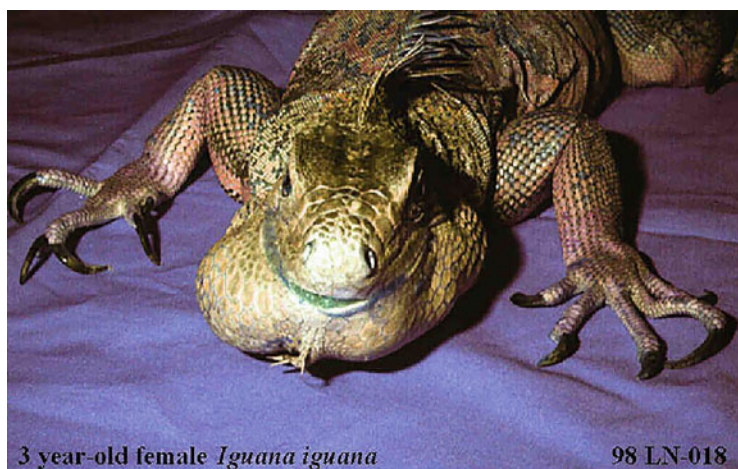


Fig. 14.1 Examples of osseous lesions associated with vitamin D-3 deficiency and/or imbalanced calcium:phosphorus. Printed with permission by Dr. F. L. Frye

Carnivorous or omnivorous reptiles pursue and catch their prey by simply grasping and immediately swallowing, aggressively attacking, envenomating, constricting, or using some other physical means of overpowering and restraint (Gillingham and Clark 2023). Some employ more than one of these strategies, depending on the amount of struggling by the prey animal. Venomous reptiles might not envenomate a prey animal if it can be overcome by restraint. When prey is envenomated, it may or may not be released to die at some distance from the attacker. The venom used to subdue the prey also plays an important role in the enzymatic digestion of the meal. When a prey animal is too large to be swallowed whole, some lizards and most crocodylians twist their bodies whilst holding onto a piece of the animal, thus reducing the carcass to smaller portions that can be swallowed more easily. Obligate herbivores and facultative omnivores grasp their vegetable food items with highly specialised toothless, yet often serrated, horn-covered nipping jaws, or with sharp-toothed mouths. Small pieces are snipped or torn from leafy vegetables; larger pieces are held down with a forelimb and then sheared with the jaws into smaller bite-sized portions before being swallowed—characteristically without chewing.

Some reptiles possess a highly cornified oesophageal lumen that resists abrasion by scabrous (rough) food items. Sea turtles possess horny, pointed oesophageal papillae that project aborally, thus aiding in the swallowing of slippery or abrasive food items that they forage from the sea such as sea jellies. Others are characterised by specialised structures that facilitate the ingestion of specific food items. These structures include hard ridges (projections of the cervical vertebrae) in the roof of the oesophagus such as those in the egg-eating snakes (*Dasypeltis* spp.): as an egg passes under these ridges, powerful oesophageal contractions compress the egg, splitting the shell and causing it to collapse and release its contents into the

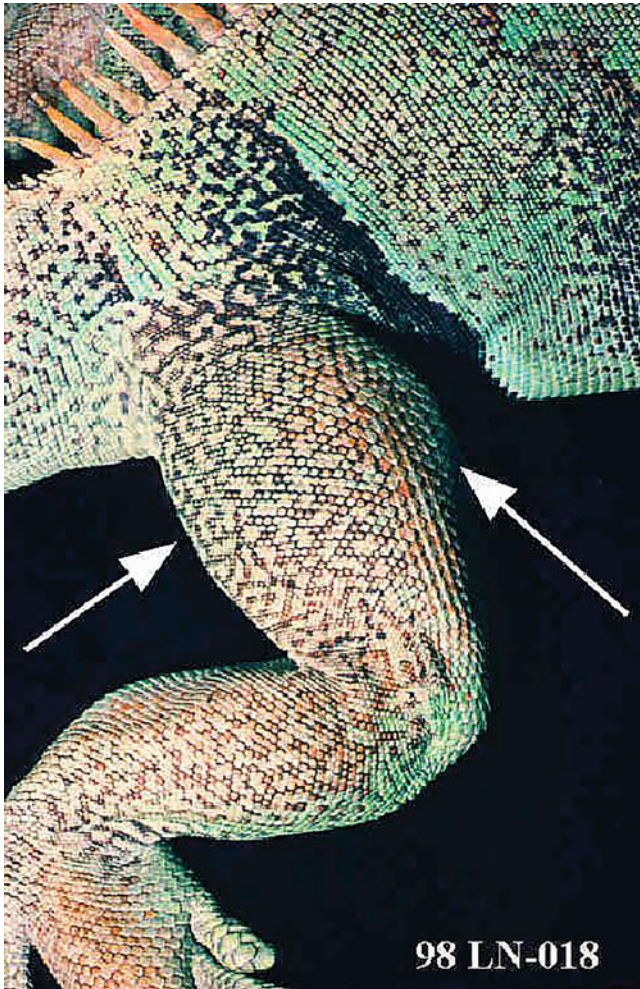


Fig. 14.2 Examples of osseous lesions associated with vitamin D-3 deficiency and/or imbalanced calcium:phosphorus. Printed with permission by Dr. F. L. Frye

oesophagus; the empty shell is then disgorged. Other reptiles, particularly many snakes, secrete copious amounts of slippery mucus with which their food is lubricated during swallowing. Some reptiles possess highly specialised teeth that reflect the nature of the diet. An example is the caiman lizard (*Dracaena guianensis*): its diet consists of molluscs whose hard shells are crushed by the lizard's large, flat-cusped molar-like teeth in order to extract the soft-bodied contents. The marine iguana (*Amblyrhynchus cristatus*) possesses sharp tricuspid teeth to enable it to scrape algae off rocks whilst submerged. Bird-eating snakes often possess long, recurved sharp teeth to secure feathered prey. Gharials (*Gavialis* sp.), that dine

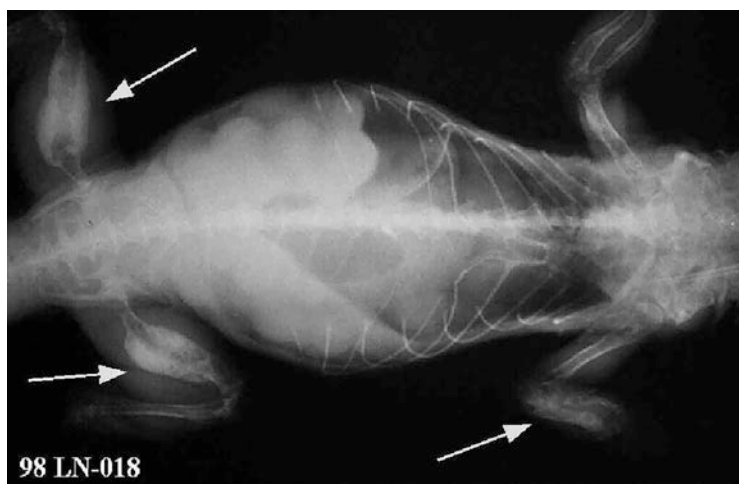


Fig. 14.3 A dorso-ventral radiograph of the iguana with typical osseous lesions of fibrous osteofibrosis shown in Figs. 14.1 and 14.2. Note the widened long bone diaphyseal shaft diameters (arrows). Printed with permission by Dr. F. L. Frye



Fig. 14.4 Necropsy specimens from the iguana shown in Fig. 14.3. The diaphyseal shaft diameter is massively expanded by soft, poorly mineralised bone. Printed with permission by Dr. F. L. Frye

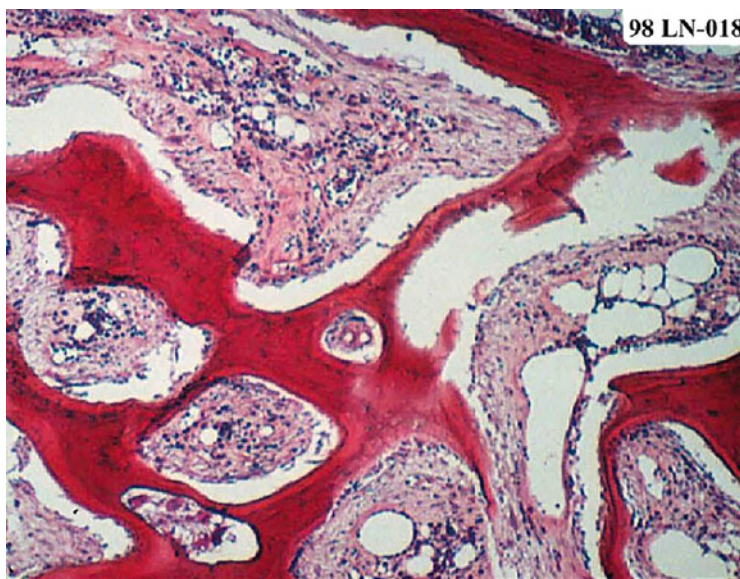


Fig. 14.5 Low power photomicrograph of fibrous osteodystrophy from a lesion identical to that illustrated in Figs. 14.1 and 14.2. Note the loss of osseous tissue and its replacement with fibrocollagenous connective tissue. H & E $\times 110$ original magnification. Printed with permission by Dr. F. L. Frye

largely on fish, possess sharply pointed and elongated homodont teeth that stud their narrow jaws.

Other reptiles, especially some lizards, possess tongues with tips that have fine papillary projections and are liberally covered with sticky mucus; this arrangement facilitates capturing insects. Perhaps the most remarkable lingual adaptation is found in members of the lizard family Chamaeleonidae: the tongues of these lizards, when fully extended, often exceed the total body length of the lizard. Lying in the floor of the mouth when not deployed, these astonishing organs can be extended and withdrawn very rapidly, thus capturing and retrieving unwary insects. As noted previously, even chamaeleons that have lost their tongue, can be trained to accept food that they have learned to grasp with their toothed jaws.

In some cases, captive reptiles will accidentally eat indigestible non-food items or develop the deliberate habit (termed 'pica') of consuming particulate material such as sand, pebbles, wood chips, ground corn (maize) cobs, sawdust, moss, cat litter, and others (Mitchell and Diaz-Figueroa 2005; Nicholas and Warwick 2011; Johnson and Doneley 2017). This consumption, alone or coupled with dehydration, can lead to serious effects such as mucosal inflammation, erosion, ulceration, or perforation of the stomach or intestines, or partial luminal obstruction, intussusception, or complete alimentary impaction and obstruction that prevents passage of ingesta and faeces, and eventually leads to death. Less serious effects include discomfort. The judicious use of one or more doses of oral lactulose solution or an osmotic laxative, or vibrating massagers (Nicholas and Warwick 2011), helps relieve

constipation and obstipation, and adequate water/humidity should be provided at all times (see Water Supply in this chapter). In order to be truly effective, the underlying aetiology of obstipation and constipation should be addressed, rather than merely treating the clinical signs of these alimentary conditions. For example, ingested particulate cage surface materials, especially sand, ground maize cob, or loamy earth, or the accumulation of fur or feathers from ingested prey, may contribute to partial or complete physical obstruction of the alimentary tract. This self-destructive behaviour can be induced or exacerbated by a lack of exercise and understimulation (Nicholas and Warwick 2011). Thus, bleak and spatially restrictive caging that is devoid of naturalistic habitat and enrichment should be avoided. When enhancing cage furniture is added, it is essential to make certain that they are either fixed in place or well supported and cannot topple over and crush or otherwise entrap the captive animal.

Sometimes, a captive reptile's excessive 'free' time can be channelled into more constructive activities such as prey pursuit and other food-related behavioural, and general behavioural, enrichment practices (Burghardt 2013; Mendyk and Augustine 2023). If, for example, live fish are included in a water pool or food items generally are dispersed, the predator reptile must spend much more energy (and otherwise surplus time) in foraging and capturing prey rather than merely being fed pre-killed, thawed frozen fish; this more closely approximates the situation present under natural conditions.

Assessment of what and how to appropriately feed reptiles begins with an understanding of their foraging strategy and how they digest their diet once procured. Reptiles represent the entire spectrum of foraging strategies; all snakes are carnivores, most lizards and aquatic turtles are carnivores or omnivores, and few lizards and most tortoises are herbivores. As described earlier, some may overlap strategies (i.e.—carnivores that consume herbivores whole, and by association, the plant material in their alimentary tracts; Frye 1995a, b) or experience ontogenetic diet shifts, transitioning from one strategy to another as they mature (such as aquatic turtles).

14.4 Water Supply

Water-balance is an important aspect of reptile nutrition and reptiles have evolved numerous structural, physiological, and behavioural adaptations to restoring and maintaining hydration. Some can sequester water from the atmosphere and may not require fluid in their diet, whilst some aquatic turtle species can absorb water through their cloaca (Chessman 1984). Most others must imbibe water at least occasionally.

Variations in provisioning water in captivity should correlate with the species' natural history. Some species, such as chameleons, will not readily drink from standing water but respond well to drip systems in artificial environments (Frye 1995a, b). Some snake species will drink from standing water, but others utilise their tight coils to collect rainwater or mist from which to drink (Aird and Aird 1990).

Although many tortoises obtain most of their water from the moisture content of the succulent tissues of the various plants that they ingest, most will drink eagerly if

water is furnished in shallow pans or similar containers. The water must be sufficiently deep to permit the immersion of the external nares so that these animals can create a vacuum and thus draw the fluid into their mouths; they lack a shelf-like complete hard palate and the external nostrils must, therefore, be immersed beneath the water's surface. Some arid-dwelling tortoises will, when necessary, excavate depressions in the soil that help facilitate the collection of water and its imbibition. In the tortoise's native habitat, relatively shallow bodies of water may be available for only a very brief time, dictated by season; the tortoises compensate for this by drinking a large volume of water in a short period of time and they further conserve vitally important quantities of water through osmotic reabsorption across the membrane of the colon and urinary bladder.

Some desert-inhabiting species of lizard such as the Australian thorny devil or moloch (*Moloch horridus*) and many North American horned lizards (*Phrynosoma* spp.) have developed a system of interscalar channels through which water collected as dew on the spiny-scaled integument is conveyed into the corners of the animal's mouth by capillary action (Sherbrooke 1990; Cormanns et al. 2016). These lizards constitute a prime example of parallel evolution in two widely disparate but morphologically similar species.

Contrary to popular belief, reptiles do not absorb significant amounts of water through their skin. As indicated previously, many lizards imbibe water as rain-drops or dew-drops, but also from foliage and often these species refuse to drink from vessels of standing water. Others can become accustomed to accepting water from one or more small emitters connected to a drip irrigation system. Such watering schemes are useful when dealing with chamaeleons and arboreal Iguanid lizards (Frye 1996). Some tree-dwelling snakes collect rain for ingestion among their tightly held coils and recently, this behaviour has also been recorded in ground-dwelling viperids (Aird and Aird 1990; Sherbrooke 1990; Abe and Andrade 2000; Phadnis et al. 2019).

Many marine or pelagic reptiles are capable of drinking sea water; the excess electrolytes are then secreted by specialised 'salt glands' located in the nasal passages or beneath the tongue as a hyperosmolar product containing sodium, potassium, chloride, and minor amounts of trace minerals present in the saline water. Some semi-aquatic and terrestrial reptiles also possess similar salt-secreting glands from which they secrete concentrated electrolytes extrarenally without the loss of appreciable—and precious—water (Dunson and Taub 1967; Dunson 1970a, b; Dantzler and Bradshaw 2009). In many lizards, such as members of the Family Iguanidae, these glands are embedded in the nares or the tongue (Anderson and Wack 2006). Some species of crocodylians (especially the Indo-Pacific crocodile [*Crocodylus porosus*] and other *Crocodylus* spp.) possess physiologically similar salt-secreting glands in their tongues (Taplin 1989).

Because most reptiles require some water to be imbibed, it should always be available in a manner that is appropriate for the individuals being managed in captivity. A chronic lack of imbibed water can lead to the failure to excrete nitrogenous wastes and the deposition of microcrystalline urates, mostly sodium and/or potassium ammonium salts in the renal cortical glomerular and tubular structures. Once a sufficient number of glomeruli and/or renal tubules have been obstructed and distorted, parenchymatous visceral gout ensues (see Figs. 14.6, 14.7, 14.8 and 14.9).

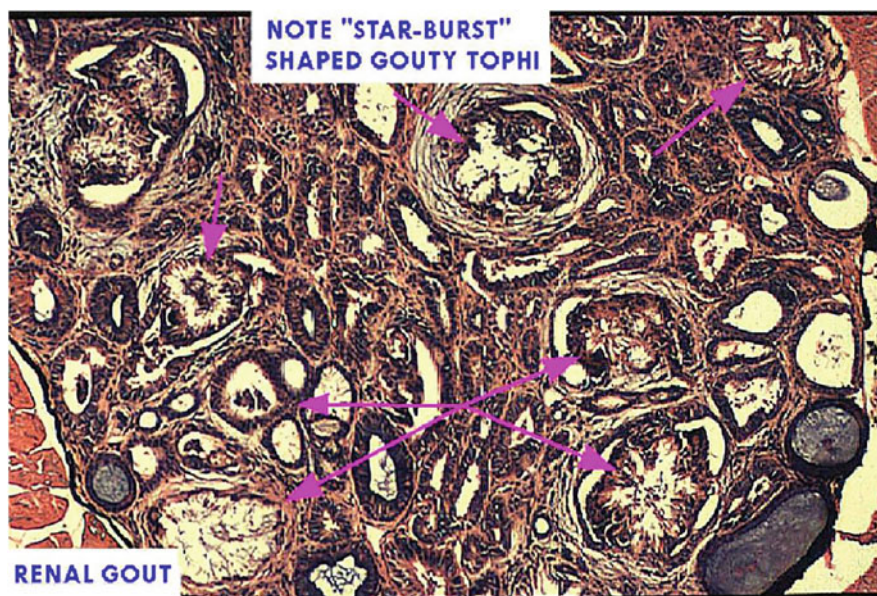


Fig. 14.6 Low power photomicrograph of stained histological section of reptilian renal cortex affected by hyperuricaemia. The violet arrows point to glomeruli which have been distorted by the presence of uric acid deposits. H & E stain, $\times 80$ original magnification. Printed with permission by Dr. F. L. Frye



Fig. 14.7 Higher power magnification photomicrograph of a single renal glomerulus which exhibits the typical 'star-burst' pattern that results from the deposition of crystalline urates that induce this characteristic chronic secondary inflammatory histological pattern in affected glomeruli. H & E stain, $\times 240$ original magnification. Printed with permission by Dr. F. L. Frye

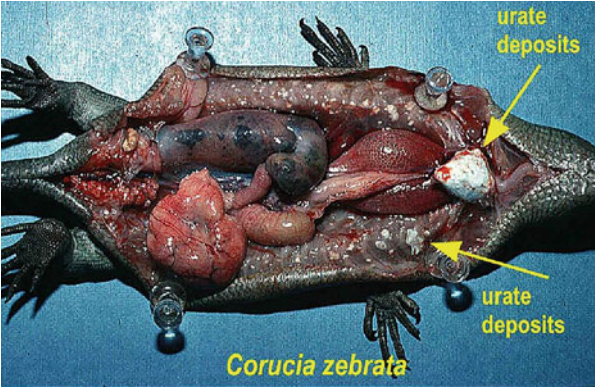


Fig. 14.8 Post-mortem image of a prehensile-tailed skink (*Corucia zebrata*) with visceral and appendicular gout. The pericardial sac and pericardium are covered with white urate crystals. Note also that both of the lizard’s articular joints (lower arrow and the opposite side, to the left and caudal to the pushpin). Lastly, both kidneys at the far left, between rear legs, contain white urate deposits. Printed with permission by Dr. F. L. Frye

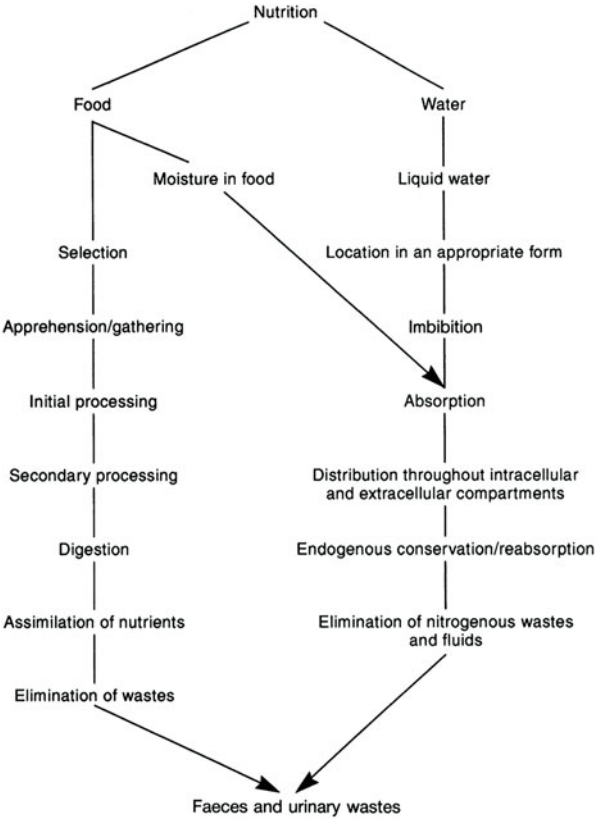


Fig. 14.9 Flow diagram depicting the fates of food and moisture once taken into the body. Printed with permission by Dr. F. L. Frye

In addition to the assimilation of water, humidity levels are also extremely important when considering an animal's hydration, and many species have adapted important physiological and behavioural adaptations to reduce evaporative or cutaneous water loss. Inappropriate humidity levels can lead to dehydration, stress, dysecdysis, and refusal to feed (Donoghue and McKeown 1999). During times of low water availability, reptiles may change their activity patterns and lower their body temperatures (Lorenzon et al. 1999; Ladyman and Bradshaw 2003) to reduce dehydration potential. For example, many species will burrow deep into substrate in order to access increased humidity and lower temperatures.

An additional consideration of provisioning water to captive reptiles is, much like the nutritional composition of prey, the mineral content of water. Hard and soft water contain very different mineral profiles. Water-inhabiting reptiles are of particular concern because the mineral content and general chemistry relationships among pH, alkalinity, and hardness should be evaluated when addressing the nutritional status of all reptiles. Water quality recommendations exist for a limited number of aquatic reptile species (Higgins 2002; Rangel-Mendoza et al. 2014; Webb et al. 2008); however, it is limited in scope and more research is needed across individual species.

Improper provisioning of water in an artificial environment can lead to dehydration, which can affect thermal preference (Ladyman and Bradshaw 2003), digestive efficiency, appetite (Mans and Braun 2014), ecdysis (Harkewicz 2002), activity patterns (Lorenzon et al. 1999), and other physiological processes. Furthermore, dehydrated animals are often anorexic, which can further contribute to their dehydrated state (Mans and Braun 2014).

14.5 Processing, Assimilation, and Elimination

Depending on the nature of the individual reptile under consideration, the meal may be swallowed whole (as by snakes, some lizards, some chelonians, and some crocodylians) or reduced into smaller portions before it is swallowed. Those animals that ingest the entire meal as intact prey are less likely to develop nutritional deficiency disorders because not only are the soft tissues of the prey ingested, but also the entire mineral-rich skeleton plus fur, feathers, or scales and, importantly, the stomach contents that were eaten by the prey prior to it being swallowed by the predator.

As indicated previously, in some instances, the venom that helped subdue the prey may also initiate the early stages of the digestive process (Cundall and Greene 2000). In snakes that have been surgically deprived of venom or a venom-delivery apparatus, the digestive process may be impeded by the absence of this often enzyme-rich substance (Klauber 1956). The act of striking and biting often serves as a powerful releaser for feeding behaviour in snakes (Kardong 1982; Chiszar et al. 1983; Cundall and Greene 2000). Similarly, the hunting and attack sequences characteristic of many crocodylians' feeding behaviour serve as stimuli to feeding and swallowing. It is for this reason that when many crocodylians are housed under crowded conditions, they may exhibit 'feeding frenzies' during which their cohorts

are injured. To a lesser extent, these frenzied episodes, that may occur in turtles and some carnivorous lizards, especially large varanids, can lead to fatal injuries. Careful husbandry of multiple captive naturally aggressive varanids, crocodylians, and/or some species of snakes together in the same 'community caging' situation (s) requires careful selective feeding to ensure that each captive animal receives its fair share, whilst avoiding competition for each prey morsel.

In those instances where food is reduced into smaller portions prior to engulfing, the meal is ground, mixed with saliva, and finally swallowed. By the time the food enters the stomach, it is partially macerated and may be reduced in particle size, therefore increasing the surface area on which the enzyme-rich digestive secretions can act. Several species of reptiles have been noted to carry gastroliths (stones, gravel, or sand) that may serve a grinding function in the maceration process (similar to material found in the avian proventriculus; Stevens and Hume 1995) or as ballast for aquatic species. Freshwater aquatic turtles and crocodylians employ this technique in order to remain submerged. However, as indicated previously, when these animals are kept in captivity, particularly under conditions of public display, this stone-eating behaviour (lithophagy) may be replaced by potentially harmful pica involving the ingestion of thrown coins, toys, and other public-deposited items. This problem is especially prevalent in semi-aquatic reptiles displayed in artificial swamp environments, particularly crocodylians.

All snakes, crocodylians, chelonians, lizards, and the tuatara possess a gland-rich gastric mucous lining, the secretions of which rapidly digest the complex animal prey meals that these creatures ingest. Bone-rich meals become demineralised and digested within three or four days of being swallowed. Even the teeth of some prey are softened by these potent acidic gastric secretions.

Reptiles tend to have tubular stomachs except for Crocodylia that exhibit an outpocketed and muscular stomach. If prey is consumed whole, such items can provide the reptile with a complement of nutrients via the soft tissues, bones, organs, and hide or feathers. However, beyond this, we should also consider the parts of the consumed diet that are more difficult to digest (and/or may not provide an obvious nutrient source). Such components may contribute to overall digestive tract health by regulating/stabilising the alimentary microbiome (as we are just beginning to learn about in a wide variety of species; felines and canines, Suchodolski 2011; primates, McKenna et al. 2008).

Ingested food is subjected to proteolytic digestion in the stomach; then moves into the small intestine, where it is mixed with bile and pancreatic enzyme-rich digestive secretions and further digested. This sequence of events depends on the size and nature of the meal, ambient (and/or animal's deep core) temperature, physical condition of the animal, and the presence or absence of gastrointestinal parasitism. Eventually, nutrients laden with dietary protein, fat and, to a variable extent, carbohydrates, are absorbed into the bloodstream. The blood flowing from the intestines travels first to the liver, where the basic 'building blocks' consisting of amino acids and peptides, fatty acids, di- and triglycerides, lipoproteins and mono-, di-, oligo-, and polysaccharides are extracted, stored, and processed into other bioactive products. In addition, essential vitamins, enzymes, trace minerals, and

co-factors are absorbed and converted to substances from which body tissues will be formed and maintained.

Enzymatic degradation that is responsible for digestion of proteins, fats, and carbohydrates is largely temperature-dependent: at temperatures lower than their thermal optimum (Michaelis Constant), the activity of each enzyme is diminished; raising the temperature beyond the optimum also results in reduced catalytic activity.

The midgut in carnivorous reptiles tends to be long, versus short in herbivorous reptiles. The opposite is true for the length and volume of the hindgut (Stevens and Hume 1995). Due to the need to slow down passage rate, allow for microbial fermentation of plant fibre, and increase the surface area available for absorption, the hindgut of herbivorous species tends to be longer and more capacious than omnivores or carnivores (Bjorndal 1997). For example, iguanas (*Iguana iguana*) possess a very complex and long hindgut owing to their primarily plant-based diet, compared to rattlesnakes (*Crotalus adamanteus*), which consume mostly vertebrate prey and have a short, unremarkable, tract. For carnivorous reptiles, the digestion of a large meal can take days or longer. Refuge to a safe space may aid in the stimulation of digestion during this period.

Some folivorous lizards possess a partially compartmentalised colon that serves as a fermentation vessel during hindgut processing of cellulose by microorganisms (Figs. 14.10, 14.11 and 14.12). Many of the iguanine, and some other non-iguanine lizards employ this form of hindgut digestion, which is enabled by single-celled microorganisms, especially *Nyctotherus* sp., and which help convert complex carbohydrates into simple sugars and fatty acids (Figs. 14.13 and 14.14).

Many reptiles become quiescent after eating a large meal. Some snakes and large monitor lizards, for example, may remain inactive for many days whilst the digestive

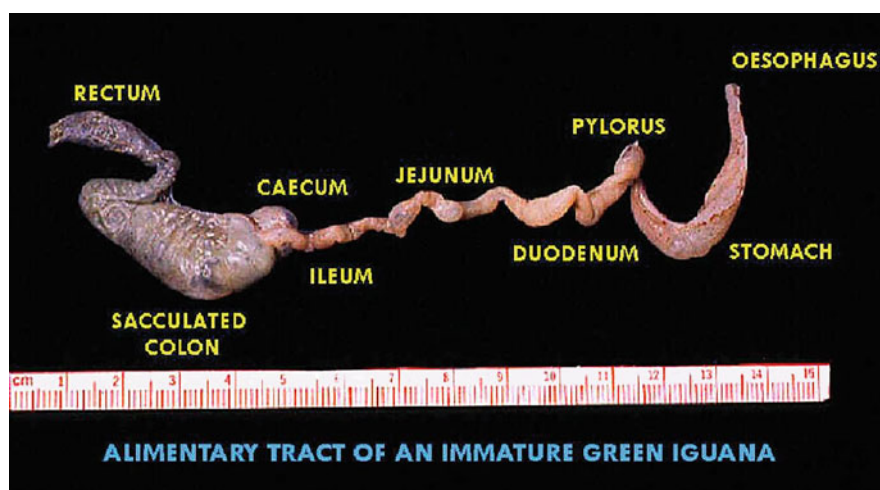


Fig. 14.10 Necropsy specimen of alimentary tract of an immature common green iguana, *Iguana*. Printed with permission by Dr. F. L. Frye

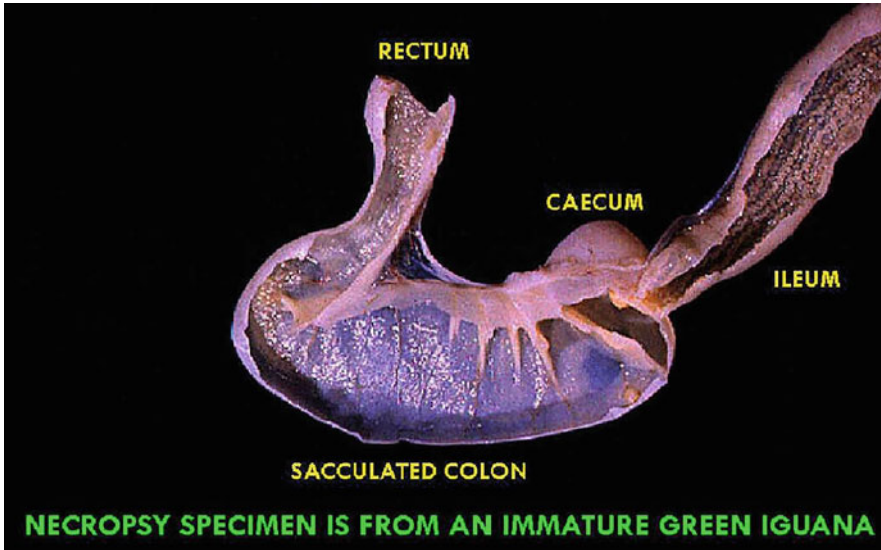


Fig. 14.11 Same specimen opened to reveal the expanded internal surfaces. Printed with permission by Dr. F. L. Frye

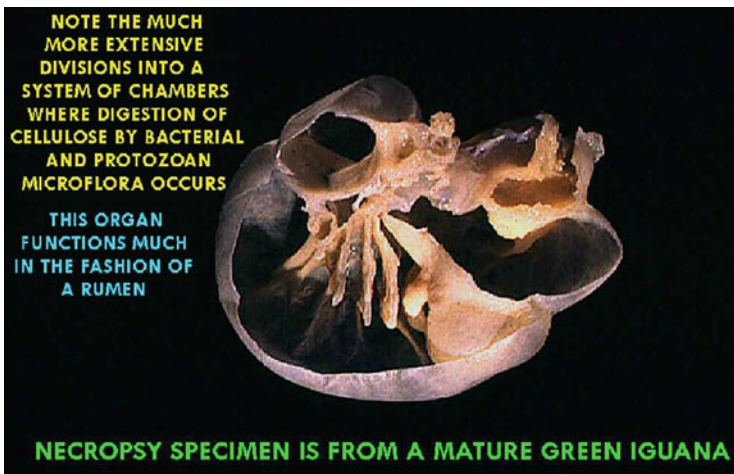


Fig. 14.12 Opened sacculated colon from an adult green iguana. Note the much more globular shape and more expanded surface area available for the absorption of nutrients. Printed with permission by Dr. F. L. Frye

process continues. Under natural conditions, the post-prandial act of moving to a safe refuge in which to hide may stimulate digestion and help to reduce intestinal gas production by increasing peristaltic motility; of note also is that the ambient temperatures tend to fluctuate between maximum and minimum during a 24-h

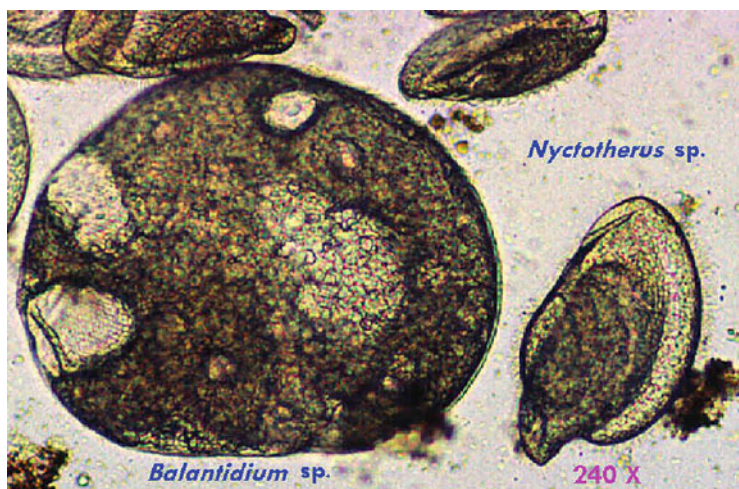


Fig. 14.13 Photomicrograph of the protozoan *Nyctotherus iguana* the principal protozoan micro-organism that is responsible for processing complex carbohydrates and converting them into simple sugars and fatty acids. This figure is unstained, $\times 240$. Printed with permission by Dr. F. L. Frye

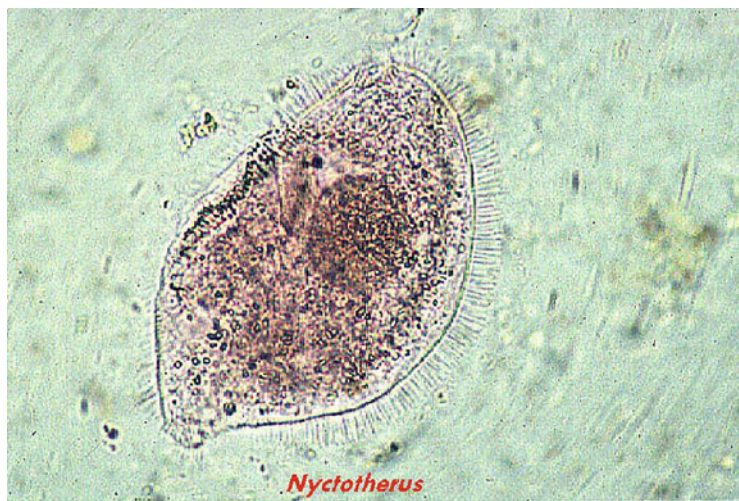


Fig. 14.14 Photomicrograph of a solitary *Nyctotherus* sp. organism stained with merthiolate, $\times 480$. Printed with permission by Dr. F. L. Frye

cycle. However, under captive conditions, exercise is limited because of cage space and other constraints and the ambient temperature tends to remain at a relatively constant level; often this temperature is intentionally close to the preferred optimum for a particular species.

Unfortunately, the lack of exercise and the level warm temperature favour the production—and retention—of intestinal gas. Because many long-term captive giant snakes often are already obese, this form of captive habit-related flatulence is exacerbated and can become life-threatening if not treated vigorously by encouraging exercise and giving gas-lysing agents (containing the dilute ingredient simethicone) by stomach tube. Permitting and encouraging the affected reptile (usually a giant boid snake) to swim facilitates the lysis and passage of this gas as flatus. When remedial action is taken, relief of this condition can be dramatic.

Mammal- and bird-eating reptiles tend to have somewhat bulky faeces containing fur or feathers. Because many of these animals, under wild conditions, vary their diet between several kinds of prey, fur and feather impactions are probably rare occurrences. However, under captive conditions when the diet is not varied, these impactions are commonly encountered and must be treated with stool softeners and lubricative laxative products. Impactions can be avoided by feeding mammal and bird prey alternately, and paying careful attention to hydration, as mentioned earlier. Again, exercising these often relatively sedentary animals is usually beneficial.

Some herbivorous reptiles, because of their high-fibre diet, tend to require a relatively long transit time between ingestion and defaecation (in comparison with carnivorous counterparts) and their faeces tend to be bulkier, and more frequently passed, than those of a carnivorous reptile. When fed a succulent diet with a very high-water content, such as squashes, melons, and cucumbers, the faeces of many tortoises tend to be near-liquid in consistency (not appropriate). Microscopic examination for parasites should be part of the evaluation of any case of diarrhoea, but if the analysis is negative for pathogens, frank diarrhoea can often be treated effectively by changing the diet to a much drier, fibre-rich ration.

A food item that has been used as both a source of dietary fibre and a treatment for loose stools is *Opuntia* cactus, fed as immature pads. Some zoos feed young beavertail cactus pads (*Opuntia* sp.) as a source of dietary fibre. When feeding these pads, it is essential to select those with still-soft spines to prevent injury to oral and oesophageal tissues. Older cactus pads can have their clusters of sharp spines scooped out with a spoon-shaped instrument that has had its bowl sharpened on its leading edge.

14.6 Target Nutrient Values for Appropriate Diets

Very few studies have examined target nutrient values for specific reptile species. Data from these few species- or nutrient-specific studies can be used to develop target nutrient values, but because of the limited scope and number, this information provides little assistance. In order to establish nutrient requirements, deficiency and toxicity studies are needed and, for most reptile species, are not appropriate to

conduct (for welfare reasons, among others). For this reason, perfectly applicable data to establish nutrient needs for various reptiles is not and will not be available. Given that lack of data and the concept that cellular-level nutrient metabolism is conserved across taxa, comparative nutritionists extrapolate information from other well-studied model species (regardless of taxa) to assist in the development of target nutrient values. Many domestic animals (avian and mammalian) have been extensively studied and can be utilised as such models. This information, combined with published species- or taxa-specific literature, can allow development of reasonable target nutrient ranges, as a guide or 'safety net' across species. Experience with exotic avian and mammalian species has proven that, in most cases, species-specific target nutrient ranges are not needed to appropriately address nutritional needs. Rather, an understanding of the species' natural history and foraging strategy-based target nutrient values or ranges are appropriate for this task. Thus, studying species that utilise the same foraging and/or digestive strategy can help to provide the best range. In the case of herbivorous reptiles, nutrition information from farmed iguanas (*Iguana* sp.) may provide a foundation, supplemented by well-studied domestic animal models, such as horses and rabbits. Similar work with alligator farms may provide insight for carnivores, paired with the well-studied domestic feline (and similarly, the domestic canine for omnivores). Obviously, in a farmed reptile, setting the management goals is often considerably different from other managed care situations (maximising average daily gains may be valued in one situation, where appropriate slow growth and reproduction may be valued in the other), and the ultimate goal (best welfare for the animal in question) should be considered when developing nutritional standards. For example, maintaining a healthy reproductively successful animal as opposed to producing large numbers of individuals of a certain size/age with diets aimed at accelerating growth rates for harvesting. As with other available data, there are limitations in the applicability of information derived from farmed animals, yet it cannot be wholly dismissed, given that, in many cases, it is species-specific.

The cognitive challenge for the comparative nutritionist and animal manager is the perceived impact of the metabolic difference between mammalian and reptilian models. Nutrient and energy needs, although inherently linked in physiology, can be addressed separately for the sake of utilising the robust data set of nutrient requirements for well-studied domestic mammals. In this way, Table 14.2 suggests target nutrient ranges across the three main foraging strategies within reptiles as a starting point for developing more species-specific targets. These are 'safety net' ranges of specific nutrients to be included in the diet for reptiles, based on their prevailing 'natural' diet and foraging strategy. It also should be noted where these target nutrient ranges contain exceptions for specific foraging strategies (i.e. the need to supplement vitamin E and thiamin for fish-eating carnivores offered frozen-thawed aquatic prey in managed care, that increases values above those outlined in Table 14.2).

Ambient environmental temperatures affect reptilian core body temperature, function, and metabolism (Donoghue 1998). Although reptile metabolic rates can be calculated using standard equations similar to birds and mammals (related to

metabolic body size—the smaller the animal the greater its metabolic rate per unit body mass), reptile metabolic rates typically average 25% those of similar sized mammals (reptile metabolisable energy [ME, kcal/d] = $32 \times \text{Body Weight [BW] in kg}^{0.75}$; Donoghue 2006). It is important to note exceptions to this generality, based on species-specific traits, such as varanids, which have a markedly higher metabolic rate than most lizards (Thompson and Withers 1997). Dietary energy sources vary across foraging and digestive strategies.

Carnivores can utilise animal-based protein (4 kcals ME/g) and fat (9 kcals ME/g), but intake and digestion of carbohydrate is considered minimal. For herbivores, dietary energy can be derived from plant protein (approximately 3.5 kcals ME/g), carbohydrate (plant fibre, approximately 3.5 kcals ME/g), and dietary fat (although usually limited in the diet, 8.5 kcals ME/g). Fermentation in the hindgut of herbivorous reptiles also contributes approximately 2 kcals ME per gram of fibre due to volatile fatty acid (VFA) production (Stevens and Hume 1995; Donoghue 2006).

Because many reptiles are quiescent in captivity, their expenditure of energy during foraging for food or other energy-expendng activities is greatly diminished compared with wild conspecifics that have to hunt for or otherwise locate sources of food. Consequently, overfeeding and obesity are commonly observed in many of less active species. Some captive reptiles, because of their high activity level, must be fed often just to maintain their normal weight. The nature of the diet is extremely important when ascertaining the frequency of feeding: items high in water content and low in dry matter, or high in fibre, contain less utilisable energy when compared with more concentrated items that contain less moisture or fibre, or are rich in fats. Yet others will suffer disuse atrophy and/or osteoporosis in captivity because these conditions can be induced by lack of exercise.

14.7 Considerations for Provision of UV Light

Ultraviolet (UV) light is a component of natural, unfiltered sunlight that is defined most broadly as light within the wavelength of 10–400 nanometres (see Lillywhite 2023; Mancera and Phillips 2023; Mendyk and Augustine 2023). Whereas many subdivisions of the UV light spectrum have biological significance (UVA is within the visual spectrum of reptiles and plays an important role in identifying conspecifics and prey), perhaps most important to appropriate reptile nutritional husbandry is a small range within the larger UVB spectrum. Exposure of skin to UVB light between 285 and 315 nm allows for the bioconversion of 7-dehydrocholesterol to previtamin D₃, in capable species, which then can be thermally converted into vitamin D₃ (bioconversion relies on appropriate wavelength and heat). Within the spectrum described, the most effective energies are from 290 to 300 nm (Ullrey and Bernard 1999). Hormonally-acting vitamin D₃ is necessary for the development of organs, maintenance of calcium homeostasis, and embryogenesis (Klaphake 2010). Depending on species, some carnivorous reptiles may obtain vitamin D₃ (cholecalciferol) entirely from their diet where others rely on ultraviolet light sources to

activate the cholecalciferol pathway and endogenously biosynthesise vitamin D₃ (Klaphake 2010).

Research on UVB requirements for reptiles has shown considerable variation among species, and between dietary and endogenously produced vitamin D₃. Certain taxa have been demonstrated to produce endogenous vitamin D₃ when exposed to UVB light, such as lizards and chelonians (Karsten et al. 2009; Ferguson et al. 2010; Oonincx et al. 2010). Lizards appear to voluntarily expose themselves to stronger UVB when their internal vitamin D is lacking (Karsten et al. 2009). Additionally, some taxa use mainly UVB endogenous sources to produce vitamin D₃, and appear unable to utilise dietary sources when housed with optimal husbandry.

Exposure to natural, unfiltered sunlight in native habitats is always preferred, but not always possible. When housing reptiles indoors, the use of artificial UV lighting can provide both UVA and UVB wavelengths. The amount and intensity of UV light needed by the reptile is variable and dependent on the species habitat and activity patterns (Baines et al. 2016). However, very few field studies have documented natural UV exposure of most reptiles (Brinker 2006; Ferguson et al. 2010, 2015; Edmonds et al. 2018). For this reason, it is important to make informed decisions based on current relevant information available and provide a gradient within an animal's enclosure with the option for access throughout their diurnal and crepuscular period. Excess UV exposure can cause deleterious effects, therefore providing a hide in the enclosure in addition to the appropriate level/gradient of UV light should be based on behavioural and morphological characteristics that optimise UV exposure for vitamin D₃ biosynthesis whilst minimising potential UV damage. These include basking behaviour, skin permeability to UV radiation, and response to UVB in the context of vitamin D production (Baines et al. 2016). Diurnal lizards have greater UVB exposure and dietary vitamin D₃ intake than a nocturnal/crepuscular lizard in the same environment (Carman et al. 2000), but even nocturnal species may utilise UVB light exposure. In fact, nocturnal geckos might have more sensitive mechanisms for bioconversion than diurnal species in order to compensate for their limited exposure (Carman et al. 2000) and diurnal snakes show less UV penetration through their skin than nocturnal snakes (Porter 1967). Nocturnal species are exposed to UV light during dusk and dawn (Carman et al. 2000) and would therefore fit into Zone 1 of the UVB guidelines (Table 14.3; Ferguson et al. 2010). However, a recurrent clinical problem arises when crepuscular or nocturnal squamates are not provided any UVB source, and several studies reveal that, for example, species of geckos and anoles have specialised capacity to absorb low levels of UVB at dusk,

Table 14.3 UVB Zone reference guidelines^a

Zone	Zone description	UV index (Median)
1	Crepuscular or shade; thermal conformer	0.1–0.7 (0.35)
2	Partial sun or occasional full-sun basker; thermoregulator	0.7–1.0 (0.9)
3	Full-sun or partial sun; thermoregulator	1.0–2.6 (1.8)
4	Mid-day baskers; thermoregulator	2.6–3.5 > (3.1)

^aAdapted from Ferguson et al. (2010)

and this increases plasma 25-hydroxyvitamin D₃ concentrations levels as stated above (Carman et al. 2000; Ferguson et al. 2005). Interestingly, recent studies evaluating corn snakes (*Pantherophis guttatus*) and Burmese pythons (*Python molurus bivittatus*) revealed that when exposed to natural environmental levels of UVB, plasma vitamin D₃ levels increased. However, this situation was not identified in the case in Royal ('ball') pythons (*Python regius*), leaving us with more questions about how its presence or absence impacts the health of snake species in captivity (Acierno et al. 2008; Hedley and Eatwell 2013; Bos et al. 2018). One study found that corn snakes (*Pantherophis guttatus*) will voluntarily expose themselves to UVB light when given the option (Nail 2011), and another study found increased basking behaviour in boas (*Epicrates subflavus*) that were not provisioned with either UVB light or given vitamin D supplementation (Bellamy and Stephen 2007). To date, no study has empirically demonstrated the benefits of providing UV lighting to snakes, although its provision may be important.

Specialised lamps may be utilised to provide captive reptiles with UVB of the appropriate wavelengths to enable vitamin D₃ biosynthesis. Several authors have reviewed the types and efficacy of commercially developed bulbs available for reptile husbandry (Bernard et al. 1997; Ferguson et al. 2010; Baines et al. 2016). The UV output of commercially produced lamps varies enormously between types and brands, and determining output is also confounded by, for example, age, total burn time and number of on-off cycles for each bulb. It is important to note that UVB output declines gradually and bulbs should be changed regularly to maintain optimal conditions.

Most lamp manufacturers provide details on UV output, minimum distance of use, and other factors important to reptile care on their labels or websites, but the same word of caution exists for artificial light sources as for vitamin and mineral supplements. It is always best for the husbandry practitioner to know the wavelength emitted and its biological relevance to the situation in which it is employed. A UV index meter can be used to evaluate the bulbs UV output over time and bulbs should be changed when they start losing effectiveness. However, keep in mind that a UVB index meter is providing an assessment of the entire range of UVB (280–320 nm). If the vast majority of the UVB measured is below 285 or above 315 nm (still within the UVB range), the information provided by the meter may be misleading in terms of assessing the ability of the bulb to allow bioconversion.

Additional things to consider when providing UV light include the size of enclosure, the ability for the animal to seek refuge from the light, as well as the temperature and humidity changes that could result from use. As ectotherms, providing reptiles with the most adequate environment possible is a vital component of husbandry and welfare. Balancing each environmental factor in an artificial environment can often prove challenging, but providing animals with choice allows them to select the desired parameters, in this case the amount of UV light. It is important to remember that bulbs, despite appropriate use, are not as effective a natural, unfiltered sun light at ensuring appropriate bioconversion in all species (Diehl and Chiu 2010; Kroenlein et al. 2011).

14.8 Miscellaneous Factors and their Effects on Nutrition

As noted earlier, stress that impinges on nutrition and health can arise from any of several conditions common to captivity. The importance of avoiding stress cannot be overemphasised. Examples of the major causes for stress are:

- thirst, hunger, improper diet;
- inadequate or excessive environmental temperature, humidity or photoperiod;
- unnatural and inappropriate environments;
- overcrowding;
- poorly matched social dominance or sexually established territorialities;
- physical or metabolic disturbances;
- psychic stress from human:reptile interactions; excessive handling;
- housing that lacks appropriate hiding refuges;
- housing of prey species with their potential predators;
- excessive differences in the size of cage mates;
- the presence of infectious or parasitic disease;
- recovery from infectious, parasitic, or metabolic disease and the post-operative period of healing following surgery;
- courtship, including male-to-male combat;
- and the production of sperm, eggs, or embryos.

Each of these stressors can result in a lack or diminishment of appetite; when more than one is present, the effect can be devastating, particularly in chamaeleons, some Iguanids, Agamids, and other usually solitary lizards.

The periodicity and amount fed to captive reptiles is largely governed by the activity level of each individual that is kept in captivity. Very active lizards and snakes require feeding much more frequently than sedentary taxa, which if fed too often, or lacking an ability to exercise, will become obese. Chronic obesity will eventually result in gross accumulation of fat, especially within the coelomic cavity as expanded adipose bodies, and, if sufficiently severe, as lipidosis in parenchymatous organs, especially affecting the liver, as hepatic steatosis (Figs. 14.15 and 14.16). The diet of obese, sedentary herbivorous reptiles should be changed to include more high-fibre vegetation and high-water content succulent fruit and less whole-grain bread, starches or sugar-laden ripe fruit, or other energy-rich items.

The opposite of obesity is inanition/starvation, which is all too often observed in captive reptiles that have failed to thrive in captivity for a variety of reasons. As mentioned earlier, because they are heterothermic creatures, reptiles may languish and, thus require a prolonged period of time to starve. First, their normal stores of fat will be called on for energy, and second, their muscular tissues. Thus, when observed, undernourished reptiles appear to have shrunken tails or other soft body tissues. Figures 14.17, 14.18, and 14.19 are examples of a lizard and a snake that illustrate chronic starvation.

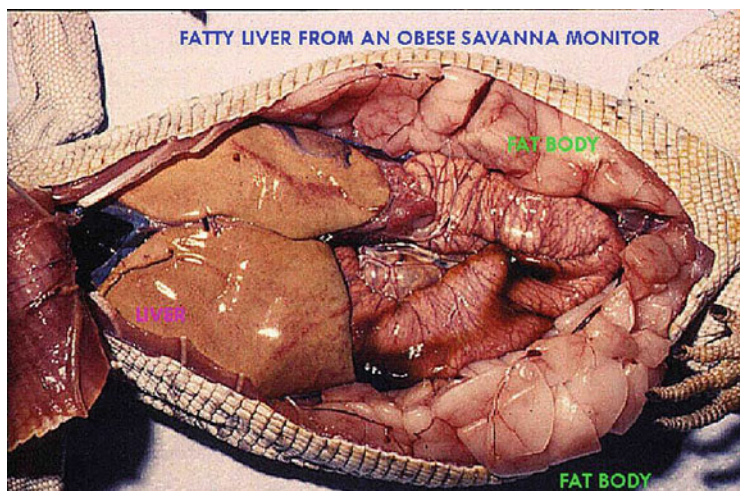


Fig. 14.15 Necropsy specimen of gross obesity in a Savannah monitor (*Varanus exanthematicus*). Note the enlarged coelomic adipose (fat) bodies and swollen fat-laden liver tissue. Printed with permission by Dr. F. L. Frye

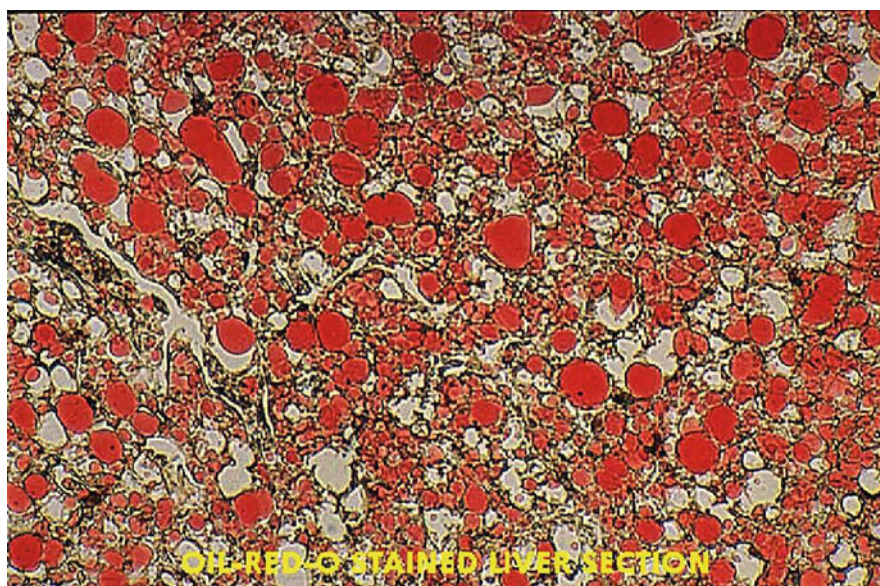


Fig. 14.16 Histological section of the liver from the monitor shown in Fig. 14.15. Note the enormous number of lipid-filled hepatocytes. Oil-red-O stain, $\times 110$ original magnification. Printed with permission by Dr. F. L. Frye

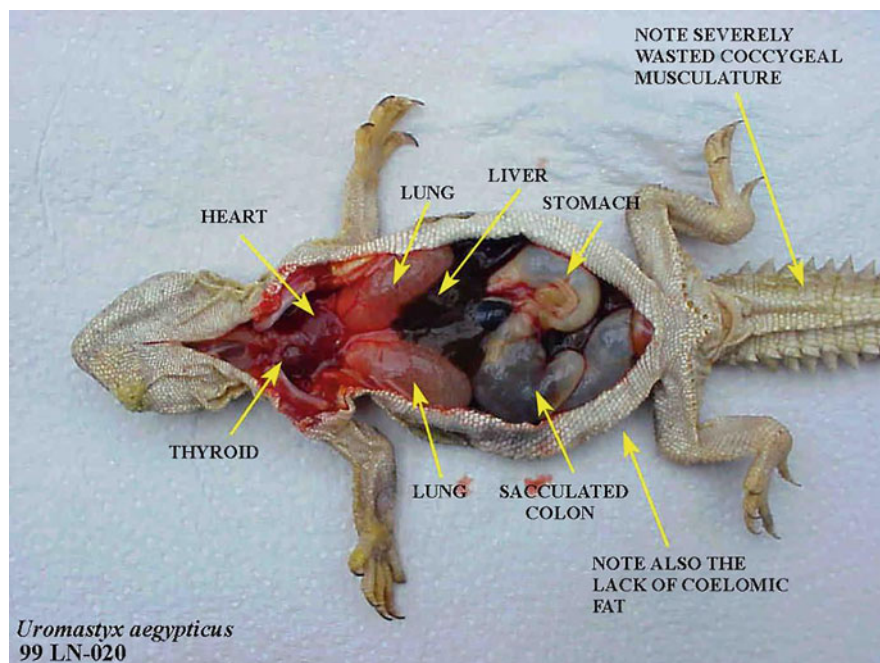


Fig. 14.17 Note the extremely thin and cachectic condition that is best shown by the muscle wasting of the skeletal muscles and the total lack of intracoelomic adipose bodies. Printed with permission by Dr. F. L. Frye

14.9 Future Research Opportunities

Knowledge of reptile nutrition is constantly growing and improving due to increased experience with specific species and increased research focused on not only areas of interest, but areas where perceived shortcomings exist (whether basic or applied). The foundation of many efforts to feed captive reptiles is a clear understanding of the identity and nutrient content of the diet consumed by free-ranging conspecifics. Such examinations will remain important to improve nutritional husbandry for captive reptiles, regardless of foraging strategy. Although the alimentary tracts of many reptiles have been examined and described for science, the microorganisms that inhabit those tracts are just starting to be described. The value of an appropriately-functioning gastrointestinal microbiome is obvious for herbivorous species (to break down cellulose and other fibre not readily available to the animal) but, as we are learning within other taxa, gastrointestinal microorganisms play a key role in health across all or most foraging strategies. The identification of the form and function of the gut microbiome in captive versus free-ranging reptiles may help determine appropriateness of diet, and can provide insight in cases of poor digestion, failure to thrive, or other non-specific health issues. Much new information has been

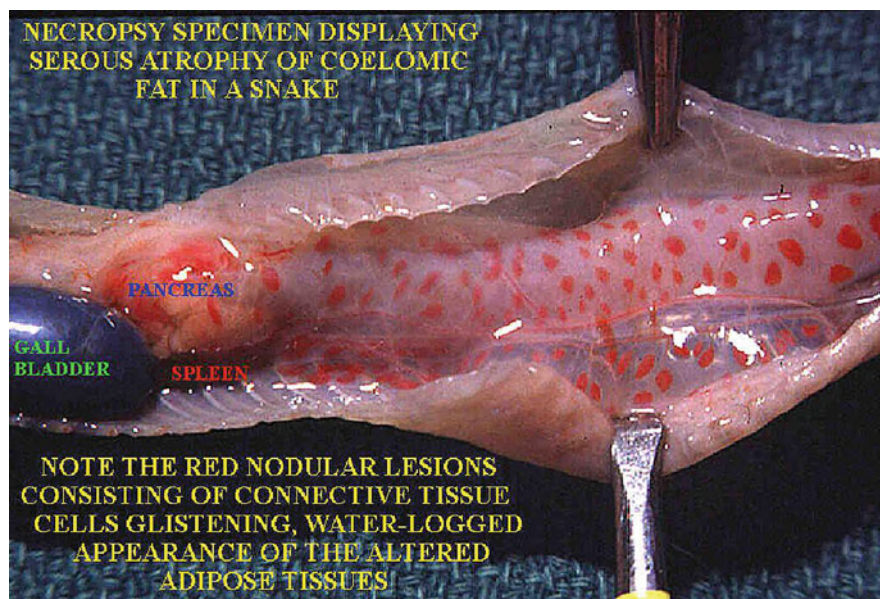


Fig. 14.18 Necropsy specimen of a snake. The small, round bright red lesions are the remnants of the former fat within the coelomic cavity. Printed with permission by Dr. F. L. Frye

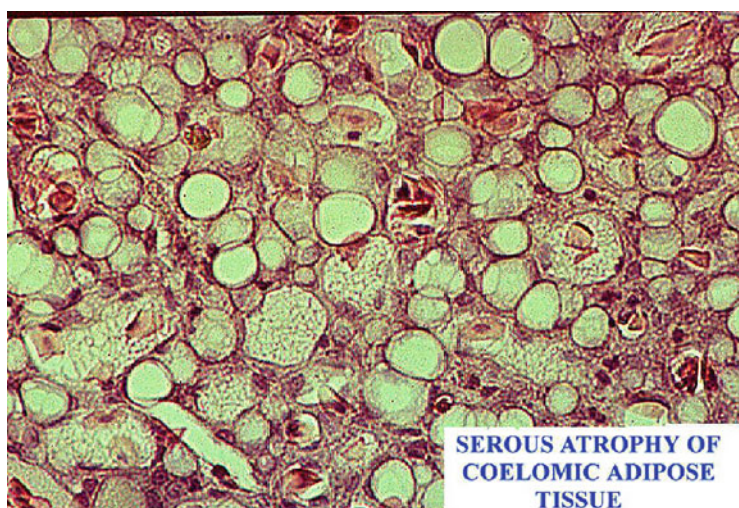


Fig. 14.19 Histopathological image of one of the typical lesions taken from the cadaver seen in Fig. 14.17. Note the relative paucity of lipocytes and their replacement by fibrovascular connective tissue. H & E, $\times 110$ Original magnification. Printed with permission by Dr. F. L. Frye

gathered over the last two decades (since the first printing of this book) about how reptiles utilise UV light. Nonetheless, there is still much to learn about vitamin D metabolism and UV light exposure in snakes and for crepuscular and nocturnal species that are maintained in captive settings.

14.10 Animal Welfare Conclusions

Reptiles are a highly diverse class of vertebrates and as such, it has been beyond the scope of this chapter to suggest individual diets for each species. Accordingly, this chapter has confined itself to generalities common to reptiles, and generalised and specific dietary guidance information is available elsewhere (Frye 1991a, b, 1994, 1995a, b, 1996, 2016; Mader 2005; Mader and Divers 2014; Divers and Stahl 2019). In the future, there may be better commercial diets for many reptiles, and perhaps even more speciality products directed toward preventing and controlling some metabolic disorders.

In the early 1970s, one animal feed company developed and test-marketed an artificial diet for reptiles that closely mimicked the taste and chemical composition of a rat; it was a canned product that superficially resembled moist dog food. It was consumed when presented to a variety of reptiles. The food was consumed by many chelonians, crocodylians, some carnivorous and omnivorous lizards, and a few naticine snakes, but was rejected by most other colubrid snakes and most boids, with the notable exception of anacondas (*Eunectes* spp.), which seem to be willing to engulf almost anything that even remotely resembles food. Today, several artificial diets are being marketed for iguanid lizards; some appear to be well balanced and accepted by these reptiles, but leafy calcium-rich vegetables and leaves such as ornamental shrub (*Hibiscus* spp.) and mulberry tree (*Morus* spp.) appear to provide a more natural diet for these folivorous animals and are much less expensive. For reptiles as 'pets', there will be an enhanced economic incentive for developing nutritionally sound artificial diets for many species.

To appropriately maintain any animal, reptile, or otherwise, in a captive situation, those caring for the animal must account for its every need. The process of placing an animal into a foreign environment within which it has not evolved means animal managers are faced with making the appropriate choices for health and welfare for that animal. Among the complexities of reptile husbandry is the provision of appropriate nutrition. It is impossible to address all of these complexities in a relatively short chapter, and so we have focused on those that we feel are most important.

We stress the need to accurately document and report current nutritional regimes (see Mendyk and Block 2023). Documenting and sharing nutritional information is the first step in developing evidence-based nutritional standards for reptiles. The nutritional care of reptiles is complex and involves much more than simply the provision of food and the nutrients they contain. The consideration of species' natural histories and the importance of how environmental factors and diet contribute to their nutritional status cannot be overstated.

Reptiles have been kept in captivity for over 4000 years (Coote 2001). Some illnesses were probably recognised even by early reptile keepers, and treatment likely discarded in favour of merely exchanging the sick creature for a newly captured healthy one. Lest the reader interpret this as an acquiescence or condonation of keeping animals in captivity, it is not.

However, in a realistic world, animal keeping will, at least for the present, be part of our civilisation. No longer can we afford—nor should we condone—the unbridled exploitation of our resources, and we must conserve and preserve the precious flora and fauna that remain; thus even the most utilitarian of minds ought to appreciate that taking the greatest nutritional and other care of captive reptiles represents a model not only of best practice, but also of ethical responsibility.

In the end, regardless of how well we have addressed all aspects of husbandry, nutritional and otherwise, each animal in our care will die. We will endeavour to determine why, hoping it was not due to some avoidable, nutrition-related under- or over-provision or other mis-step within a management approach. Aiding this approach, clinical necropsies can provide us with some of the last, and most valuable, information that we can learn from a specific animal. By utilising this information, even the loss of a single individual can be a net gain for the care and management of an entire species—if we can learn and apply the knowledge gained in a timely and appropriate fashion. Applying this whole life (and into death) management and learning process to reptile husbandry should be considered a standard for appropriate animal care and welfare, providing a constant honing mechanism for our nutritional approach. We encourage this continued learning, growth, and ultimate success.

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Naturalistic Versus Unnaturalistic Environments

15

Clifford Warwick and Catrina Steedman

Abstract

Reptiles are kept in diverse husbandry situations, including zoological collections, private pet or hobby keeping, scientific and laboratory studies, quarantine, and numerous commercial settings such as for livestock, skin, and meat production, and this chapter is relevant to all these areas. In recent years, a major paradigm shift has occurred favouring naturalistic conditions for the health and welfare of captive reptiles. Increasing data and opinion indicate that the physical, ethological, and psychological well-being of animals (including reptiles) is best served in naturalistic conditions. Despite the generally accepted and growing use of naturalistic environments, husbanders could make greater efforts to incorporate spacious, naturalistic environments across all captive reptile situations. Given now wide acceptance that naturalistic environments infer positive benefits over unnaturalistic conditions, husbanders across all captive situations should evaluate their responsibilities with a refreshed sense of obligation towards developing animal housing to reflect the natural environments in which reptiles evolved.

Keywords

Natural · Environmental diversity · Complexity · Habitat · Space · Stimuli

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15.1 Introduction

Reptiles are kept in diverse husbandry situations, including zoological collections, private pet or hobby keeping, scientific and laboratory studies, quarantine, and numerous other settings, such as for livestock, skin, and meat production (Schlaepfer et al. 2005; UNEP/WCMC 2009; Mason 2010). This chapter has relevance across all the aforementioned areas, in particular concerning concepts and principles relevant to biological needs and husbandry. Numerous early works must be recognised for their foundational influence in the evolution and principles of reptile welfare biology (including Cowan 1980; Greenberg et al. 1989; Morton et al. 1990; Lance 1990; Warwick 1990a, b, 1991; Bielitzki 1992; Ford 1992; Greenberg 1992; Lance 1992; Mason et al. 1992; Pough 1992; Chiszar et al. 1993; Kreger 1993; Burghardt 1996; Burghardt et al. 1996, as well as the first edition of this volume). Nevertheless, the past quarter-century has produced many important contributions to, and in many examples reinforcements of, our understanding of reptile biology and welfare, as well as its association with essential and advanced reptile husbandry (for further examples see¹). Within this cited body of work and its extended reference resource, numerous directly consider the different husbandry approaches involving naturalistic (e.g. based on natural provisions) or unnaturalistic (e.g. based on minimalistic and clinical provisions) environments (including: Warwick 1990a, b, 1991; Pough 1991; Chiszar et al. 1995; Newberry 1995; Burghardt et al. 1996; Bernard et al. 1997; Mellen and Sevenich MacPhee 2001; Almlı and Burghardt 2006; Ferguson et al. 2010; Phillips et al. 2011; Burghardt 2013; Whitham and Wielebnowski 2013; Allgood and Leighty 2015; Baines et al. 2016; Bashaw et al. 2016; Januszczak et al. 2016; Oonincx and van Leeuwen 2017; Mendyk 2018; Warwick et al. 2018; Warwick et al. 2019).

In the first edition of this chapter (Warwick and Steedman 1995), and largely with the intention of promoting debate, we deliberately adopted a more critical approach towards minimalistic and clinical environments. Since then, a major paradigm shift has, as predicted, occurred favouring naturalistic environments. Also, for the first edition a table was provided outlining suggested summary terminology concerning environments associated with captive reptiles (Table 15.1), and those definitions are retained herein. However, whereas originally the focus of this section compared naturalistic (typically elaborate zoological) with clinical (typically minimalistic or

¹Examples of recent relevant publications: (Mason and Mendl 1993; Bernard et al. 1997; Blake et al. 1998; Hayes et al. 1998; de Vosjoli 1999; Mellen and Sevenich MacPhee 2001; Scott and Warwick 2002; Moore and Jessop 2003; Burghardt 2005, 2013, 2015; Case et al. 2005; Almlı and Burghardt 2006; Morgan and Tromberg 2007; Therrien et al. 2007; Manrod et al. 2008; Ferguson et al. 2010; Phillips et al. 2011; Rosier and Langkilde 2011; Leal and Powell 2012; Wilkinson and Huber 2012; Arbuckle 2013; Doody et al. 2013; Kuppert 2013; Warwick et al. 2013a, 2018, 2019; Whitham and Wielebnowski 2013; Mancera et al. 2014, 2017; Martinez-Silvestre 2014; Rose et al. 2014; Mellor and Webster 2014; Wilkinson 2015; Baines et al. 2016; Bashaw et al. 2016; Mellor 2016; Howell and Bennett 2017; Moszuti et al. 2017; Waters et al. 2017; Oonincx and van Leeuwen 2017; Siviter et al. 2017; Mason and Burn 2018; Mendyk 2018; Benn et al. 2019; Lambert et al. 2019; Whitehead 2018; Tetzlaff et al. 2019).

Table 15.1 Suggested summary terminology concerning environments associated with captive reptiles

Term	Concept and design
Natural	Free-living wildlife in natural habitat. Example: the natural world
Captive natural	Natural habitat and indigenous fauna and flora within human-made boundaries, but still in concert with wider natural environment. Example: natural habitat that has been partitioned off as a study site or display
Naturalistic	Use of natural (rather than derived or artificial) provisions in (species-specific) simulated natural environments and organisation. Example: a reasonably detailed caricature of a species' natural environment - present in some elaborate formal zoological and other collections. Such features may include both overt characteristics (e.g. essential space, habitat diversity, animal control over environment, and social conspecifics) and covert characteristics (e.g. essential thermal zones, light wavelengths, chemical cues, and views from enclosure)
Pseudonatural	Can mean 'naturalistic', but literally means 'false-natural', which could also be taken to imply use of only derived or artificial provisions (for example, artificial plants and rocks) in a non-natural environment, that is largely unnaturalistic. Important, therefore, to clarify term specifically, where used
Unnaturalistic	Use of provisions (whole, derived, or artificial) in a non-simulated natural organisation. Example: randomly or poorly chosen or arranged provisions - often found in pet animal cages where keeper has little or no knowledge of species' natural lifestyle
Clinical	Use of simplest and/or least amount of (typically derived or artificial) provisions, usually intended to produce a 'clean' and 'easily managed' facility. Example: hospitalisation enclosures
Minimalist	Can mean 'clinical', otherwise similar but not necessarily intended to manage disease, or assist targeted research programmes. Example: some commercial captive-breeding operations
Reductionist	Can mean 'clinical' or 'minimalist' but perhaps more appropriately used with specific research protocols. Example: progressively reducing complexity of environmental stimuli to increase focus on targeted factors

reductionist laboratory or quarantine) environments, the proliferation of pro-naturalistic conditions across various use sectors warrants a less narrow remit. Accordingly, this revision will look more holistically at naturalistic versus unnaturalistic environments because this approach offers a broader and thus more representative assessment.

15.2 Terminology for Types of Environment

Various terms and meanings exist that refer to relevant environments in the wild and in captivity. The situation is not particularly straightforward. Reptiles in the wild can be completely free of direct, and possibly indirect, human interference. They also can be effectively wild but conceptually captive where one or another form of artificial human-made boundary surrounds a natural area. In regular captive situations there exist, as outlined above, diverse categories wherein reptiles can be placed. Unsurprisingly, husbandry perspectives, as well as the conditions for

reptiles, vary greatly between and within these categories. Table 15.1 provides descriptions for commonly used terms relating to wild and captive reptiles that might assist to clarify and standardise relevant terminology, although there is likely overlap in certain situations.

Terms such as ‘sterile’ and ‘semi-sterile’ have been intentionally avoided because where animal husbandry is concerned these descriptions are largely self-contradictory in that they suggest incomplete absolutes. Such terms offer little or no advantages over the suggested preferred terms in Table 15.1 and, unless specifically qualified when used, potentially add to existing confusion over meanings.

15.3 Naturalistic Versus Unnaturalistic

Animal enclosures and associated husbandry vary considerably both between and within different settings. Typically, the two major applied environmental concepts and types can be characterised as ‘naturalistic’ and ‘unnaturalistic’. This division is based according to whether the essential intention achieves conditions that strongly mimic nature or artificiality. It is inarguable that nature offers greater diversity, complexity, and ecological context than artificial conditions. However, clearly, there is a continuum between natural diverse and complex environments (highly stimulatory, organism-occupying, conditions) at one end of the scale, and artificial minimalist environments (deprived conditions) at the other, with positive, neutral, and negative implications for welfare varying along this continuum.

In some instances, for example, where zoological collections and private pet reptiles are concerned, it is widely accepted that, in principle, there are few or no constraints on why animals should not be provided with carefully organised environments that seek to simulate the natural one, and which are intended to fulfil, as much as possible, species-specific physical, ethological, and psychological needs (Warwick et al. 2013a; Benn et al. 2019; Warwick 2023). In other cases, for example, where scientific studies and veterinary scenarios are concerned, it is widely believed that, for various reasons outlined later, reptiles should be housed in very basic, ‘clean’, and ‘easily managed’ environments, even though these offer less potential to fulfil biological needs (Cooper and Williams 1995).

Reptiles that are physically, ethologically, and psychologically compromised due to inappropriate environments probably experience greater stress (Cowan 1980; Frye 1991; Warwick et al. 2013a, b; Benn et al. 2019; Warwick 2023). Depending on the nature, context, and extent of stress-inducing influences, as well as species, individual character, and condition of the animal, a reptile may either deal with its stressors utilising normal coping mechanisms or fail to cope, languish, and die (Warwick et al. 2013a, b; Phillips et al. 2015; Benn et al. 2019; Jessop et al. 2023; Warwick 2023). The loss of a single animal due to poor welfare management can be regarded as both a heavy moral and a miniature ecological disaster.

Where formal zoological collections, and especially pet animals, are involved, these usually are the major ethical aspects to consider. However, in the case of many

scientific investigations, further specific considerations must be made. Whether the effects of stressors are mild, moderate, or severe, any serious adverse alteration of an animal's holistic health probably alters the purity of the experimental subject and raises serious questions regarding the quality of research data in such cases (Warwick 1990b; Gangloff and Greenberg 2023). Those involved in research, therefore, arguably have even greater responsibilities than others to ensure the good health and welfare of the animals that they are studying (National Research Council 2011).

15.4 Naturalistic Environments

In captivity, it is probably impossible to create anything more than a partial simulation of a reptile's natural habitat. Accordingly, a 'naturalistic' environment is necessarily one that aims towards providing an animal with as many features as possible that replicate nature including relevant: space, temperature gradients and thermoregulatory opportunities, lighting, circadian cycles, diet, water, substrate, furnishings, and conspecifics (see Arena and Warwick 2023; Doody 2023; Mendyk and Augustine 2023), as well as eliminating unnatural aversive stimuli such as noise and light disturbances (Arena et al. 2023; Mancera and Phillips 2023). Naturalistic environments accommodate and stimulate normal positive behaviours (consistent with quiescence and comfort; see Warwick 2023) and states that are also important to promoting good welfare. Understimulating and unnaturalistic environments may impose negative and possibly inescapable stressors, such as thermoregulatory deficiencies, lack of control of environmental interactions, 'boredom', as well as exposure to excessive light and disturbance. Complex, naturalistic, and appropriately stimulating environments cannot objectively be considered negative, and today their value is broadly and widely recognised (e.g. Webster 1994; Mellen and Sevenich MacPhee 2001; Burghardt 2013; Warwick et al. 2013a, b; Martinez-Silvestre 2014; Rose et al. 2014; Carter et al. 2015; Bashaw et al. 2016; Mellor 2016; Oonincx and van Leeuwen 2017; Brando and Buchanan-Smith 2018; Greggor et al. 2018; Mendyk 2018; Benn et al. 2019; Brando and Burghardt 2019; Burghardt 2019; Gangloff and Greenberg 2023; Jessop et al. 2023; Warwick 2023).

15.4.1 General Captive Conditions

An assessment of 62 environmental enrichment studies published between 1985 and 2004 found that only 0.57% concerned reptiles, whereas 92.2% involved mammals (de Azevedo et al. 2007). Years on, despite the raft of significant advancements in understanding captive reptile management, along with recognising the value and application of naturalistic principles, there remains much to do in order to align reptile-based academic study with that of mammals. Although Eagan (2019) found

that 95% of zoos practise some environmental enrichment for reptiles (e.g. thermal, humidity and light range diversity, choice of seclusion sites, and habitat variation), Burghardt (2019) points out that increased enrichment in zoo exhibits and general welfare concerns are far greater for mammals than for reptiles, and stresses the need to 'alter biases' against reptiles, especially snakes.

Spacious, naturalistic enclosures typically incorporate more examples of normal behaviour, although abnormal and problematic behaviour can also be observed (see e.g. Benn et al. 2019; Loughman 2020; Spain et al. 2020). However, unnaturalistic or clinical conditions always include abnormal and problematic behaviour (see Warwick 2023), and frequently little normal behaviour.

It is important to consider that whilst the absence of normal behaviour and the presence of abnormal behaviour are often associated with captivity stress (see Warwick 2023), the presence of some normal behaviour may not conclusively indicate that an animal is in harmony with its environment (Warwick 1990a; Kreger 1993; Warwick 1995; Warwick 2023). There is clearly a need for careful comparative monitoring of both normal and abnormal and problematic states in reptiles, and at present behavioural assessments appear favourable over physiological measures (see Martinez-Silvestre 2014; Gangloff and Greenberg 2023). Obviously, demands made on an animal's evolved coping mechanisms are greater in those conditions where the individual must try to adjust. Similarly, animals cared for in the least natural environments may require the greatest input from humans to promote optimal health and well-being.

More specific research has highlighted a number of issues where naturalistic environments are superior to unnaturalistic environments. Naturalistic conditions are synonymous with environmental enrichment, which can provide a positive outlet for frustration and other problem behaviours or a means of allowing an individual to adequately address, escape, or retreat from stressors (Kuppert 2013; Sneddon et al. 2016). Indeed, environmental enrichment, or naturalistic environments, may be both an essential component of good management (Burghardt 2013) and a problem-solver in terms of a remedy for under-stimulation ('boredom') (Mason and Burn 2018).

The most naturalistic environments are generally associated with formal zoological collections. There is a significant collection of studies illustrating the benefits of naturalistic environments and environmental enrichment in zoo animals (Alligood and Leighty 2015). Boissy et al. (2007) pointed to the wide acceptance that good animal welfare involves not merely absence of negative experiences, but primarily the presence of positive experiences for animals. Keepers with good understanding of an animal's biological and behavioural needs are more likely to have zoo enclosures that promote positive experiences.

Research by Therrien et al. (2007) using behavioural assessment in enriched conditions found that environmental enrichment (such as novel play items and slow food release devices) was as effective for marine reptiles as for other animals and encouraged its use for all captive sea turtles. Relatedly, Arena et al. (2014) found that marine turtles in a naturalistic lagoon showed no signs of captivity stress (effects of stressors in captive conditions), such as hyperactivity, rapid body movement, boundary exploration, surface congregation, and apprehension, aggression, and

cannibalism, aside from occasional boundary exploration. Case et al. (2005) used preference tests to study box turtle physiology and behaviour and found that turtles preferred naturalistic conditions and made less attempts to escape, and both physiological and behavioural assessments positively correlated with enriched rather than barren enclosures. Mehrkam and Dorey (2015) found that naturalist environmental enrichment (such as scented coconut shells for primates) was often preferred by the animals in their study and discuss the importance of appropriate enrichment in increasing species typical behaviours and reducing abnormal behaviours.

Although frequently under-considered, spatial factors are important and integral to reptile welfare (Warwick 1990a; Warwick et al. 2018, 2019; Arena and Warwick 2023). Appropriate environmental diversity undoubtedly provides greater opportunities for animal-environment interaction. Some empirical evidence indicates that reptiles recover more successfully from disease under natural or naturalistic conditions (Warwick 1991; Arena et al. 2023), which could result from fewer or no negative influences or the impact of positive influences on immune competence (see Gangloff and Greenberg 2023).

However, a naturalistic enclosure that is space-restrictive applies a highly significant constraint whereby it is, in effect, at least partially devolved into a reductionist environment. Phillips et al. (2011) found that where food was spread about the environment lizards became more active and spent less time hiding. Also, when space was increased the lizards walked longer and further on their first day, thus stimulating exploratory behaviour, and then longer and further for the rest of the experiment, thus increasing general activity.

Reduced space also infers a lack of naturalistic conditions such as appropriate lighting, temperature, and humidity gradients (Arena and Warwick 2023). Perhaps the view should be more widely fostered that generally reduced naturalistic conditions are simply a move in the wrong direction for animal welfare, as are spacious environments with few or no furnishings. Therefore, whilst small naturalistic environments might be thought of as reasonable natural microcosms, the true inference of a naturalistic environment requires an increasing, not decreasing, relationship with the natural world, that is, spaciousness and diversity. Broadly, in terms of improved welfare, reptiles probably benefit from environmental enrichment as much as any other captive animal (e.g. Burghardt et al. 1996; Almlı and Burghardt 2006; Therrien et al. 2007; Arena et al. 2014; Wilkinson 2015; Bashaw et al. 2016; Brando and Burghardt 2019).

15.4.2 Research Conditions

In nature, a myriad of interconnected genetic (e.g. innate drives), internal (e.g. physiological dynamics), and external (e.g. thermal) factors affect physiological, behavioural, and psychological states. These states change from moment to moment; thus, life in nature is highly dynamic. Dynamic implies variability, and variables are resistant to control. Classically, scientific experiments are designed to limit or control variables. Because naturalistic conditions are favoured for studying

normal behavioural expression, the type of ethological research contemplated here refers to work under the reductionist approach.

Reduction of environments to simplify systems and expose targeted behaviours is commonly practised. This distinctly non-holistic concept presents complications of its own in that, for example, deliberate isolation of behaviours from human-perceived undesirable influences also unavoidably reduces the diverse gross and subtle behavioural interactions found under more naturalistic situations. Studying biological features (e.g. physiological, behavioural, or psychological) in captivity arguably significantly limits their relevance within situations of captivity. Yet, the rationales and protocols associated with a reductionist policy are widely accepted as valid. Moreover, is a reductionist environment ethically acceptable in a purely animal welfare context?

Garner (2005) noted that enrichment may improve research validity, reliability, and replicability by reducing the number of abnormal animals in experiments. Warwick (1990b) and Snowdon and Burghardt (2017) highlighted the need for researchers to be mindful that highly clinical environments, where animals lack the facilities needed to express normal behaviour, may impact the validity of behavioural studies. Moreover, without an in-depth understanding of normal behaviour in the wild, or in highly naturalistic settings, there is no control baseline on which to test hypotheses in behavioural studies.

Thus, captive-based studies instil incongruency at the interface of natural and artificial conditions, not least because the experimenter must select or deselect biological and environmental factors precisely to assess and analyse them in the controlled environment. Accordingly, information based on free-living reptiles can and should inform our approaches to the captive situation whether for research or general husbandry.

15.4.3 Summary Conclusion

In general husbandry, there appears to be no justification for failing to provide environments that are as naturalistic as possible for the species concerned. In some situations where the express purpose is targeting specific biological or research factors, reductionist or minimalistic environments can be rationalised, but in the majority of study conditions, there also appears to be no restrictive reasons why naturalistic conditions should not be maintained.

15.5 Unnaturalistic Environments

Some authors continue to comment on the welfare suitability of unnaturalistic environments for reptiles. For example, Divers and Stahl (2018) suggested there was an absence of scientific evidence that snakes require more intellectual stimulation beyond the clinical conditions of, for example, minimalistic rack housing. However, apart from the wider acceptance of naturalistic environments by the

scientific community, absence of evidence does not infer evidence of absence. Furthermore, small typically minimalistic conditions, such as snake racks, are countered by research and strong criticism regarding increased risk of self-injury, under-stimulation, and stress-related disease, and other work that shows snakes prefer larger more diverse environments (Warwick 1990a, b, 1995; Mendyk 2018; Warwick et al. 2018; Lambert et al. 2019; Warwick et al. 2019; Spain et al. 2020; Arena and Warwick 2023; Font et al. 2023). Diminutive enclosures such as snake racks involve major behavioural restrictions due to enforced inability for snakes to fully stretch (Warwick 1990a, b, 1995; Astley and Jayne 2007; Hu et al. 2009; Cannon and Johnson 2012; Warwick et al. 2013a, b; BVZS 2014; Hedley 2014; Jepson 2015; Wilkinson 2015; Scott 2016; Arena et al. 2018; RSPCA 2018; RVC 2018a, b; Warwick et al. 2018; Warwick et al. 2019; Arena and Warwick 2023; Mendyk and Warwick 2023).

A study by Rosier and Langkilde (2011) employed raised basking platforms as a form of climbing enrichment to assess habitat use among lizards and found no difference in hiding or active behaviours between the control group and the ‘enriched’ habitat group; thus, the authors concluded that researchers need to objectively evaluate the effectiveness of any environmental enrichment. Others have emphasised the importance of using species-specific and appropriate environmental enrichment in research for such studies to be meaningful (e.g. Mellen and Sevenich MacPhee 2001; Case et al. 2005; Borgmans et al. 2018; Loughman 2020; Spain et al. 2020).

It is also possible that studies into the effectiveness of environmental enrichment that appear to show no positive effect on the animals’ physiological or behavioural parameters may be compromised by many variables, such as length of the study, possible unaccounted for negative stimuli, and plasma corticosterone as an indicator of stress taken out of context (Moore and Jessop 2003; Warwick et al. 2013a; Martinez-Silvestre 2014). Oonincx and van Leeuwen (2017) concluded that studies into enrichment should take account of several welfare indicators (e.g. neural, behavioural, endocrine, reproductive, metabolic, psychological), and risk factors (e.g. phylogenetic, ecological), and cautioned that no single measure corresponds directly to an animal’s holistic welfare state.

Razal and Miller (2019) found that observers consistently rated naturalistic enclosures as their preferred environment for ‘livability’ of zoo animals. However, conditions that may look naturalistic to a human onlooker may not be at all appropriate for the species concerned (Fàbregas et al. 2012). Hare et al. (2007) wrote that even though harm and fatal consequences have resulted from well-furnished diverse environments, keepers are ethically obliged to provide enriched environments for the animals’ physical and psychological well-being; such environments also allow for greater choice or ‘individual agency’ by animals over control of interactions with their environments.

15.5.1 Veterinary Management

Veterinary management presents special considerations where naturalistic and clinical environments are concerned (Cooper and Williams 1995). It can be appreciated that microorganisms and megaparasites that may be innocuous to healthy animals might become opportunistic secondary pathogens in diseased or otherwise immunocompromised individuals. Relatedly, injured animals might be at greater risk of local (possibly leading to systemic) infection or other forms of wound contamination if there are open lesions. Also, as outlined previously, it is worth considering the potential compromising effects of greater captivity stress in clinical environments, and possible associated increases in susceptibility to secondary opportunistic and primary diseases (Martinez-Silvestre 2014). Similarly, the rate of an animal's recovery might be slowed or hindered in high-stress conditions; for example, wound healing has been shown to be slower in restraint-stressed lizards (Gouin and Kiecolt-Glaser 2011a, b). This perspective, does, of course, apply to all aspects of clinical (including veterinary) situations.

Collection of samples, such as faeces, is occasionally necessary for a variety of purposes, and these obviously should be as free as possible from environmental (including co-occupant) contamination. Sometimes, such management may be simpler in clinical environments, but it should not be presumed that it is possible only in such facilities. Samples collected even from the most clinical environments may not mean zero contamination. Prompt and effective removal of droppings from a cage (regardless of whether it is a naturalistic or clinical one) may be the most important procedure in minimising contamination of samples. Of course, faecal and other relatively 'solid' samples are easier to collect than highly fluid ones, such as urine, which are quickly absorbed into a deep substrate in a naturalistic environment. However, a paper floor covering in a clinical environment also might absorb fluids to the point where useful collection is also very difficult.

Clinical environments, at least during veterinary treatment, are clearly suitable much of the time. Temporary clinical environments do not have to imply bare conditions, and some elements for retreat can still be provided, such as species- and individual-specific seclusion zones (e.g. disposable cardboard boxes). In some cases, naturalistic environments may lead to greater chances of recovery, because captivity- and disease-related stresses may contribute to poor prognoses (Warwick 1991). That said, carefully managed clinical environments for numerous aspects of short-term veterinary treatment and related research may offer a justifiable solution to a potentially complicated dilemma. A highly significant justification for clinical conditions in all veterinary aspects (treatment, investigation of disease, and quarantine) may reside in the fact that most treatment involves short-term hospitalisation, thus avoiding chronic captivity stress. Although some stress is probably experienced in the clinical setting, and such stresses can have long-term consequences, its impact may be moderated and balanced with the benefits of remedial and regular expert supervision. However, it must be noted that should chronic captivity-stress situations develop, then conceivably this could tip the balance away even from any clinical setting.

15.5.2 Quarantine

Quarantine facilities are often associated with the housing of animals short term or at short notice. In these circumstances, healthy animals may be included for straightforward observation, or diseased and injured animals for segregation and treatment. As far as healthy animals are concerned, naturalistic facilities seem to be the best candidates because of the greater comfort afforded animals by these conditions, as indicated by their preference behaviours, greater behavioural normality, and probable greater perceived security (e.g. Case et al. 2005; Rose et al. 2014; Benn et al. 2019; Spain et al. 2020). There is obvious merit in a simple, standardised, housing system for short-term accommodation of animals. Nevertheless, in principle, naturalistic conditions cannot be precluded even from such management situations.

15.5.3 Summary Conclusion

In some, but not all, examples of veterinary treatment, research, and quarantine, a number of reasonable arguments appear to exist for providing clinical environments. It also seems reasonable that the use of naturalistic conditions even in the most stringent clinical situations is feasible and at least open to debate. Overall, the advantages of clinical environments over naturalistic environments may be more perceived than real, and in a purely welfare context, such approaches require precise and careful justification.

15.6 Practical Considerations

In addition to environmental suitability in fulfilling an animal's biological needs, preference for either naturalistic or unnaturalistic environments may be influenced by other practical considerations, such as access to animals, efficacy of maintenance, and hygiene. Managing preferences may vary according to situation; for example, zoological collections, private pet or hobby keeping, scientific and laboratory studies, quarantine, and numerous commercial settings. Nevertheless, certain considerations may also be generally applied.

15.6.1 Access to Animals

Access to animals for inspection or capture is obviously necessary on occasion. The ease or difficulty with which inspection or capture is achieved can be, but is not necessarily always, affected by whether or not the environment is naturalistic or unnaturalistic. For example, a human presence can elicit specific responses from reptiles - both wild and captive. Observations of free-living lizards awoken at a regular rest site by a distant human presence (and which showed no overt response on that occasion) were nevertheless sufficiently affected by the experience to avoid

the same resting place the following night (Sugerman and Hacker 1980; Bowers and Burghardt 1992). Human handling may also disrupt important periods of thermoregulation (Arena et al. 2023; Arena and Warwick 2023; Mancera and Phillips 2023; Warwick 2023). Stockley et al. (2020) showed that even gentle handling of a normally 'placid' species (bearded dragons (*Pogona* sp.)) appeared to increase anxiety-related behaviour (tongue flick rate), which may suggest that direct contact with these animals should be minimal.

These two very different examples illustrate potentially profound effects of subtle disturbances. It is important to consider that consequences of some disturbances may themselves be subtle or profound, and act earlier, later, or continuously (see also Bowers and Burghardt 1992; Gillingham and Clark 2023; Lillywhite 2023). Intentional or incidental human contact with reptiles is, therefore, something that has to be evaluated very carefully - perhaps especially where the researcher-reptile relationship is involved. Further, disturbance of animals during their rest cycle (which may differ from human activities) should be avoided wherever possible (Arena et al. 2023; Arena and Warwick 2023; Warwick 2023). Accordingly, careful training is now used by numerous professional facilities to condition reptiles to certain handling requirements and procedures (see Font et al. 2023).

15.6.2 Maintenance Efficiency and Hygiene

Certain concerns regarding threats to hygiene in well-maintained naturalistic environments relate to potential contamination risks associated with water, substrata, and plant life. In naturalistic environments, substrata or bedding contaminated by faeces or sloughed skin is practically removed as dry solid matter, often along with a small quantity of substratum, during 'spot-cleaning' - which helps prevent contaminant accumulation. Fluid waste deposits are absorbed into substrate until a 'bowl' of moist material forms, which can then be easily removed as a single 'unit'. Small amounts of waste products inevitably remain in the environment, but build-up is slow and often easily managed. Drinking and bathing water that is heavily contaminated presents the potential threat of disease, but water quality management of both small and large bodies of water is similar across all captive settings.

In unnaturalistic or clinical situations, artificial substrate (e.g. paper) has comparatively low absorption potential, and requires frequent removal; floor surfaces also require cleansing on a very regular basis - which infers more handling. Zoological collection managers anecdotally report that well-managed substrata can remain viable furnishings for several years, although clearly this is not a specific recommendation. Proponents of unnaturalistic or clinical environments routinely recognise that naturalistic substrata are required for certain species. Such reasoning could be far more broadly applied. Cautionary hygiene is widely accepted as important both for non-human and human animal health. Clearly, excessive build-up of waste and decaying organic matter is to be avoided. However, the extent and not the mere presence of contamination (as well as the animal's existing state of health) imply

relative risk. Nevertheless, caution must be exercised not to introduce potentially harmful contaminants (e.g. pesticides) via introduced natural furnishings (Murphy 2015).

During a survey by Warwick et al. (1992) researchers expressed far greater difficulty in experimentally infecting reptiles in naturalistic conditions than reptiles in unnaturalistic or clinical conditions. Indeed, this apparently was so evident that reptiles to be infected were deliberately rehoused in clinical environments to increase the chances of them acquiring a forced disease. A. Lambiris (pers. comm.) reports on experiences that suggest that free-living reptiles presented with normal biological (including immunological) stresses are at an advantage over captive animals facing problems in the artificial environment. In captive reptiles maintained in scrupulously hygienic conditions, and where keepers had perceived them to be free of stress, disease occurred with far greater virulence than in wild populations. The aetiology, at least in part, was attributed to captivity-related chronic stress and compromised immune competence arising from environments that were too clean and/or resulted in related stress. One could argue that there exists the possibility that over-cleaning reduces or eliminates conceivably important subtle stimulation of an animal's immune system. Exercise of the immune response due to background microbiology may be integral to overall maintenance of immune competence.

As indicated above, threats to animals from normally innocuous factors may only be realised as a result of compromised immune competence. This negative effect may be reduced by naturalistic, and thus biologically more comfortable, environments. At what level of microorganism infestation in an environment should one start to become concerned for animal health? If the mere presence of potentially pathogenic organisms is always to cause alarm, then alarm will be caused constantly; the point here being that truly dirty water, decaying sloughed skin, and other bacteria-laden organic debris, as well as chemically noxious substances, present unreasonable, greater-than-natural threats to animal health than naturalistic biotic conditions. A well-maintained naturalistic environment ought to present minimal hygiene risk.

Extreme cleaning of an environment may have other adverse implications. For example, cage-cleaning can delete familiar chemical cues that are known to have a calming effect on reptiles (see Chiszar et al. 1993, 1995). What level of stress might regularly repeated hygiene protocols have on individual animals? In addition, might frequent disinfection lead to the emergence of mutant, antimicrobial resistant, and possibly more serious pathogens?

Arguably, when one accepts the highly limited value of striving for substantial cleanliness, then one has to consider carefully the negative implications of captivity stress in a clinical environment. General clinical protocols should perhaps be considered as ways of keeping over-contamination out, rather than ways of keeping 'sterility' in.

In nature, animals are exposed to a myriad of microbial organisms and particles, as well as many contaminants throughout all living conditions, and indeed such factors continue to operate after death. Whilst all such environmental characteristics may present potential challenges to good health, they are also frequently integral to

it. What constitutes good versus bad hygiene is significantly a matter of balance between the nature of a potential threat and individual immune competence. Therefore, good hygiene management is a target of responsible husbandry, which implies appropriate cleanliness, and does not infer sterility. Access to animals may be an important occasional requirement. However, the proliferation of naturalistic environments in use globally offers testimony to their reasonable practicality. Accordingly, naturalistic conditions should not be interpreted to suggest impractical or problematic hygiene or access to animals.

15.7 Animal Welfare Conclusions

Historical and some current preferences for unnaturalistic environments appear primarily founded on long-established habits rather than scientific approaches. Increasing data and opinion indicate that the physical, ethological, and psychological well-being of animals (including reptiles) is best served in naturalistic conditions.

Providing environments that allow animals to fulfil natural behaviours is probably essential to promote welfare, and thus optimise health. Innate (inborn) drives or needs are importantly met in order to aid welfare in both human and non-human species (Ross and Mason 2017). Innateness is a fundamental characteristic of reptilian biology where psychological and behavioural attributes and needs are hard-wired or pre-set to the natural conditions of life in the wild (Warwick 1990a, b, 1995; Warwick et al. 2013a; Warwick 2023). In humans, environmental enrichment has been shown to improve cognitive performance (e.g. Singhal et al. 2019). Assuming such considerations may be applicable to reptiles, then greater environmental complexity may also be related to the cognitive capacities of these animals.

Despite the generally accepted and growing use of naturalistic environments, husbanders could make greater efforts to incorporate spacious, naturalistic environments across all captive reptile situations. Early attention should be given to factor in spatial, environmental complexity, and cost issues to provide naturalistic accommodation for animals when captivity-based facilities or projects are considered. This approach offers the potential to contemplate more fully animal requirements over the conveniences of an establishment's extant architecture, rather than vice versa.

Also, general managers and researchers who are reluctant to employ naturalistic conditions could make greater efforts to record and balance perceived advantages and disadvantages, both practical and conceptual, of naturalistic and unnaturalistic conditions, with an overview bias towards reptile welfare. Placing or producing a reptile in captivity may constitute the most challenging environment in which it might be expected to survive (Warwick 1995).

Just as 'environmental enrichment' ought to be thought of as a baseline norm of nature, naturalistic environments should be considered as fundamental to enclosure concept and design (see Greenberg 2023); they are not, and should be, viewed as 'additional' or 'extra' provisions or facilities. Given now wide acceptance that

naturalistic environments infer positive benefits over unnaturalistic conditions, husbanders across all captive situations should evaluate their responsibilities with a refreshed sense of obligation towards developing animal housing to reflect the natural environments in which reptiles evolved.

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Evidential Thresholds for Species Suitability in Captivity 16

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Abstract

Collectively, across all relevant sectors, millions of reptiles representing a wide range of species are kept in captivity, despite commonly being maladapted to the conditions in which they are held. In general, little data on the behavioural needs and welfare risks are available for the diversity of reptile species found in captivity. Accordingly, the amount and validity of objective scientific information available is a critical factor in determining the suitability of species to keep. Despite advances in our knowledge and understanding of reptile biology and care, the majority of captive reptiles continue to suffer for numerous and varied reasons. Because of these and allied issues, a reasonably reliable ‘scoring’ system should be applied to more objectively determine the suitability or otherwise of reptiles for captivity, as well as the suitability of the person to keep them. We propose suitability tools that are divided into two parts: *Animal* suitability and *Keeper* suitability. If followed, this two-pronged ‘precautionary’ principle would help to avoid keepers entering a quagmire of bad practices, with negative animal welfare and other consequences, and then struggling to find detailed evidence on husbandry—which may not exist.

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Keywords

Welfare measurement · Knowledge deficits · Species suitability · Suitability tools

16.1 Introduction

According to various reports, reptiles have been ‘kept’ either partially or fully captive for over 4000 years (Coote 2001) and, within the ‘modern scientific’ era, certainly for over a century (Bateman 1897). Throughout this history, both husbandry and welfare advancements and detriments, from minor to major, have paralleled each other, and it remains debatable whether these effects are positively or negatively balanced.

Within the background of reptile keeping are many issues of concern, all of which form important recurring welfare themes. These include, but are not limited to: sourcing, handling, transportation, stocking, deficient enrichment, and general captivity adaptational and maladaptational considerations, and the increasingly recognised point that even the best information for the most well-known species is incomplete. Within the foreground are also numerous persistent themes, including: costs, practicality, and maintenance of vivaria-associated ‘life-support’ equipment; essential dietary supplementation; and acquisition of reliable and objective information—all frequently challenging factors with welfare implications. At the heart of all these factors reside the fundamental issues of the welfare needs of reptiles, which derive from evolved environmental, physiological, behavioural, and practical requirements. Consequently, as elaborated elsewhere in both this chapter and volume, providing artificial conditions that replicate the obviously suitable and clearly optimal environment of the natural world so as to adequately meet the animals’ welfare needs, is difficult to conceive and probably impossible to achieve in most circumstances (Burghardt 1996; Mendyk 2018; Mendyk and Warwick 2023; Mendyk and Augustine 2023).

Basic or short-term care for reptiles can be provided using broad principles, for example, by applying natural regional climate and habitat parameters to develop ‘safety net’ conditions (Warwick et al. 2018a; Maslanka et al. 2023). However, long-term management must be considered at the class, order, species, and individual levels—because providing the necessary tailoring of good husbandry requires both generalised and specific delineation of applied information (Mendyk 2018). In addition, many keepers across all husbandry situations maintain or seek out rare and unusual reptiles for which information on natural lifestyles and biological needs are particularly scarce, leading to husbandry practices that are less likely to meet the animal’s needs and thereby raising animal welfare concerns even further.

Primary causes of regular illnesses in captive reptiles include deficient husbandry and environmental injury (Hunt 2019). Deficient husbandry involves such factors as: malnutrition, hypo- and hyperthermic surroundings, inadequate or inappropriate space, exercise, lighting, humidity, and ventilation. Environmental injury includes

injury caused by physical boundaries and hazards, infection, micro- and macroparasite infestation, injury from live prey and co-occupant aggression. All can be compounded by the species' general limitations in normal biological adaptive capabilities or 'coping mechanisms' (Cowan 1980). Often several factors together act as combination causalities of illness. Collectively, these issues constitute a major animal welfare concern residing in plain sight, although often unidentified until late, too late, or not identified at all.

Many biologists now recognise that natural (or at least naturalistic) environments provide for better welfare (Case et al. 2005; Martínez-Silvestre 2014; Bashaw et al. 2016; Gangloff and Greenberg 2023; Warwick 2023; Warwick and Steedman 2023). There may be factors particular to the complex and holistic system of nature and fundamental to health and welfare that are not yet understood by scientists. These may be either incidentally included by naturalistic conditions or excluded by minimalistic husbandry practices. However, good welfare is more than merely achieving physiological homeostasis and absence of disease—it also infers actively reviewing, conceiving, designing, and providing protocols that stimulate positive psychological and behavioural outcomes (Webster 1995; Burghardt 2013; Mellor 2016). Importantly, animal keepers need to recognise the related yet distinct difference between naturalistic environments and environmental enrichment, and their relationship to the animals' positive or negative affective states. Naturalistic environments are natural-like enclosure designs and furnishings. Such naturalistic conditions in themselves often provide environmental enrichment relative to minimalistic keeping conditions, but environmental enrichment may require more specific provisioning, namely, adapting or introducing features within the environment to offer non-aversive stimulation and choice of diversity to the occupant. Positive affective state is the good welfare resulting from such endeavours (e.g. Webster 1995; Burghardt 2013; Martínez-Silvestre 2014; Bashaw et al. 2016; Mellor 2017; Gangloff and Greenberg 2023; Warwick and Steedman 2023).

Related to this, our increasing scientific understanding of reptiles reveals greater biological complexity compared with, for example, domesticated animals, including such issues as degree of hard-wiring and precocity (inherent attributes and relatively advanced early development), diversity of species and associated biological needs, limitation of biobehavioural data, and degree of control required for environmental, physiological, and behavioural needs, as evidenced throughout this volume. Thus, genuinely meeting reptiles' welfare needs may be increasingly unreachable—the more we learn, the more we know is missing! It is clear that a great deal of fruitful research has been conducted on reptile husbandry and has advanced captive animal welfare. However, many welfare-related issues remain because they are not recognised or appropriately addressed. Regardless, the fact that many problems are persistent and go largely unresolved is not only concerning, it should also tell us something more fundamental. Move beyond the misperceptions of reptiles being content with life in a glass box, and it is clear that conjoining reptilian and human lifestyles commonly just does not work out for the reptile; whether as consequences of their suitability or unsuitability to live outside of their natural environments, our ability to provide suitable environments for them or our inability to accurately assess their welfare.

In this chapter we present and discuss the issue of information and its use based on evidence, or its misuse based on deficits from ignorance of biological and husbandry factors, arbitrary practices—many of which are historically traditional in the keeping community, miseducation, and malcompliance (see Mendyk and Warwick 2023). We then summarise some existing methods to assess species suitability. Finally, in order to promote informed decision-making for the benefit of animals and humans alike, we introduce self-assessment tools for determining both the suitability or otherwise of reptile species for captivity and of the people who aim to keep them.

16.2 Information, Compliance, and Knowledge Deficits

Readers of this book will be aware that ‘herpetology’ is regularly defined as the study of reptiles—moreover, implying the *scientific* study of these animals. This somewhat pedantic description is used here to mark contrasting degrees or levels within the framework of relevant educational backgrounds for those who are involved with captive reptiles. Given modern drives towards professionalisation, the true ‘herpetologist’ might be further categorised as someone trained and/or qualified in reptile science to a high academic and professional standard, and who typically occupies the academic or professional environment such as a university, highly regarded zoological facility, or scientific institution such as a laboratory. The herpetologist utilises, or should utilise, the best available objective science for the understanding and maintenance of captive reptiles, and should regularly ‘challenge’ its relevance and authenticity. Little information should be accepted without corroborating evidence, and the evidential bar should be set high. Allied to this category are many who possess relevant, but less specialised, education, such as general biological, zoological, or veterinary qualifications and who maintain a strong interest in reptiles.

Most other reptile keepers may be loosely divided into two categories: the ‘hobbyist or enthusiast keepers’ (i.e. those who often possess few to hundreds of reptiles of less common or rare species or types bred by artificial selection); and the ‘regular pet keepers’ (i.e. those who typically have one or two common species of ‘pet’ reptile and acquire them in much the same way as someone acquires a dog or cat). Thus, loosely, one might regard those associated with the study and/or keeping of reptiles to fall into one of four essential categories: (1) professional scientifically trained/qualified herpetologist; (2) semi-professional scientifically trained/qualified biologist, zoologist, veterinarian with interest in reptiles; (3) amateur herpetologist/hobbyist or enthusiast; and (4) regular reptile pet keeper.

These two latter categories approximately mirror other animal keepers, such as for pet cat ‘owners’ and cat breeders who typically acquire their knowledge informally or through experience, and with varying degrees of quality. Accordingly, even at the ‘higher’ level of ‘hobbyist’, a reptile keeper or breeder is not necessarily any more a ‘herpetologist’ than a cat breeder is a ‘mammologist’. However, for some individuals the term ‘amateur herpetologist’ may be justified.

Raising this issue is not a critique of people who do not possess a particular scientific background. Cat keepers generally do well with their charges regardless of not being mammalogists. However, a key difference here is that keepers of cats and other domesticated species have access to genuinely qualified expert assistance that is frequently no further away than the local high street, where highly regulated and accountable veterinary help is at hand along with other key elements of ‘societal infrastructure’ such as longstanding human-domesticated animal associations, and experience. Basically, providing at least good, if not always excellent, care for domesticated dogs and cats is relatively easy and common, whereas providing good care for reptiles is much harder, and uncommon or rare.

Where reptiles are concerned, veterinary science lags behind that for domesticated species, and local availability of modest assistance is hit and miss, mostly miss (Whitehead and Forbes 2013; Grant et al. 2017). Furthermore, the factors confounding reptile keeping are substantially greater than those affecting dogs or cats. Essentially, the availability of quality information and practical assistance for reptile keeping is low whereas the problematic demands are high. Whilst it is acknowledged that there is also misinformation concerning dogs and cats, this can be quickly countered, and health and welfare issues prevented by regular, good quality local support. Significantly, local professional (e.g. veterinary) support and biological data for domesticated species requires a knowledge base relevant to only a handful of species (e.g. dogs and cats represent two species), whereas there are over 11,000 reptile species, many of which are known to be kept in captivity.

Unsurprisingly, given the large demand for information on reptile husbandry, sources and providers manifest via a multitude of media, of which almost all is formally unregulated, scientifically untested, and factually dubious (Williams and Jackson 2016; Grant et al. 2017; Howell and Bennett 2017; RSPCA 2017; Mendyk and Warwick 2023). Decades of poorly researched and anecdotally evidenced books, reptile magazines and online forums have inflated the ‘information problem’ by filling knowledge gaps with opinion, much of which is often erroneous. New digital media could assist to distribute valuable information. Instead, new media has massively compounded misinformation issues by enabling free and wide dispersal of misleads or falsehoods where not only does poor quality information gestate universally, but also searches for better answers are not pursued (see Mendyk and Warwick 2023). Disturbingly, even some respectably produced ‘scientific’ works retain somewhat outmoded concepts and other erroneous information, effectively promoting reptiles as being: ‘good pets’, ‘adapted to captivity’, ‘domesticated animals’, ‘thrivers in captivity’ and a raft of other pseudoscientifically rationalised claims (e.g. Bartlett and Bartlett 1999; McCurley 2005; Engler 2010; see also Mendyk and Warwick 2023; Mendyk and Augustine 2023). Fortunately, such claims are relatively infrequent among genuine herpetologists, although they are a mainstay of the reptile keeper and breeder community.

Scientific intervention and robust, objective testing cannot halt a process where passion is consuming and scientific moderation is absent. In other words, among most reptile keepers, the knowledge base and allied practices are commonly fuelled by hearsay, keeper traditions, and bad habits (see Mendyk and Warwick 2023).

These problems in turn, partly feed back to the earlier point regarding certain recurring and unresolving husbandry issues. This phenomenon was summarised by Grandin and Muir (2016) as ‘bad becoming normal’—i.e. the normalisation of bad information and husbandry. Assessments of husbandry approaches within the reptile-keeping fraternity have specified the prevalence of non-evidence-based arbitrary husbandry practices and ‘folklore husbandry’ and the need to break that cycle (Arbuckle 2013; Mendyk 2018; D’Cruze et al. 2020; Mendyk and Warwick 2023).

A serious problem with arbitrary or folklore husbandry is that once ingrained, it is very difficult to ‘undo’, especially when near constantly reinforced by ill-informed advisors. Incorrect or distorted information suggesting that reptiles are ‘easy to keep’ under certain, usually minimalistic, husbandry regimes clearly is more attractive to people aspiring to acquire reptiles as pets, exhibits, or research animals. For commercial sellers and hobby groups, maintaining the aforesaid misperceptions is good for business and membership. Telling someone that they have most or all of their advice wrong, and that beginning to resolve a wide range of extant and often unrecognised problems will require additional and probably expensive resources, is likely to be poorly received and ignored. Erroneous advice advocating the suitability of minimalistic enclosures in which snakes cannot fully stretch, and feeding insectivorous reptiles highly restrictive commercially produced items with poor nutritional quality, remains common yet supported by many keepers (Mendyk and Warwick 2023; Mendyk and Augustine 2023). Accordingly, compliance with ‘better’ information provided to potential or actual husbanders is frequently poor (Kohler 2010; Pees et al. 2014; Vonk et al. 2016; Howell and Bennett 2017; Krautwald-Junghanns et al. 2017; Moorhouse et al. 2017; Alves et al. 2019; Howell et al. 2020). Relatedly, if a keeper has insufficient scientific knowledge to recognise problems requiring advanced understanding in his or her own ‘collection’, then undoubtedly things may seem acceptable and change unnecessary. Relevantly, Burghardt (2013) described husbandry for captive reptiles as ‘depauperate’, and even in the best zoos as ‘controlled deprivation’—or inferior to the spatially and environmentally diverse and stimulating conditions of nature.

16.3 Essential Principles for Animal Welfare

Welfare should refer to the measurable state of the individual, generally from very good to very poor. Keepers should have a system or systems available that enable them to determine and grade animal welfare (see Greenberg 2023; Mendyk and Augustine 2023; Mendyk and Block 2023). These measurements should be based on objective evidence and proven remedial methods for adverse situations, not merely popularly accepted information. Grading should be frequent and recorded to encourage a desire to constantly improve the welfare score. Scientific assessment of welfare might not consider ethical judgement, but such information may lead to ethically-led decisions. Typically, reptile welfare assessment has been based largely on presence or absence of negative features, whereas it should aim to assess both ‘positive’ and

‘negative’ states, i.e. it should recognise that good welfare is not just the absence of negative welfare factors.

Poor welfare can be associated with an animal’s lack of control over or synergy within its environment. Thus, maladaptation may be due to fundamental lack of adaptive plasticity and/or lack of keeper understanding regarding how or whether an animal can adapt. Stress is a part of poor welfare that involves failure to cope. Malnutrition, disease, trauma, and exposure to predators do not lead to good welfare. Health is part of welfare because disease states have a negative impact, and because aspects of health can be made worse when general welfare is poor. Points of reference for animal ‘welfare compromise’ include defining the objectionable affects (feelings) animals may experience, in both quantitative (e.g. mild to severe) and type terms (e.g. hunger, pain, discomfort, fear). The primary objective of regularly assessing welfare throughout an animal’s life is to facilitate management practices designed to minimise negative experiences. It is necessary to identify particular welfare issues and problems and their related measurable indices, and then to devise remedies. For example, Table 16.1 lists some fundamental measures of welfare that are utilised in general animal science, and that can be applied to assessments in reptiles, and which indicate complexity of issues. Some of the listed issues (e.g. body damage prevalence, reduced ability to grow or breed and reduced life expectancy) may be assessed using regular record-keeping, whereas others (e.g. physiological indicators of pleasure, behavioural indicators of pleasure, and physiological attempts to cope) require species-specific knowledge, comprehensive data regarding normal versus abnormal comparative parameters, and awareness of concepts and principles for animal welfare science.

Certain models are widely incorporated into welfare assessments. The Five Freedoms (FAWC 1979; Webster 1995; RSPCA 2005; FAWC 2009) may be the original standard-setter aimed at ensuring that welfare is not compromised, and these criteria are:

Table 16.1 Measures of welfare

Physiological indicators of pleasure (positive affective state)
Behavioural indicators of pleasure (positive affective state)
Extent to which strongly preferred behaviours can be shown
Variety of normal behaviours shown or suppressed
Extent to which normal physiological processes and anatomical development are possible
Extent of behavioural aversion shown
Physiological attempts to cope
Immunosuppression
Disease prevalence
Behavioural attempts to cope
Behaviour pathology
Brain changes
Body damage prevalence
Reduced ability to grow or breed
Reduced life expectancy

Derived from: Broom (1991)

1. Freedom from hunger and thirst—by ready access to fresh water and a diet to maintain full health and vigour;
2. Freedom from discomfort—by providing an appropriate environment including shelter and a comfortable resting area;
3. Freedom from pain, injury, or disease by preventing animals from getting ill or injured and by making sure animals are diagnosed and treated rapidly if they do;
4. Freedom to express normal behaviour—by providing sufficient space, proper facilities, and company of the animal's own kind;
5. Freedom from fear and distress—by ensuring conditions and treatment, which avoid mental suffering.

Since established, the 'Freedoms' have been valued for encompassing both the physical and mental wellbeing of animals, and should be considered a part of any assessment concerning species suitability. The concept is universally applicable to animals in zoological, farming, biomedical research, pet, or other situations. The Five Freedoms were and are well recognised in the animal welfare arena; however, their aspirational, rather than outcome-led, objectives and a marked increase in scientific information during recent decades suggests that they may not capture the breadth and depth of current understanding regarding animal welfare biology and essential management.

Another model, The Five Domains, for assessing animal welfare has roots in The Five Freedoms and was initially used in research and teaching, although also developed to address certain deficiencies of the 'Freedoms'. The 'Domains' model was designed to provide a more thorough, systematic, and comprehensive means to assess negative welfare impacts, and these criteria are: nutrition, environment, health, and behaviour—each with detailed sub-divisions (see Mellor and Beausoleil 2015; Mellor 2017). Since its formulation, The Five Domains model has been regularly updated to incorporate developments in animal welfare thinking, such as the inclusion of the fifth domain of negative, neutral, and positive effects and states to give greater definition and to facilitate its application to animal uses beyond research, teaching, and testing. The most recent update has incorporated far-reaching consideration of a broad range of positive affects—directed at achieving 'a life worth living' for all animals (Mellor 2016).

The Five Welfare Needs (RSPCA 2005) theoretically also advance the original ideas of The Five Freedoms to adopt outcome-led rather than aspirational principles, and these criteria are:

1. Need for a suitable environment;
2. Need for a suitable diet;
3. Need to be able to exhibit normal behaviour patterns;
4. Need to be housed with, or apart, from other animals;
5. Need to be protected from pain, suffering, injury, and disease.

A recent Welfare Quality[®] Protocol was developed using behavioural, health, and husbandry indicators in scincid lizards with the aim of providing foundation for broader application to reptiles generally (Benn et al. 2019). For example, the protocol advocates using multifactorial welfare criteria, including absence of prolonged hunger, appropriate diet, absence of prolonged thirst, comfort around resting, thermal comfort, ease of movement, interaction with burrows, absence of injuries, absence of disease, absence of pain induced by management procedures, expression of social behaviours, expression of other behaviours, good human–animal relationships, and positive emotional state—with each criterion have subdivided measures.

16.4 Assessing the Suitability of Reptiles for Captivity

Numerous factors must be considered when assessing the suitability of reptiles for a life in captivity, including that many species are specially adapted to multiple features of their natural environments and thus risk poor acclimatisation to artificial conditions (Pasmans et al. 2017). The welfare detriments that result from poor adaptability to captivity are compounded by the fact that it can be difficult, even for expert keepers or veterinarians, to assess the welfare of reptiles in anything other than very basic terms. Many keepers have expressed the outdated view that ‘if a reptile is moving around and eating, then it is OK’ or ‘if it looks healthy, grows and breeds, then this must be a product of good welfare’. These common attitudes and social norms within society make good captive reptile welfare highly uncertain. The resulting welfare problems may be obvious or less apparent and manifest in many ways, including problematic behaviours and unnecessary suffering caused by undue stress and sub-clinical illness (i.e. illness not apparent to human observers, but which may be causing the animal to suffer), overt illness, and death. Additional factors to consider are various handling, storage, husbandry, and transportation practices inherent to wild capture and captive breeding for the global live animals and body parts trades, and which may strongly impact on reptile life histories. In addition to welfare issues, the keeping of reptiles can also be associated with species conservation threats, ecosystem disruption, the introduction of exotic diseases to native wildlife, and zoonotic disease potential.

In all captive reptile situations, welfare may become compromised due to a raft of reasons relating to reptiles’ complex needs, including (in no particular order): spatially restrictive enclosures; insufficient exercise opportunities; a unnaturalistic, barren, and psychologically and behaviourally understimulating conditions; inadequate temperatures; seasonal variations and thermal gradients; incorrect photo- and scoto-phase regimes; lack of ventilation; poor humidity; poor quality, species-inappropriate, and insufficiently varied diets; insufficient UV-B; poor hygiene; inappropriate substrates; poor hibernation procedures and conditions; use of transparent boundaries and related stress and injuries; insufficient provision of relevant hides; and negative interactions with humans and other kept pet species, (see also Maslanka et al. 2023; Mendyk and Warwick 2023; Warwick and Steedman 2023).

Relatedly, the veterinary community reports that poor husbandry is a principle endemic feature of causes of morbidity and premature mortality among captive reptiles. Thus, poor quality husbandry guidance and practices dominate captive reptile care, despite availability of higher quality scientific and veterinary information. However, a related consideration involves the reported general adaptational limitations of reptiles to unnaturalistic and atypical conditions, which may further compound morbidities and premature mortalities (see Arena et al. 2023; Warwick 2023; and Warwick and Steedman 2023).

These issues vary across species, and include specific dietary, thermal, humidity, spatial, enviro-feature, enviro-chemical, enviro-sonic, photo/scoto-phase period, strongly predetermined genetic traits, and psychological and behavioural (including social) factors that are commonly challenging to accommodate in captivity. The likelihood of these needs being met is influenced by: the availability of accurate knowledge about them (which is highly limited for many and incomplete for all reptile species), by individual keepers' awareness and understanding of that knowledge, and by keepers' abilities and motivation to apply this knowledge in provision of appropriate captive care. The probability of animals' needs being met is further influenced by the general difficulties of assessing captive reptile welfare. In particular, many (mostly pet) keepers have little knowledge and understanding of reptile biology, physiology, ethology, and welfare, resulting in seriously deficient husbandry, which they simply do not recognise. These deficiencies—mismatches between the animals' requirements and the captive environment provided—frequently result in severe stress and metabolic and immune-compromised states, leading to disease susceptibility, maladaptation, subclinical illness, overt disease, and mortality. Furthermore, legal obligations for welfare protection and evidence-based husbandry are often lacking, allowing poorer standards to proliferate.

It should be self-evident that, as for any animal of any taxa, captive reptiles require responsible, knowledgeable, and motivated keepers; regrettably, these requirements are often not met. Given modern understanding of the biological complexities of animals, it can be argued that only trained persons who have detailed species-specific scientific and husbandry knowledge should care for reptiles—and indeed other exotic or specialised animals. A recent study found that 'lack of time' for care was the single largest factor responsible for people relinquishing their reptiles, which further underscores that these animals are not 'easy to keep' by casual acquirers (Tedds et al. 2020). Furthermore, high premature mortality rates among reptiles in private keeping offer testimony to lack of husbandry knowledge and difficulty of care (Toland et al. 2012).

Academic and amateur herpetologists, including zookeepers and some reptile hobbyists/enthusiasts, have good access to the known facts about individual species from the scientific literature and databases as well as contacts with other experts with access to relevant information. Many such keepers also have a good understanding of biology and ethology, as well as practical husbandry abilities, allowing them to more correctly apply available data—i.e. better provide for animals' health and

welfare needs. However, other hobbyist/enthusiast and most pet keepers are not aware of the specialised knowledge required, and/or have little understanding of general biology, ethology, and/or may have less ability and resources for practical husbandry and good welfare (Benn et al. 2019). This situation is compounded by how difficult it is for humans to assess the welfare state of reptiles beyond the gross level of ‘does it appear ill?’, which is arguably subjectively associated with keeper perception and knowledge.

Difficulties in assessing reptile welfare arise partly because most keepers have little knowledge for animal welfare assessments in general, let alone for reptiles specifically, and partly because it is difficult even for many experts to assess reptile welfare. Combined, these factors very commonly result in scenarios in which ‘exotics’ veterinarians are presented with reptiles that are very ill and suffering the effects of chronic poor husbandry by keepers who believe that their care is good. Unfortunately, it remains common that even the most difficult to keep species are allowed to be kept without specialist knowledge and skills.

16.5 Suitability Tools

Various approaches or ‘suitability tools’ have been developed to evaluate whether or not a species may be suitable for captivity, and each has its own merits. Below, we summarise these approaches as background to a recent impetus for incorporating informed decision-making as early as possible into the process of captive reptile (and other animal) management.

16.5.1 Example Existing Suitability Models

Several models exist for assessing species suitability. Warwick et al. (2013) produced the ‘EMODE’ (‘Easy’, ‘Moderate’, ‘Difficult’ or ‘Extreme’) algorithm, which classifies animals according to the husbandry difficulty they represent as well as human health and safety factors, and incorporates a series of six pre-weighted closed questions that accumulate points towards an overall score to indicate keeping challenge. Schuppli and Fraser (2000) developed a 12-question self-assessment framework directed primarily at scientific professionals in relation to companion animals, human health and safety, conservation, and invasive species factors, which aimed to highlight key considerations with potential impact on animal welfare, human health and safety and environment. Schuppli et al. (2014) presented, discussed, and prioritised a checklist for four major welfare concerns regarding pet animals, promoting that animals: ‘function well biologically’, are ‘free from negative psychological states’ and are ‘able to experience normal pleasures’, and thus are able to ‘lead reasonably natural lives’. The term ‘pleasure’ may seem somewhat anthropomorphic, although it is increasingly incorporated into modern scientific literature, and more stoically the issue may be considered to imply positive mental states.

Fraser et al. (1997) consider pleasure in animals in a species comparative context, thus human examples of pleasure are in some instances not dissimilar. Balcombe (2009) implies that pleasure would be the perceived experience of both avoiding negative states and selectively enhancing positive states. Zoonotic risks and invasive potential were also integral. Koene et al. (2016) designed a method that utilises a species-specific bibliographic input algorithm including animal biology, behaviour, husbandry, welfare, health, zoonoses, and human-animal relationship.

The veterinary profession recognises the need for tools and other approaches to assess species suitability. For example, Wensley et al. (2014) representing key British veterinary organisations proposed principles whereby only approved species may be sold and kept *if* published evidence and professional experience indicate there is a reasonable expectation of meeting the Five Welfare Needs (FAWC 1979), *and* that an animal's needs are fully researched and understood prior to acquisition. The British Veterinary Zoological Society (BVZS 2014) proposed a 'traffic light' system to flag species as either red ('species that should never be kept except for specific conservation purposes'), amber ('species that require a DWA [Dangerous Wild Animals Act, UK] license and/or a greater degree of expertise') or green ('species considered suitable species for all, provided the owner has demonstrated suitable education and ability to fulfill their welfare needs at point of sale'). However, it remains unclear how individuals would demonstrate their competence to meet any of these categories, although formal high-level qualifications, accountability, and regulation would provide a framework in line with other competence bases.

Manifestly, an amalgamating theme of these tools is their animal-centric nature, being pertinent to measurable features in animals, and predominantly aimed at pet ownership. All the aforementioned approaches have merit and, although being 'pet'-centred, offer broadly applicable principles for assessing suitability across a range of captive situations. However, all these systems are omni-species, non-reptile-focused approaches and the target users vary, with some systems being essentially confined to professional biologists (see Warwick et al. 2018b for review). In contrast, captive reptiles per se include a wide range of private pet, commercial, zoological, laboratory, and even field situations where animals are brought into captivity for temporary (short- or long-term) handling and release.

To greater or lesser degrees, the aforementioned tools can be applied to any of the preceding situations, but with reduced specificity and with little to no account of the particular knowledge, abilities, and resources of the keeper. Accordingly, the aims of this chapter include outlining and introducing reptile- and keeper-oriented assessment tools that allow evaluation both of animal needs and keeper knowledge and abilities with relevance to all captive situations. The suitability tool presented below has been adapted from the EMODE system (Warwick et al. 2013) because of its conciseness and clarity of scoring, and aims to refine the model towards reptile suitability.

16.5.2 Proposed Suitability Tools

The proposed suitability tools are divided into two parts: *Animal* suitability (where prospective and actual keepers can assess species' biological needs, including behavioural, psychological, and environmental); and *Keeper* suitability (where prospective and actual keepers can assess themselves based on such factors as knowledge, resources, and abilities). Notably, these determinants for species suitability preferably should *precede* keeping an animal, and not involve first acquiring an animal and then conducting suitability assessments or demanding information to rationalise keeping it once that animal is captive, and likewise, for assessing keeper suitability. If followed, this two-pronged 'precautionary' principle would help to avoid entering a quagmire of bad practice and then struggling to find detailed evidence on husbandry—which may not exist. This principle is relevant to the keeping of any species, subspecies, or breed of any taxa.

16.5.2.1 Using the Algorithm-Based Tools: Difficulties and Weaknesses of the Self-Assessment Approach

In this section, we suggest a preliminary example of a reptile-specific self-assessment approach based on the already published EMODE system (Warwick et al. 2013; EMODE Pet Score 2019). Other self-assessment approaches could be devised. However, all such approaches confront substantial difficulties in implementation such that they can provide accurate answers for the great majority of, but not necessarily all, potential users. Obviously, no system that attempts to provide guidance for a wide variety of users for a wide variety of species with very different requirements will be perfect. The modified EMODE system below may provide useful guidance in most instances when used by educators, acquirers, and keepers of reptiles with adequate knowledge of the subject, such as expert herpetologists and many hobbyists/enthusiasts. Indeed, the process of completing the EMODE task may promote self-education because some degree of research and analysis is likely needed to address relevant questions. However, this modified EMODE system is likely to be less reliable when used by the typical 'pet reptile owner'—members of the public with no expertise or particular knowledge about reptiles, and the reasons for this include:

1. *Acquirer/Keeper Understanding of the Terminology* Some of the terms used in the questions are specialist, e.g. microhabitat (highly niched environmental systems), fossorial (burrowing), environmental mosaic (varied elements within an environment), ontogenetic (origination and developmental of an organism), aestivation (dormancy during warm or hot climatic conditions), and brumation (partial dormancy during cold climatic conditions). Many keepers of, in particular pet, reptiles may not know the meanings of these terms. Thus, certain questions may need to be rephrased before widespread implementation for use by non-expert acquirers/keepers.
2. *Acquirer/Keeper Knowledge of Reptiles and their Husbandry, and of Science and Evidence* If acquirers/keepers do not have a good knowledge of reptile biology,

welfare needs and husbandry—then they may not be able to answer some questions accurately, even when motivated to do so, and possibly even when they believe they are doing so. This problem is further compounded by four issues: *first*, members of the public generally may not have a good understanding of scientific methodologies, and thus what constitutes objective, scientifically-validated evidence; *second*, members of the public generally often may not have access to most of the scientific literature; *third*, members of the public generally do not understand how to access and interpret scientific literature to find relevant information; *fourth*, whereas scientifically validated information is often difficult for the public to find and to access, there is a large amount of non-evidence-based and potentially misleading information freely available on the internet.

3. *Subjectivity of Some Questions* Some of the questions involve subjective assessment. Whether an animal is dangerously toxic or venomous or able to cause serious injury is generally clear. However, what constitutes an ‘especially sensitive’ species or ‘exceptionally high’ disease susceptibility can involve greater rationalisation. Likewise, dividing lines between specialised and non-specialised habitat may be broad. Such issues facilitate imprecise and incidentally self-serving answers, even for users attempting to be accurate and objective in answering questions. Decades of psychological research have demonstrated that when people make decisions about something they want, they often do not do so in a rational, objective manner (Kahneman 2011; Howell and Bennett 2017; Moorhouse et al. 2017). Just the process of self-assessment using a modified EMODE system such as this will help to make people think more about their considerations, but a downside is that if users unconsciously make self-serving errors, they may believe the self-assessment process indicates a species to be suitable for them when in reality it is not.

Murphy et al. (2020) discussed and proposed education standards for staff in the zoological community, and suggested formatted interviews, journal clubs, workshops, fieldwork, and education targets, as well as presented essential reading materials for herpetologists. However, clearly, a self-assessment system could be very difficult or even impossible to implement where animal acquirers/keepers with little knowledge of the field use inaccurate information. For this reason, other methods require adoption to protect the animal’s welfare, including education, formal validation of keepers (e.g. prospective keepers being required to provide proof of relevant knowledge, training, or experience before being able to keep a species), and restricting or banning keeping of certain species by members of the public. Assessment approaches including EMODE, when used by experts can provide the basis for certain educational protocols and permissive systems such as positive lists (Toland et al. 2020; Warwick and Steedman 2021). For example, a labelling system for ‘ease/difficulty’ of keeping a species can also be provided at the point of acquisition (Warwick et al. 2018b) or to aid decision-making with regard to which species may or may not be kept as part of a voluntary or legislated system for the keeping of certain species.

For reasons outlined elsewhere (Warwick et al. 2013; Mendyk and Warwick 2023), no reptile may objectively be described as ‘easy to keep’, except possibly for the atypical occasion where an indigenous or enviro-compatible species might, for example, occupy a healthy outdoor pond, and is under the conscientious guardian experienced in scientific welfare observation. Accordingly, whilst the EMODE table commences at ‘Easy’ (e.g. species that are less delicate or sensitive, not long lived, not threatened or endangered, have dietary needs that are easily met, benefit from widely available objective care advice, and are of low health and safety threat to people), this is essentially for contextual purposes and this category may be considered practically redundant in most reptile-keeping situations.

16.5.2.2 Instructions for Use of the Algorithm-Based Tools

Tables 16.2 and 16.3 contain ‘*Specific questions*’ (column 1). Obtain objective evidence-based answers to these questions. When responding to the questions in Tables 16.2 and 16.3 it is important to answer as objectively and accurately as possible to avoid unrepresentative scores. Aim to acquire information from scientific sources (e.g. published peer-reviewed articles, veterinary books and manuals, and other academic materials—such as this volume). For Table 16.2 unless there is a clear reason for answering ‘no’ to any question, then the precautionary principle should apply and the response should be ‘yes’.

Table 16.2 shows the EMODE species suitability scale (range 0–35+), which corresponds to categories ‘Easy’, ‘Moderate’, ‘Difficult’, or ‘Extreme’, indicating degree of challenge associated with a reptile and its husbandry (e.g. a score of 21 would indicate ‘low difficult’). ‘*Examples*’ (column 2) are provided for clarification regarding the specific questions. Refer to these clarifying examples to help understand how to ‘grade’ the nature of the specific questions. *Answers* (column 3) to the specific questions are binary/= ‘yes’ or ‘no’. Record ‘yes’ or ‘no’ in the answer column. *Points* (column 4) accumulates the scores; if the answer is ‘yes’ add the relevant number of points and if ‘no’ simply move to the next question. *Total points* (row under question 6) records the final cumulative score (e.g. ‘21’).

The original EMODE system is pre-weighted for reptiles with 18 points, which was arrived at following consensus with independent experts, to account for certain inherent husbandry challenges inherent to managing environmental provisions and practices in artificial, enclosed systems, then further scored 5 points per question, whereas the present reptile-specific EMODE system uses the same pre-weighted 18-point scores, but with 3 points per question.

In addition, to the original rationale for use of a pre-weighted score of 18 points for reptiles, replicating this value provides a high degree of consistency between the original and reptile-specific EMODE algorithm, thereby enabling direct comparison of reptiles scores obtained using the reptile-specific EMODE to scores for non-reptile species. The reptile-specific EMODE system contains questions with a greater potential for the respondent to obtain more point-scoring answers, thus points have been adjusted downwards from 5 points to 3 points per question to avoid over-scoring.

Table 16.2 Reptiles—indication of degree of ease or difficulty (suitability or otherwise) to keep

Pre-weighted score = 18 points			18 points +
<i>Specific questions</i> <i>If answer is 'yes' to any part of each question then assign 3 accumulator points.</i> <i>If answer is 'no' to all parts of each question then move to next question.</i>	<i>Examples</i> <i>All examples listed indicate that a 'yes' answer is required.</i> <i>If unsure of answer indicate 'yes'.</i>	<i>Answer</i> <i>Yes/No</i>	<i>Accumulator</i> <i>points</i>
1. <i>Sensitivity</i> : Is the animal widely considered to be an especially sensitive species or individual, including small and/or delicate animals; wild-caught; exceptionally high disease susceptibility?	Chamaeleonids; geckonids, anolids, green iguanas; very small or baby animals of small species of turtles, lizards, and snakes	Yes = 3 points	
2. <i>Lifespan</i> : Does animal have a long potential lifespan; ≥10 years?	Probably most reptiles, other than certain diminutive lizard species	Yes = 3 points	
3. <i>Diet</i> : Does the animal have specialised feeding habits that can make its dietary requirements subject to restricted supply; unusual live foods, unusual plants, specific seasonal foods?	Moloch, caiman lizard, uromastids, chamaeleonids/ insectivores, Asian box turtle	Yes = 3 points	
4. <i>Habitat</i> : Does the animal require a specialised habitat or microhabitat (small environment containing distinct flora, fauna, or both); is the animal dependent on sharing its life with a particular environment type or plant; combination habitat, (aerial/ arboreal/terrestrial/aquatic); burrowing?	Chamaeleonids, uroplatids, sauromalids, larger iguanids, larger varanids, larger agamids, crysopelids, chondropythonids, erycids	Yes = 3 points	
5. <i>Behaviour</i> : Does the animal have particular behavioural, spatial, locomotor needs; requires social grouping/ pairing; subject to co-occupant aggression; nocturnality?	Varanids, chameleonids, iguanids, agamids, terrestrial (and many semi-aquatic) chelonians, most snakes	Yes = 3 points	
6. <i>Threat</i> : Is the animal venomous, capable of growing large or inflicting appreciable injury at any point in its life?	<i>Toxicity risk</i> : Elapids, higher toxicity viperids, helodermatids, komodo dragons <i>Injury risk</i> : Crocodilians; larger semi-aquatic/aquatic chelonians; larger varanids, teiids, iguanids; larger boids	Yes = 3 points	
Check total points in row below to find <i>species suitability</i> score. Total points: =			
'Easy'		'Moderate'	
'Difficult'		'Extreme'	
1 2 3 4 5 6 7 8 9 10	11 12 13 14 15 16 17 18 19 20	21 22 23 24 25 26 27 28 29 30	31 32 33 34 35 +

Table 16.3 Keepers—indication of degree of suitability as prospective keepers (training, experience and knowledge bases)

<i>Specific questions</i> <i>If answer is 'yes' add 10 or 5 accumulator points as indicated.</i> <i>If answer is 'no' move to next question.</i>	<i>Examples</i>	<i>Answer Yes/No</i>	<i>Accumulator points</i>
1. <i>Relevantly qualified</i> : Are you a professional scientifically trained/qualified herpetologist experienced in reptile care/husbandry?; or a semi-professional scientifically trained/qualified biologist, zoologist, or veterinarian with interest/experience concerning reptiles?; and do you have access to objective and scientific information?	Possess relevant scientific high-level training or qualifications, existing high-level successful species-specific management experience, access to reputable independent scientific sources, familiarity with scientific information research methodologies, occupy a professional role in a university/highly regarded zoological facility/other scientific entity such as a laboratory.	Yes = 10 points	
2. <i>Unqualified/amateur</i> : Are you an amateur herpetologist ('hobbyist' or 'enthusiast') with detailed husbandry experience concerning reptiles?	Self-taught or experiential knowledge, no or low- to moderate-level academic or professional training concerning reptiles.	Yes = 5 points	
3. <i>Recognising health and welfare</i> : For this species, are you able to recognise signs of health and comfort, normal behaviours, and departures from normal, such as signs of stress, disease, and injury, soon enough to seek help or make necessary changes?	Ability to effectively determine if a reptile is under stress, sick, or in need of medical intervention, including detailed knowledge of normal behaviours, changes related to hormonal state, season, or metabolism. This means the ability to identify at least 40 welfare-related signs, including: At least 10 positive signs of behavioural and psychological condition and 10 signs of negative behavioural and psychological condition; and to identify at least 10 signs of physical health and 10 signs of physical injury and disease.	Yes = 10 points	
4. <i>Veterinary care</i> : Is there adequate veterinary care available including emergency services?	Local availability of relevantly qualified or experienced veterinarians and suitable emergency clinics require	Yes = 5 points	

(continued)

Table 16.3 (continued)

<i>Specific questions</i> <i>If answer is ‘yes’ add 10 or 5 accumulator points as indicated.</i> <i>If answer is ‘no’ move to next question.</i>	<i>Examples</i>	<i>Answer Yes/No</i>	<i>Accumulator points</i>
	confirmation. Not all veterinary practices will treat reptiles.		
5. <i>Resources</i> : Do you have access to adequate financial resources for the species?	Costs of long-term accommodation, environmental furnishings and ongoing enrichment provision and redesign, energy (e.g. heating, lighting), food, veterinary fees can be substantial and unexpected.	Yes = 5 points	
6. <i>Human health risk (zoonotic disease)</i> : The household/environment (or extended circle) is free from occupation by any immunocompromised persons?	Under 5 years, elderly, pregnant, diagnosed with HIV or other immune disease, drug user, receiving chemotherapy such as cancer and anti-rejection drugs, severe allergies. CAUTION: It is not advisable to keep reptiles where anyone in the home or extended circle meets this description.	Yes = 5 points	
Check total points in row below to find <i>keeper ability</i> Total points score =			
‘Low’	‘Moderate’	‘High’	‘Very high’
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 +			

The pre-weighting of 18 points accounts for the fact that even for those reptiles with ‘easier’ welfare needs, meeting those needs is harder than for many species in other taxa. However, as discussed earlier, there is wide variation in the training, experience, and knowledge bases (and self-perceptions thereof) among prospective and current keepers; thus the ‘18 points’ takes account of relatively low abilities versus reptile-keeping challenge, and is included only as a reference point for scale because no reptile can score below 18 points (see Warwick et al. 2013 for further explanation).

Accordingly, a highly qualified and experienced reptile biologist operating in a professional and well-resourced environment may reasonably regard ‘Moderate’ or ‘Difficult’ and beyond to be within their abilities, given the resources of their specific facility. Table 16.3 (suitability of keepers) does not utilise pre-weighted scoring, because whereas key biological and managerial factors are known in advance for reptile species (Table 16.2), individual factors relevant to keepers’ reptile-husbandry

ability are not known in advance. Table 16.3 also scores individual questions differently because certain questions (e.g. Qs 1 and 3) carry fundamentally greater significance than others regarding keeper suitability.

Tables 16.2 and 16.3 may be used entirely independently or as two related tools. When used together, an allied objective is that keeper ability and animal suitability should approximately correlate, for example, where a keeper scores up to 20 points or ‘Moderate’ then their ability to keep a reptile may be limited to those species that score within the Moderate suitability category. Similarly, where a keeper scores 35 points or ‘Very high’, then their ability to keep a reptile may be extended to those species that score within the ‘Extreme’ category, and higher correlating scores generally ought to imply better welfare outcomes for animals.

16.5.2.3 Worked Examples

Below (Appendix) are worked examples for Table 16.2. ‘Q’ is an abbreviation for ‘Question’; numbers ‘1–6’ that follow ‘Q’ indicate which of the six questions is relevant; ‘y’ indicates a positive or ‘yes’ response to the relevant question in Table 16.2; ‘n’ indicates a negative or ‘no’ response to the relevant question in Table 16.2; 3 points are accrued per positive ‘yes’ response; all positive ‘yes’ scores are added together to give a final ‘Total’ score; the Total score is viewed in the bar indicating the species’ score: up to 10 points = ‘Easy’ (to keep); 11–20 points = ‘Moderate’ to keep; 21–30 = ‘Difficult’ to keep; 31–35+ = ‘Extreme’ difficulty to keep.

Questions included in Tables 16.2 and 16.3 are derived from published (Warwick et al. 2013) and novel consultation results, and were selected because of reasonable availability of on-topic information and their ability to produce essentially binary answers that promote clarity. Many other questions salient to both animal and keeper suitability may be asked, and towards this Tables 16.4 and 16.5 list illustrative examples that are advisable to consider when assessing matters of suitability. Thus Tables 16.4 and 16.5 are not intended to factor in the EMODE scores, but are merely additional consideration prompts.

Table 16.4 Additional questions salient to animal suitability

Animals
Does the animal have specific daily or seasonal thermal requirements (e.g. daily fluctuations in temperature, hibernation for winter)?
Does the animal have specific lighting requirements (e.g. UV-B exposure with specialised lamps)?
Does the animal naturally utilise an environmental mosaic (diverse range of elements)?
Does the animal habituate to observers or handlers?
Does the animal have a complex and evolving diet—i.e. dietary shift?
Does the animal naturally range over a wide geographical area?

Table 16.5 Additional questions salient to keeper suitability

Keepers
Are you aware of the legality of keeping the relevant species?
Are you aware of and prepared for ontogenetic (developmental) alteration in habits (e.g. behavioural and dietary changes as animals mature and later enter old age)?
Are there local good options for rehoming if necessary?, and do you have plans to deal with situations (e.g. starting a family, changes in finances, move to less suitable facilities, your illness, your death) that may necessitate rehoming?
Do you understand quarantine procedures as well as safe and effective cleaning and disinfection?
Will you develop a relationship with a suitable exotic species veterinarian for wellness and preventive care (thus not only when the pet is sick) and trust and follow their recommendations?
Are you prepared to deal with a range of environments (e.g. aquatic and semi-aquatic) that may be required for optimal care?
Do you understand the concepts of aestivation, brumation, and hibernation?
How will the animal be temporarily cared for if you are on holiday or away ill/hospitalised?
Will you put effort towards environment and individual enrichment?

16.6 Conclusions

In general, little data on the behavioural needs and welfare risks are available for the diversity of reptile species found in captivity. Experts may be able to estimate or assess behavioural needs, welfare, and health risks of animal species. However, varied problems and controversies exist concerning captive reptiles, especially in relation to the hobbyist/pet sectors. Whether an individual animal is captive-bred or wild-caught may be an important consideration, and it is arguable that more information exists about behavioural needs and welfare risks for regularly captive-bred species than for regularly wild-caught species. Accordingly, the amount and validity of objective scientific information available is a critical factor in suitability determination. Also, fundamental is the issue of general deficits in adaptive plasticity—or the ability/inability of reptiles to adapt to the overly restrictive, limited, and artificial conditions inherent to almost all captive situations.

Despite advances in our knowledge and understanding of reptile biology and what are generally considered to be requirements for successful care, the majority of captive reptiles continue to suffer for numerous and varied reasons. Thus, the clinical and non-clinical aspects of species suitability for life in captivity raise significant concerns from a welfare standpoint. Current concerns regarding captive reptile husbandry are also numerous and farther reaching than many often consider when taking on a reptile.

The dissemination of objective, independent, current, and correct information to educators in responsible positions, such as veterinarians, inspectors, and other professional advisors, as well as reptile keepers, remains challenging. In particular, pet stores, breeders, dealers at expos, shows, or fairs, and most internet-derived husbandry resources also lack both authoritative knowledge bases and the training

needed to offer guidance for captive reptile care. It is unfortunate that arbitrary husbandry and historical acceptance of substandard practices typically prevail. In addition, concepts of quarantine procedures remain foreign to most keepers, and financial status of many also result in poor overall welfare.

Because of these and allied issues, a reasonably reliable and legitimate ‘scoring’ system should be applied to more objectively determine the suitability or otherwise of reptiles for captivity, as well as the suitability of the person to keep reptiles. It is hoped that the EMODE-derived tools herein may go some way to assisting with improvement of such objective evaluations.

16.7 Animal Welfare Conclusions

Collectively, across all relevant sectors (pet, professional zoological, laboratory, commercial) millions of reptiles representing a wide range of species are kept in captivity, despite commonly being maladapted to the conditions in which they are held. Maintaining reptiles indoors, subjection to climates quite different to those for which their species have evolved, confinement in diminutive enclosures, extreme divergence from normal diet, atypical stimulation, or understimulation, exposure to unusual microbes and potential pathogens, and simply not being understood, are among many confounding factors and stressors imposed on most if not all captive reptiles.

Inherent adaptability or nonadaptability of species to unnatural conditions and stressors occupies a deterministic outcome for individuals, which may answer the ‘suitability’ question—i.e. reptiles are typically unadapted and unsuitable for most captive situations. However, being locked-in to arbitrary husbandry and bad practice is likely to catastrophically override even the most adaptable of species and hardest of individuals. In contrast, using the best objective evidence, based on the natural lifestyles of reptiles and an awareness of the limitations imposed by captivity, can provide a basis for a better quality of care.

No amount of information, good or bad, has any effect on reptiles until it is applied. The human carer is the link in the chain between better or worse information, and the animal itself. Accordingly, it is as important for the prospective or actual reptile keeper to candidly assess their suitability or otherwise as it is to assess the suitability of the reptile to be kept. At the very least, by conscientiously seeking to address both the animal- and human-centric questions in our assessment system, a positive degree of self-learning and perhaps motivational direction may be instilled simply by taking the time and energy to consider the issues that these questions are intended to represent.

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Appendix: Worked Examples of the EMODE Method for Table 16.2

Order/group	Pre Weighted points	Q1 Sensitivity/ points	Q2 Lifespan/ points	Q3 Diet/ Points	Q4 Habitat/ points	Q5 Behaviour/ points	Q6 Threat/ points	Total
<i>Crocodylians (crocodiles, alligators, caiman): Species</i>								
American alligator (<i>alligator</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	Yes/= 3	27
Spectacled caiman (<i>Caiman</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	Yes/= 3	27
<i>Chelonians (turtles, terrapins, tortoises): Species</i>								
Red-eared terrapin (<i>Trachemys</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	No/= 0	24
Snapping turtle (<i>Macrochelys</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	Yes/= 3	27
Florida soft-shelled turtle (<i>Apalone</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	Yes/= 3	27
Hermanns tortoise (<i>Testudo</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	No/= 0	24
Sulcata tortoise (<i>Geochelone</i> sp.)	18	No/= 0	Yes/= 3	Yes/= 3	No/= 0	Yes/= 3	No/= 0	27
<i>Saurians (lizards): Species</i>								
Collared lizard (<i>Crotaphytus</i> sp.)	18	No/= 0	No/= 0	No/= 0	No/= 0	No/= 0	No/= 0	18
Leopard gecko (<i>Eublepharis</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	No/= 0	24
Green anole (<i>Anolis</i> sp.)	18	Yes/= 3	No/= 0	No/= 0	No/= 0	Yes/= 3	No/= 0	24
Bearded dragon (<i>Pogona</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	No/= 0	24
Green iguana (<i>Iguana</i> sp.)	18	Yes/= 3	Yes/= 3	Yes/= 3	Yes/= 3	No/= 0	No/= 0	30
Nile monitor (<i>Varanus</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	Yes/= 3	Yes/= 3	Yes/= 3	30
<i>Serpents (snakes): Species</i>								
Garter snake (<i>Thamnophis</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	No/= 0	No/= 0	21
Corn snake (<i>Pantherophis</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	No/= 0	No/= 0	21
King snake (<i>Lampropeltis</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	No/= 0	No/= 0	21
Royal python (<i>Python</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	No/= 0	24
Burmese python (<i>Python</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	Yes/= 3	Yes/= 3	Yes/= 3	30
Rattlesnake (<i>Crotalus</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	No/= 0	Yes/= 3	Yes/= 3	27
Green mamba (<i>Dendroaspis</i> sp.)	18	No/= 0	Yes/= 3	No/= 0	Yes/= 3	Yes/= 3	Yes/= 3	30

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Record Keeping as an Aid to Captive Care

17

Robert W. Mendyk and Judith Block

Abstract

Record keeping is a fundamental component of reptile husbandry, yet it is often undervalued and underutilised by keepers and the types of records kept can vary widely in their scope and adherence to detail. Without detailed records, keepers may not have sufficient information to make informed decisions about the health and management of their captives and may be basing their husbandry practices largely on anecdote or speculation. A broad range of data and information collected from captive reptiles can enable keepers to effectively monitor, evaluate, and improve husbandry practices, which can have direct impacts on animal health and welfare, and long-term keeping success. This chapter describes different types of records that can be collected on captive reptiles and emphasises the importance of this information in advancing standards of herpetological husbandry and welfare.

Keywords

Records · Record keeping · Measurements · Captive husbandry · Veterinary · Pathology · Behaviour

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17.1 Introduction

Record keeping is a fundamental component of reptile husbandry. Information collected from captive specimens can have profound impacts on the ability to monitor, evaluate, and improve on husbandry practices, which can ultimately affect animal health, welfare, and long-term keeping success. There are still many gaps in what is presently known about the biological requirements of reptiles in captivity, and many keeping practices today are still based largely on anecdote or tradition rather than direct evidence (Arbuckle 2013; Mendyk 2018; Mendyk and Warwick 2023). Careful record keeping can serve as the basis for informed decisions and help explain the success or failure of captive management efforts. Moreover, this information can provoke or address questions relating to challenges that may impact the lives of reptiles in captivity; yet, record keeping is often underemphasised or underutilised in captive management efforts.

The types of records kept on captive reptiles can vary widely in their scope and adherence to detail. In some cases, record keeping may be a legal requirement for establishing provenance or maintaining reptile keeping licenses, or a criterion that zoological parks must satisfy for accreditation (EAZA 2014; AZA 2018). In other situations, particularly in some private collections, record keeping may not be practised at all. When record keeping is minimal or neglected altogether, keepers may not be able to document legal ownership in order to trade specimens or have sufficient information for knowledgeable decisions about the health and management of their captives. The goal of this chapter is to provide an overview of the many types of records that can be collected on captive reptiles and discuss how they can inform and enhance captive management practices. Improved standards of record keeping can help bring about positive changes in and across collections and transcend current standards of herpetological husbandry and welfare.

17.2 Historical Records

Knowing the history of an animal prior to its arrival in a collection can be important for developing appropriate keeping practices as well as understanding its individual habits, preferences, temperament, physical condition, and health status. Associated documents such as correspondence and permits for collecting, importing, or exporting can help establish ownership and verify the taxonomic identities of individuals (see Murphy 2015). Although not always available, especially for specimens collected from the wild or acquired through the reptile trade, prior records detailing an animal's age, sex, origin (i.e. place where wild-caught or captive-bred), length of time in captivity, reproductive and medical histories, and supportive care can provide a basis from which to build sound husbandry practices. This information can also offer avenues for investigating health- or husbandry-related issues. For example, multigenerational inbreeding can lead to deleterious genetic anomalies (Murphy 2018), which can be easily recognised with good record keeping. A sample of an acquisition record for a specimen is provided in Fig. 17.1.

ACQUISITION RECORD				
SPECIES: Speckled kingsnake (<i>Lampropeltis getula</i>)		SEX: 0.1	ID #	14R038
ARRIVAL DATE: 22 August 2014		ORIGIN: WC	LOCALITY:	St. Tammany Parish, Louisiana
PARENTAGE: Unknown - collected from the wild		PERMITS: n/a		
DATE OF BIRTH/COLLECTION: 5 July 2014		SOURCE: John Smith, 123 Fake Street, Tallahassee, FL 32302; 850-555-0111		
AGE CLASS ON ARRIVAL: Sub-adult		TYPE OF TRANSACTION: Purchased for \$150		
TRANSPONDER ID: 1034-3019-303-7714 (Trován)		ADDITIONAL IDENTIFYING MARKS: Two large yellow blotches on top of head between eyes; has a scar on left side of body ca. 10 cm cranial to vent		
QUARANTINE ARRIVAL: 22 August 2014		QUARANTINE CLEARANCE: 4 December 2014		
COMMENTS: This animal was purchased together with a male (14R037) and an additional female (14R039) of similar sizes. The male died unexpectedly whilst in quarantine on 22 September.				

Fig. 17.1 Sample acquisition record card with all pertinent information relating to the origins of an individual

On their arrival, subjecting new animals to quarantine can be an important measure for preventing the transmission of pathogens to a collection (Miller 1996; Jacobson et al. 2001; Pasmans et al. 2008), and knowing the history and origins of an individual can influence the length of its quarantine period. For example, wild-caught specimens or those of uncertain origins that may have passed through one or more dealers' facilities or private collections (and potentially exposed to other species and pathogens) might raise more serious concerns about disease risk. Such risk might warrant longer quarantine periods than captive-bred individuals with known medical histories originating from reputable zoological parks or private collections. Even with strict quarantine measures and testing in place, it may still be possible for some pathogens to pass through quarantine undetected and affect a collection. With accurate records of an individual's provenance, it may be possible to trace the etiology of a pathogenic agent to a particular source, which could offer clues for diagnosis and treatment.

Abrupt changes to an animal's captive environment and supportive husbandry can have profound impacts on stress levels (Chiszar et al. 1995). For captive reptiles originating from other collections, it is usually best practice to first replicate the certain conditions and care practices they had previously been accustomed to, and then gradually adjust these parameters over time towards the desired conditions. Here, historical records outlining an individual's prior husbandry including dietary preferences and feeding regimens, environmental parameters, substrate types, refugia, enclosure furnishings, social groupings, and enrichment can be used to minimise the disturbance of a new set of conditions and routines. Although it may be less commonly practised among private reptile keepers, animal transfers between zoological parks today almost always involve the exchange of detailed husbandry records well before the actual transfer of an animal, facilitating better preparations for the animal and a gentler transition through acclimation.

The medical histories of individuals, including laboratory test results, can be useful for alerting keepers to potential health- and husbandry-related issues, as well as sensitivities to watch out for in new specimens. This information can also help keepers and veterinarians develop customised strategies for managing chronic medical conditions, as well as preventive measures to avoid future complications. Similarly, records of prior health issues and their treatments can also aid veterinary clinicians when diagnosing new issues and identifying appropriate treatments for them.

17.3 Identification Records

Having the ability to distinguish between individual animals is crucial for tracking and monitoring the health and husbandry of reptiles, as well as meeting administrative and financial responsibilities (Block et al. 1977; Braverman 2010). In zoological parks, individual accession numbers are typically assigned chronologically to specimens new to the collection, which are used to track husbandry practices, reproduction, medical treatments and pathology, and transfers between institutions

(Earnhardt et al. 1998; Miller and Block 2004; Lackey 2010; Miller 2013). For diminutive species or neonates that are maintained together in groups, a single group number may be assigned to keep track of multiple individuals sharing an enclosure. Private keepers, breeders, and research laboratories may not adhere to such rigid identification systems, but often have some numbering system in place for identifying and keeping track of individual animals within their collections.

Visually identifying individual reptiles can be challenging, especially in taxa lacking discernible physical characteristics. For species exhibiting unique intraspecific differences in body colouration and patterning, or individuals with scars or irregular scalation, descriptive and photographic records of these discernible features can be used to reliably identify individual animals (e.g. Schofield et al. 2008; Ziegler et al. 2009; Knox et al. 2013). Depending on the identifiers, periodically updating photographic records of these features may be necessary if they change in appearance over time.

For species and individuals lacking visually perceptible features, physical marking techniques may be necessary for positive identification (Dietlein 1968; Pough 1991; Crook 2013). Honegger (1979) outlined several criteria for reptile identification systems in zoos, noting that they should be readable from a distance, permanent and adaptable for individuals of varying sizes, as free of pain and stress as possible, limit the opportunity for infection, and should not inhibit normal behaviours or physiological functions. Passive integrated transponder (PIT) tags have become a popular marking technique for captive reptiles, where implanted tags can be scanned with a handheld reader device and matched up with corresponding transponder numbers maintained in the records. Because implanted PIT tags can sometimes migrate in the body over time (Keck 1994; Wyneken et al. 2010), it is useful to document the location of PIT tags during implantation and in subsequent scans to aid future scanning attempts. Other marking techniques such as shell notching or scute painting in chelonians may be based on numerical patterns or coding (e.g. Cagle 1939; Nagle et al. 2017), for which the coding system should be described in the records and kept consistent over time and across individuals in a collection. Additional marking techniques for reptiles are reviewed in detail by Ferner (2007).

17.4 Husbandry Records

Reptile husbandry is dynamic. As new information becomes available, conscientious keepers adapt and modify their keeping practices to more effectively meet the biological needs of their animals. Maintaining accurate and detailed records of daily husbandry practices enables keepers to closely monitor the progress, health and welfare of their captives, and evaluate the success or appropriateness of their keeping practices. Noting the dates of changes to husbandry or physical manipulations of an animal can be important for understanding changes in its activity, behaviour, health, or physical condition that may follow. Because behavioural responses to such changes may not appear right away, it can be difficult to link such changes to any alterations in husbandry or potential stressors without

any records of when they took place. Husbandry records can also call attention to problematic keeping practices, as well as inform veterinary diagnoses and treatments. A sample husbandry record, here presented as a specimen cage card for routine feeding and diet, is provided in Fig. 17.2.

SPECIMEN CAGE CARD																															
SPECIES <i>Rhinoceros viper</i> / <i>Bitis nasicornis</i>															SEX 1.0					ID # 15R066											
CARD DATES 1/1/2019 - 12/31/2019										CARD # 5					ENCLOSURE # RH-134																
SOURCE Captive-born to WC female Born - 3 June 2015 Audubon Zoo										IDENTIFICATION MARKS / TRANSPONDER # #1038-8239-511-1296 (Biomark); located on left side, ca. 10 cm up from the vent *Animal has distinct L-shaped marking on the neck, just anterior to the skull																					
DIET CODES (<u>underline/highlight</u>): SA - salad / G - gel / N - nectar / LB - leaf biscuits / PM - pinky mouse / FM - fuzzy mouse / SM - sm. mouse / LM - lg. mouse / PR - pinky rat / SR - sm. rat / MR - med. rat / LR - lg. rat / JR - jumbo rat / RA - rabbit / FL - fish / A - anole / HG - house gecko / C - Chicken / CH - chick / Q - quail / CE - chicken egg / QE - quail egg / CR - crickets / CO - cockroaches / MW - mealworms / SW - superworms / WW - waxworms / BW - butterworms / HW - hornworms / SI - silkworms / EW - earthworms / NC - night crawlers / FF - fruit flies / BB - bean beetles / T - termites / ST - springtails / IS - isopods / CF - crawfish / SP - shrimp / SN - snail /																															
SPECIAL FEEDING INSTRUCTIONS / SUPPLEMENTATION *No dietary supplementation needed * Has not accepted dark-colored rodents															ADDITIONAL INFORMATION *Housed together with female conspecific #15R067																
ADDITIONAL CODES: / = refused meal O = opaque S = shed F = fecal R = regurgitation																															
JAN	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
FEB													LR																		
MAR							F													S			LR								F
APR																					Q				LR						
MAY														F																	
JUN																			LR							S					
JUL		LR																													
AUG																															
SEPT																															
OCT																															
NOV																															
DEC																															

NOTES AND OBSERVATIONS	
SPECIES <i>Rhinoceros viper</i> / <i>Bitis nasicornis</i>	ID # 15R066
DATE	COMMENTS
10-Feb-19	Struck at and seized large rat, but did not consume
12-Feb-19	Animal starting to go opaque -likely why it did not eat on 10 Feb
19-Feb-19	Shed in one, intact piece
16-Mar-19	Weight: 5.1 kg
15-May-19	Enclosure substrate replaced with fresh soil and leaf litter
16-Jun-19	Was not interested in quail
17-Jun-19	Animal opaque
25-Jun-19	Animal shed in pieces with possible retained spectacle; enclosure sprayed to help with shedding difficulties
26-Jun-19	Remaining shed skin and spectacle resolved
2-Jul-19	Took considerably longer than usual to consume rat
16-Jul-19	Weight: 5.4 kg

Fig. 17.2 Sample specimen cage card noting dietary intake, ecdysis and defaecation on the front, and other observational notes on the back

Appetite can be a useful indicator of health and welfare in captive reptiles. Dietary intake for many species may normally fluctuate throughout the year in response to changing environmental conditions such as temperature, rainfall, or photoperiod, or physiological changes associated with reproductive cycling. Review of an individual's feeding records can highlight normal seasonal trends in dietary intake, which can then be used as a barometer for identifying irregularities in feeding patterns. It is important to record the dates in which food was offered, the type, quantity and size of food items, whether each food item was consumed, rejected, or regurgitated, as well as any vitamin or mineral supplementation. These data can be used to identify possible health issues or nutritional deficiencies, as well as provide information that can assist veterinary clinicians in diagnosing disease. Along similar lines, faecal output can be used to monitor animal health, where recording the dates of defecation as well as its appearance and smell—at least for irregular-looking faecal material—can help with identifying illnesses or nutritional issues.

Tracking changes in dietary intake and individual feeding preferences over time could also enable keepers to identify potential ontogenetic shifts in a species' diet (e.g. Burghardt and Layne 1995), particularly those offered varied diets. For example, some freshwater turtles shift from largely carnivorous to herbivorous diets through ontogeny (e.g. McCauley and Bjorndal 1999; Bouchard and Bjorndal 2006), whereas the diet of the varanid lizard (*Varanus niloticus*) shifts from mostly insects and arachnids to hard-shelled mollusks and crustaceans due to ontogenetic changes in dentition (Reippel and Labhardt 1979; Bennett 2002; D'Amore 2015). However, for most species, very little is known about ontogeny-related dietary shifts. Recording feeding patterns over time can identify such shifts, where this information can then be used to adjust captive diets to reflect better nutrition.

Environmental parameters such as lighting, heating, and humidity represent some of the most critical elements of reptile husbandry. Although conscientious keepers try to maintain control of all environmental aspects of their husbandry, sometimes these conditions may naturally fluctuate seasonally and go unnoticed. Physiological processes in reptiles, including immune response (Warwick 1991; Gangloff and Greenberg 2023; Mendyk and Augustine 2023) are largely governed by body temperature (Cowles and Bogert 1944; Huey 1982; Seebacher 2005). Therefore, ensuring that captives have access to an appropriate range of temperatures at all times can help keepers consistently provide optimal conditions, which is aided by regularly monitoring and recording temperature ranges within enclosures (Fig. 17.3).

Changes in rainfall, humidity levels (Fig. 17.3), and photoperiod can also affect the activity, behaviour, and physiology of captive reptiles; thus, documenting natural seasonal changes in these parameters, or physical manipulations of them, could help explain changes in an animal's behaviour or physical condition. For individuals provided with access to ultraviolet (UV) lighting, periodic documentation of UV-B exposure within enclosures (Fig. 17.3) is vital for ensuring that levels are maintained within a safe and appropriate range for the species (Baines et al. 2016), as well as for determining when lamps need to be replaced as their UV-B outputs degrade over time (see also Arena and Warwick 2023; Mancera and Phillips 2023).

TEMPERATURE / UV / HUMIDITY LOG									
SPECIES: Black tree monitor (<i>Varanus beccarii</i>)			SEX:	ID #	ENCLOSURE: RH117				
DESCRIPTION OF ENCLOSURE: Fiberglass enclosure measuring 200 x 100 x 60 cm; large tree trunks and branches, hide boxes, and live foliage, 30 cm deep soil and leaf litter substrate				DESCRIPTION OF LIGHTING/HEAT:			150 W halogen spot lamp, 48" T5 HO fluorescent UVB lamp - twin fixture		
DATE	TIME OF DAY	LOW TEMPERATURE °C	AMBIENT TEMPERATURE °C	SURFACE BASKING TEMPERATURE °C	UVB OUTPUT µW/cm ²	RELATIVE HUMIDITY %	HUMIDITY INSIDE HIDE 1 %	HUMIDITY INSIDE HIDE 2 %	COMMENTS
14-Sep-18	1100	24.7	27.9	36.6	36.0	77%	84%	100%	Prolonged basking observed - basking temperature may not be hot enough
21-Sep-18	1130	26.7	29.6	45.8	-	85%	86%	92%	Basking lamp wattage increased to raise basking temperature; animals appear to be more active and spending less time basking
28-Sep-18	1200	28.0	30.3	51.4	-	86%	87%	100%	-
05-Oct-18	1100	27.8	30.0	50.0	18.0	91%	91%	98%	UVB output degrading
12-Oct-18	1045	24.1	27.5	27.5	11.0	88%	88%	88%	Basking lamp burnt out; bulb replaced in afternoon
17-Oct-18	1215	28.0	30.1	50.4	87.0	86%	86%	98%	Both UV bulbs replaced

Fig. 17.3 Sample temperature, humidity, and UV exposure logs

Tracking the dates when enclosures are serviced can help to ensure that captive environments are well maintained, but there are other reasons why recording this information can be useful. Changes to an individual's physical environment can cause acutely elevated stress levels in reptiles that may subsequently affect behaviour, including feeding patterns and other important biological functions. For example, transferring skinks to new enclosures had a greater effect on elevating stress hormone levels than toe clipping (Langkilde and Shine 2006). Manipulating objects within enclosures can have similar stressful effects for some species (Chiszar et al. 1995). Cleaning enclosures and thereby removing familiar chemical cues can cause an increase in behaviours that may be stress-induced (Conant 1971; DeFazio et al. 1977; Chiszar et al. 1980, 1995), and handling and restraint can have similar stress-inducing effects in reptiles (Schuett et al. 2004). Given the apparent effects that at least some of these common maintenance-related activities can have on reptile behaviour and welfare, maintaining records of the dates of any such manipulations to an animal or its physical environment could help explain changes in appetite, activity, behaviour, or health.

Many aquatic and semi-aquatic reptiles require specific water conditions to live healthy lives in captivity. When certain water quality parameters deviate from normal levels, animals may experience increased stress and develop health issues. For example, snakes of the genus *Acrochordus* appear to require low pH aquatic environments; when kept in systems with higher pH levels, they can develop chronic skin diseases (Banks 1989). Aquatic chelonians can also develop skin and shell lesions and associated health issues resulting from poor water quality (Rangel-Mendoza et al. 2014). Testing for parameters such as pH, chlorine, nitrogenous wastes (ammonia, nitrite, and nitrate), and coliform counts can provide valuable insight into the safety and appropriateness of aquatic systems. Maintaining detailed records of water quality test results over time will alert keepers to spikes in certain parameters that occur, as well as identify what are normal cyclical trends in these conditions. This information can then be used to make corrective changes to husbandry practices, as well as develop schedules for routine water changes and filtration equipment maintenance.

Body size measurements are often used to evaluate an animal's health and welfare. Routine length and weight measurements can be used to generate growth curves that track an individual's progress and development. These data can also help identify factors that could be affecting an individual's growth or physical development. For example, if an individual has not been growing at a rate comparable to its siblings or previously published records regarding normal growth for the species, then corrective changes to husbandry parameters, such as diet or thermal conditions, or more individualised care, may be necessary (see also Maslanka et al. 2023). Closely monitoring weights can help establish normal trends for a species or individuals (e.g. body mass fluctuations), identify potential health issues, and evaluate body condition (e.g. obesity). However, there is a likely trade-off between the importance of monitoring such changes and the need to minimise stress from handling during measurements, where the frequency of measurements will depend on the species, age, and temperament of the individual.

For nervous or cryptic individuals and specimens maintained in group situations whose feeding behaviours may be difficult to observe, periodic weight measurements can indicate whether or not an animal has been feeding appropriately. Chronic or acute weight loss in an individual could point to various issues including, for example, insufficient diet, stress, or disease, whereas unexpected weight gains could be suggestive of excessive diets, thermoregulatory difficulties, reduced activity and exercise, reproductive cycling or gravidity, disease or a combination of factors. Flawed husbandry or incidental phenomena may be responsible for such signs and states.

Many reptiles, particularly snakes, exhibit observable patterns in shedding cycles (e.g. Jacobson 1977; Alexander and Brooks 1999; Lillywhite and Sheehy 2016). Recording the dates of ecdysis and the quality of sheds (e.g. whole, or in pieces, in the case of snakes) can be useful for determining what may represent a normal shed cycle for an individual. Deviations from normal cycles or shedding difficulties could point to husbandry issues that may require corrective changes (e.g. humidity level, misting frequency, and substrate or furniture alterations) or underlying disease (Harkewicz 2001, 2002).

Changes to an animal's physical condition or appearance including changes in body colouration or the appearance of lacerations, swellings, other lesions, or discharges may be linked to stress, injury, or disease, and should be carefully documented. Medical intervention at the onset of such problematic signs could keep a minor health issue from advancing into a more serious one. Recording when physical changes are first noticed, with detailed descriptions of those changes, can be useful for determining the cause and origin of potential health issues, and informing veterinary diagnostics and treatments.

17.4.1 Reproductive Data

Collecting reproductive data aids understanding of the various factors involved in successfully breeding a species in captivity; however, a discussion of how these data can benefit reptile breeding programs is beyond the scope of this text (see Gangloff and Greenberg 2023). Nevertheless, many of the same reproductive data can also be used to monitor and evaluate keeping practices, as well as track the health and physiological states of captives, particularly females (Figs. 17.4 and 17.5).

Breeding success is often used as a measure of welfare, health, and keeping success. Although poor reproductive performance is usually indicative of inadequate, missing or overlooked husbandry components, stress, poor nutrition or underlying health issues, successful reproduction may not always denote good health and welfare (see also Gangloff and Greenberg 2023; Warwick 2023). For example, excessive reproduction, such as multi-clutching in species whose females are not known to produce more than a single clutch of eggs per annum in nature, could be an artifact of excessive captive diets or inappropriate nutrition (Mendyk 2012a). In such cases, multi-clutching may signal the need for corrective changes to husbandry such as dietary reductions or the separation of paired individuals. Here,

REPTILE EGG DATA SHEET											
SPECIES: Weber's Sailfin Lizard/ <i>Hydrosaurus weberi</i>		CLUTCH #		2018-2		ENCLOSURE: RH16					
DAM: 15R012		SIRE: 16R003		DATE OF PAIRING: 2-Feb-18		DATE(S) OF COURTSHIP: not observed		DATE(S) OF COPULATION: not observed			
EGG DEPOSITION											
DATE OF OVIPOSITION: 22-Sep-18				TOTAL # EGGS: 6.4		# NON-VIABLE EGGS: 1					
DESCRIPTION OF NEST SITE: Eggs laid in planter box in upper right of enclosure				NEST DEPTH: 30 cm		NEST TEMPERATURE: 29.4 °C					
APPEARANCE OF EGGS: All but one egg appear healthy, white and turgid				SUBSTRATE TYPE: soil/coir mix		SUBSTRATE DEPTH: 45 cm					
POST-OVIPOSITION WEIGHT OF FEMALE: 0.92 kg				APPEARANCE OF FEMALE: thin in overall appearance, with hip bones visible							
NEST-GUARDING BEHAVIOUR? n/a											
ADDITIONAL OBSERVATIONS: Female was observed test digging for the 24 hour period leading up to oviposition. At least two other sites excavated, but abandoned. Eggs were deposited in a nest hole, but were not buried. One non-viable egg was laid on top of surface the following day.											
EGG MORPHOMETRICS											
EGG #	DATE	NESTED/ SCATTERED?	EGG WEIGHT (g)	EGG LENGTH (cm)	EGG WIDTH (cm)	HATCH DATE	HATCHLING WEIGHT (g)	SVL (cm)	TOTAL LENGTH (cm)	ACCESSION #	COMMENTS
1	22-Sep-18	N	10.2	3.1	1.2	28-Nov-18	7.1	6.8	13.8	18R006	Healthy in appearance
2	22-Sep-18	N	10.8	3.1	1.1	27-Nov-18	6.8	6.4	13.6	18R007	Healthy in appearance
3	22-Sep-18	N	11.1	3.0	1.0	28-Nov-18	6.8	6.4	13.7	18R008	Large egg yolk remaining
4	22-Sep-18	N	10.7	3.1	1.1	27-Nov-18	6.2	5.9	13.1	18R009	Egg pipped, but hatching died prior to emerging. Was smaller in size than surviving siblings
5	22-Sep-18	N	9	3.2	1.2	-	6.9	6.8	13.8	-	Egg manually opened on 2 Oct; fully-developed dead embryo inside
6	23-Sep-18	Y	5.1	3.2	1.2	-	-	-	-	-	Egg discolored and misshapen, clearly non-viable and subsequently discarded

Fig. 17.4 Sample egg data sheet

BEHAVIOURAL LOG					
SPECIES:	South American Bushmaster/ <i>Lachesis muta</i>		SEX:	0.1	
			ID #	09R018	
			ENCLOSURE:	RH233	CARD DATES: 27 Feb -
					CARD # 2008-2
DATE	TIME OF DAY	DURATION	CONSPECIFICS INVOLVED	TYPE OF BEHAVIOUR	OBSERVATIONS
4-Mar-18	1400	3+ hours	n/a	Irregular activity	Animal was seen perched in a tree in its enclosure for the duration of the afternoon; largely terrestrial, this behaviour has never been observed in this individual or any other bushmasters in the collection.
23-Apr-18	0800	8+ hours	11R131	Conspecific interactions	Animal observed sharing the same shelter as male (11R131) for entirety of the day
24-Apr-18	0800	8+ hours	11R131	Conspecific interactions	Animal observed sharing the same shelter as male (11R131) for entirety of the day
26-Apr-18	1630	30 mins	11R131	Reproductive	Courtship and successful copulation observed. Male observed rubbing on female for several
2-Jun-18	-	~ 4 days	n/a	Thermoregulation	General note - beginning around 28 June, animal has been observed spending noticeably more time basking under its heat lamp than normal
18-Jun-18	0800	-	n/a	Reproductive	Female laid a clutch of 6 eggs in nest box overnight. Animal was temporarily removed from enclosure to retrieve eggs for artificial incubation. No defensive nest guarding was observed; animal retreated to nest box upon return to enclosure.
14-Sep-18	1200	~ 1 hour	n/a	Feeding	Animal struck frozen-thawed rat, but spent close to an hour nudging and repositioning the prey before finally beginning to consume it. Normally the animal begins swallowing prey within a few minutes of striking it.
7-Oct-18	1600	3+ hours	n/a	Irregular activity	Animal has been restless, observed circling around enclosure in the late afternoon for at least several hours.
8-Oct-18	0800	n/a	n/a	Irregular activity	A large fecal mass was discovered in enclosure in the morning and could explain animal's restlessness the previous evening.

Fig. 17.5 Sample behavioural log, noting noteworthy and unusual behavioural observations

documenting reproductive output in females including clutch size, egg morphometrics, relative clutch mass, and the amount of time between successive clutches can play an important role in evaluating supportive husbandry. Reductions in fecundity or departures from normal reproductive trends, such as declines in clutch size, egg size, or egg viability, might suggest underlying health issues or possibly the onset of reproductive senescence; either of which may necessitate changes to husbandry practices or social groupings.

Nesting is a critical component of reptile biology, with strong implications for the health and welfare of females of many oviparous species in captivity. When appropriate nesting conditions are not available, gravid females may experience nesting distress and associated reproductive complications, such as dystocia, which remains a significant cause for morbidity and mortality among captive reptiles (e.g. Raiti 1995; Lock 2000; Stacy et al. 2008; Mendyk et al. 2013). By recording specific nest site parameters such as the location, substrate type and depth, nest temperature, moisture content, and time of oviposition for both successful and unsuccessful nesting events, keepers can gain familiarity with individual females' nesting preferences. Once established, these conditions can be offered consistently in an effort to meet the nesting requirements of a female and avoid future reproduction-related health complications. Additionally, because comparable data from wild populations are lacking for most species maintained in captivity, documenting the gestation periods of females over successive reproductive events can help establish expected timeframes for females, which can then be used as a reference for predicting the timing of birth or oviposition. Divergence from expected gestation periods could be indicative of underlying reproductive complications that may require rapid medical intervention.

17.4.2 Behavioural Data

Behavioural observations may provide the most compelling information needed to assess whether keeping practices are appropriate for a species or individual, or when an animal's health or welfare may be compromised (Warwick 1995; Warwick et al. 2019; Greenberg 2023; Warwick 2023). Whilst it is not feasible for keepers to observe all activities, documenting any noteworthy behaviours through written descriptions, photographs, or videos can be valuable for understanding normal activity patterns, thermoregulatory and feeding behaviours, social interactions, and how individuals interact with and utilise their physical environment. Deviations from what may be considered normal behaviour and activity can point to potential husbandry problems, stress, or compromised health (Warwick 1995; Warwick et al. 2013).

When documenting behaviours, it is important to record details pertaining to the context in which a particular behaviour was observed (Fig. 17.5). Such contextual information can assist with determining the true underlying circumstances or cause for the behaviour, and should include the time of day, location, duration and

frequency of the behaviour, any recent changes or manipulations to husbandry, and the location and activity of conspecifics at the time of the event.

Animal behaviour records usually focus on unusual behaviours, as defined by observant keepers, and it is beneficial to classify the nature of the observation as it is being recorded; for example, courtship, copulation, and nesting are usually subcategories of reproduction. Consistent definitions and categories are important for record retrieval. Interesting observations could lead to a more rigorous template and concentrated study. In some cases, the discovery of novel behaviours performed by captive individuals, such as forelimb-assisted extractive foraging in varanid lizards (e.g. Mendyk and Horn 2011), has had important applications to captive management, including the development of novel forms of enrichment (Mendyk 2012b; Kuppert 2013).

Carefully collected behavioural data can be used to generate ethograms or activity budgets that characterise and evaluate the behavioural repertoires of individuals. Specific behavioural observations may also highlight husbandry deficiencies needing attention. For example, prolonged basking activity could indicate that thermal conditions are inadequate for an animal to reach its preferred body temperature within a reasonable timeframe (Arena and Warwick 2023). Lethargy and hypoactivity could be suggestive of inadequacies in thermal husbandry, stress, illness, or understimulation ('boredom') due to a lack of stimuli within their enclosure, whereas hyperactivity could point to underlying stress, excessive temperatures, aggression, disease, or other issues (see Warwick 2023).

Agonistic interactions between conspecifics can elevate stress levels and sometimes lead to serious injuries or death. Limited enclosure space, or adequate space lacking appropriate refugia, and unnatural social groupings may contribute to the establishment of dominance hierarchies that can increase stress levels and negatively affect the health and welfare of subordinate individuals (e.g. Barker et al. 1979; Alberts 1994). Documenting both positive interactions such as courtship and copulation and negative interactions such as aggression and dominance can be useful for assessing group compatibility and identifying problematic individuals, as well as determining when animals should be separated to avoid potentially harmful situations. Maintaining records of the dates when individuals are introduced to one another can help keepers track the phenology of reproductive cycles and events because negative interactions may peak at particular times during the reproductive cycle. By noting when aggression is first seen, keepers can trace back the origins and underpinnings of aggression or other conspecific-related stressors that could be adversely influencing the health and welfare of captives. Observations should match a species' normal activity patterns (e.g. conducted during relevant diurnal, crepuscular, or nocturnal periods) (see Warwick 2023).

As enrichment becomes a more significant component of reptile husbandry (Hayes et al. 1998; Burghardt 2013; Mendyk and Augustine 2023), documenting the types of enrichment offered to captives and the behavioural responses to them will be important for gauging their appropriateness and effectiveness. Although uncommon in private collections, many zoological parks maintain detailed records of the enrichment they provide to captives as part of their behavioural management

practices (EAZA 2014; AZA 2018), and typically evaluate the success or failure of enrichment stimuli by rating the response and determining whether the ultimate predetermined goal of the enrichment was achieved. Detailed behavioural data are needed for formal assessments that seek to objectively evaluate the success of enrichment programs and their ultimate impact on reptile welfare (Mendyk and Augustine 2023).

17.5 Veterinary and Pathology Records

From a veterinary perspective, many aspects of an animal's behaviour and physical condition, including activity levels, feeding and defecation patterns, and body weight over time, are helpful when determining the nature of an injury or illness and deciding on a course of treatment. Just as husbandry records can inform the medical management of reptiles in captivity, veterinary and pathology records can play an equally important role in guiding the husbandry of reptiles.

Species and individual animals may respond differently to the same or similar medical treatments and therapies. Maintaining detailed records of all medical procedures, treatments, medications (including dosages [i.e. amount, route of administration, and frequency] and dates of administration) and descriptions of physical and behavioural responses to them, can be important for directing future therapies (Fig. 17.6). Signs of complications arising from certain treatments or procedures can sometimes take several days or weeks to appear. For such cases, detailed records of the described parameters will aid linking physical or behavioural changes to previous treatments and therapies. Records documenting how an individual has reacted to or tolerated a particular medication or procedure can affect future therapies and management decisions for the individual. For instance, if an individual is not faring well from a particular treatment (e.g. lethargic, not eating and losing weight), then this could warrant the discontinuation and re-evaluation of that therapy.

Diagnostic test results should be paired with husbandry records to identify potential health- and husbandry-related issues that may not be immediately apparent, or to explain changes in an animal's activity and behaviours. For example, minimally invasive physiological assessments such as blood and faecal testing can be valuable for identifying potential health issues including infections, parasites, and stress, as well as monitoring physiological states such as reproductive cycling.

Necropsy and histopathology reports provide valuable feedback that can help pinpoint potential flaws in husbandry or specific disease processes that contributed to an animal's death. In large collections with numerous individuals, a recurring cause of mortality can indicate serious deficiencies in husbandry that need addressing. For example, multiple female deaths attributed to reproductive complications, such as dystocia, may suggest inadequacies in nesting conditions, or recurring cases of gout and renal failure may raise suspicion of chronic dehydration related to inadequate humidity levels or available drinking water.

Consistent veterinary care and record keeping for all animals in large collections is beneficial for early detection of disease processes and husbandry deficiencies.

HEALTH RECORD			
SPECIES: Chinese box turtle/ <i>Cuora flavomarginata</i>		Sex: 1.0	ID# 09R098
D.O.B: 3 March 2006		DATE OF ACQUISITION: 22 May 2009	
		ORIGIN: CB	
DATE	TREATMENT/PROCEDURE	COMMENTS	
22-May-09	Entered quarantine	Animal housed individually; appears to be in good physical condition	
28-May-09	Faecal sample submitted	Faeces appeared normal; no reported issues	
7-Jun-09	Faecal sample submitted	Faeces appeared normal; no reported issues	
15-Jun-09	Faecal sample submitted	Faeces appeared normal; no reported issues	
24-Jun-09	Cleared from quarantine	Animal moved to general collection; housed together with 09R097	
3-Feb-10	Faecal sample submitted	Faeces appeared abnormal - loose and poorly formed; pinworms detected	
4-Feb-10	Medical treatment*	0.05 mL Fenbendazol orally administered for pinworms (100% success). Repeat once every 7 days for three treatments	
11-Feb-10	Medical treatment*	0.05 mL Fenbendazol orally administered (100% success)	
18-Feb-10	Medical treatment*	0.05 mL Fenbendazol orally administered (100% success)	
28-Feb-10	Faecal sample submitted	Faeces appeared normal; no reported issues	
24-Apr-10	Faecal sample submitted	Faeces appeared normal; no reported issues	
10-Dec-11	Physical exam and radiographs*	Animal has not been defaecating normally; concerns over possible intestinal obstruction. No obstruction found on radiographs- continue to monitor	
17-Dec-11	Follow-up exam*	Problem appears to have resolved itself - animal now defaecating normally; continue to monitor	

*Under veterinary supervision.

Fig. 17.6 Sample health record, noting veterinary tests, treatments, procedures, and outcomes

Furthermore, diagnostic records should periodically be reviewed by a veterinarian, because many reptiles are long lived, and disease trends may not become apparent early on in their management.

17.6 Record Keeping Systems

Record keeping systems should be simple, efficient, easy to search, and standardised as much as possible across all taxa within a collection. Regardless of the system, maintaining the core data elements (e.g. identification, sex, age, source) along with accuracy, consistency, and retrieval ability are key considerations (Earnhardt et al. 1998; Miller and Block 2004; Lackey 2010; Miller 2013). Historically, private reptile keepers and zoological parks have independently developed their own record keeping systems (e.g. Dietlein 1968; Dowling and Gilboa 1968; Slavens 1989; Hoser 1995; Miller 2013), ranging from miscellaneous hand-written notes and memoranda, to personal journals and notebooks, specimen feed cards, daily summary reports, and large-scale electronic databases.

The most common form of captive management records has been hand-written notes (e.g. Dowling and Gilboa 1968; Miller 2013), presenting challenges in archiving and searching for specific information, and interpreting the hand-writing of different individuals. Digital records have helped address issues concerning data storage and retrieval in recent decades, with electronic reports becoming widely used, and allowing for more efficient organisation, standardisation, and sharing of data. Although digital records offer many benefits over traditional hand-written documents, there may still be some value in hand-written records, at least when used in conjunction with electronic record keeping. For example, many zoos and private keepers continue to use individual specimen cage cards at each enclosure for recording general husbandry and behavioural observations as they occur. These hand-written cage cards allow information to be noted immediately, preventing pertinent information from being lost or forgotten if a keeper waits until later to record an observation. However, it is important that these data are then added to digital records in a timely manner; physical paper copies can easily be lost or destroyed, whereas digital records can be searched, duplicated, backed up, and shared electronically. Keepers at zoos are increasingly being fitted with handheld electronic devices for direct entry of their data into central databases.

Photographic and video records can serve as valuable tools for captive management. In addition to aiding in the identification of individuals, photographs also can be used to keep track of husbandry practices and captive environments. Archived photos and videos can provide useful comparisons of keeping techniques, growth and development in individuals, and offer historical perspectives on how species were formerly kept in a collection. Photographic and video series of an individual can also be important for recording behaviours and monitoring changes in physical condition over time, such as during recovery from an injury or illness. Whereas traditional photographs and analog video footage may be difficult to archive, index

or search for, digital media files can easily be duplicated, archived, and organised into searchable electronic files and folders.

The types of information recorded have also changed considerably over time. For example, record keeping in many zoos was once limited to documentation of when animals were received or born in a collection, and when they died (Braverman 2010); today, they often include more detailed information relating to various aspects of an individual's origins, biology, life history, and health. However, this increase in the amount of data collected has created some challenges particularly in distinguishing between what may be valuable and redundant information. Superfluous data can be just as useless to captive management as no records at all and can interfere with captive management and impose additional time costs (Braverman 2010).

One major challenge of animal record keeping systems is that the format, types, and quality of information recorded have not been consistent across collections (Earnhardt et al. 1995). In an effort to address this issue and standardise record keeping across zoological parks and aquariums (e.g. Teare 1991; Flesness 2003), several animal-record keeping databases have been developed over the past few decades, which have now become important everyday fixtures in captive animal management (Flesness 2003). Current centralised databases such as the Zoological Information Management System (ZIMS; Species360[®], Minneapolis, MN, USA) and Tracks[®] Software (Tracks Data Solutions, Inc, Salida, CO, USA) offer many ways of tracking historical and institutional records of individuals, as well as documenting ancestry, daily husbandry practices, behavioural observations, reproduction, medical management, enrichment, and welfare.

There is great utility in the ability to retrieve information from these databases, compare notes, and exchange records between institutions. Zoo staff, including curators, keepers, veterinarians, and registrars, are working to further standardise these data and identify additional useful parameters to record; constant refinements and improvements are being made, based on need and usage. Whilst most private keepers and research laboratories do not participate in or have access to ZIMS or Tracks[®], there are other digital applications that allow users to record, track, and manage individual captive reptile collections. As the technologies for digital record keeping and reptile husbandry advance, there are many possibilities for new and improved applications that can aid captive care.

17.7 Record Keeping for Retrospective and Comparative Studies

Beyond tracking the history, husbandry, and health of individual animals within a collection, data collected in captivity can be employed to address broader questions and challenges facing the captive management of reptiles. Retrospective and comparative studies utilising data sourced from numerous specimens within and across collections can be used towards evaluating current husbandry practices, reproduction, health, and welfare. Moreover, comparisons of equivalent data between captive

and wild individuals, when available, can be used to assess the biological appropriateness of captive environments and management practices.

There is much need for comparative studies that seek to determine how specific keeping practices differ across taxa, collections, and keeping communities (e.g. zoos vs private keepers), but limited research has targeted broad captive datasets to address these and other questions. However, in one example, Mendyk et al. (2016) collected temperature data from a large sampling of zoological parks and private keepers to assess the biological appropriateness of current thermal husbandry practices in use with varanid lizards. These data also were used to compare keeping practices between private hobbyists and zoos, as well as between keepers from different geographical regions. Similar studies that seek to compare husbandry data from other taxa could help develop a better understanding of the variation in care practices across the reptile keeping community, as well as identify additional husbandry challenges that may need to be addressed.

In contrast to veterinary case studies that may identify a particular disease and its aetiology, retrospective studies of morbidity and mortality can shed light on significant diseases and their prevalence within captive populations. Some studies focus on morbidity or mortality in a particular taxon or taxonomic group (e.g. Braz et al. 2012; Mendyk et al. 2013; Schmidt-Ukaj et al. 2017), whereas others concentrate on specific pathogens or disease processes (e.g. Ramsay and Fowler 1992; Ramsay et al. 1996; Graczyk and Cranfield 2000; Garner et al. 2004; Soldati et al. 2004; Sykes and Trupkiewicz 2006; White et al. 2011; Hedley and Eatwell 2014; Dietz et al. 2016). At the individual collection level, retrospective studies can identify issues that may be unique to a collection and that could be adversely affecting animal health, welfare, and keeping success.

Life history data sourced from zoo studbooks and animal record keeping databases offer many opportunities to evaluate welfare and keeping success through the lens of life expectancy, longevity, and reproduction, and can be useful for identifying specific husbandry practices that may be affecting these parameters. Although studies evaluating captive lifespans and their relation to keeping practices and welfare have widely been used as a tool for captive management with mammals (e.g. Wiese and Willis 2004; Müller et al. 2010, 2011), few studies of this nature have focused on reptiles (Braz et al. 2012; Mendyk 2015). The full potential of these data as a tool for advancing standards of reptile care has not yet been realised.

As centralised electronic animal record keeping databases such as ZIMS and Tracks[®] become more robust, sophisticated, and widely used, more data and opportunities will inevitably become available for retrospective and comparative studies focused on captive reptiles. For private keepers and zoological institutions that do not participate in ZIMS or Tracks[®], comparable databases to collect and share many of the same types of information could be extremely valuable, although no such consolidated programs presently exist. Such databases could provide opportunities to explore captive management using data from collections that historically have not been available for analysis.

17.8 Animal Welfare Conclusions

Record keeping is an essential tool for improving the lives of captive reptiles. However, for record keeping to be an effective aid to captive management, reptile keepers themselves must recognise the value and utility of records. Records should not be kept for the sake of keeping records, but rather for piecing together information that has practical applications, and can be utilised to monitor and improve the quality of life for captives, as well as answer broader questions about their care and well-being. This may only be possible when records are regularly employed and reviewed, whether on a daily, weekly, monthly, or yearly basis, or whenever something unusual occurs or is observed. Utilisation may be in the form of checking record cards and logs, and/or managing reports from a centralised electronic specimen record. The importance of having and using good records extends well beyond private reptile keepers and zookeepers being able to learn from, and care for, their captives, in that it also benefits the work of zoo curators, veterinarians, registrars, behaviourists, and other researchers.

Careful attention must be paid to the types, quality, and consistency of the information being recorded. Even in zoos or veterinary clinics where record keeping systems may have been in place for decades, compliance with standards or follow-through actions may be inconsistent; record keeping ‘drift’ can occur and inevitably affect the quality and utility of the information collected. Staff training and codification of records standards, along with daily oversight or review, can counter this trend. Another way is to regularly utilise records for analysing and evaluating captive management practices to improve animal welfare.

Whilst data collected from captive reptiles can have immediate implications for captive management, it is also important to acknowledge that we may be unable to comprehend fully the extent of the value and applicability of this information at this time. Much like voucher specimens deposited decades ago in natural history museum collections being used to address contemporary questions and challenges (e.g. Green 1998; Suarez and Tsutsui 2004; Wandeler et al. 2007; Hoeksema et al. 2011; Lister and Climate Change Research Group 2011), information recorded from captive reptiles today may prove useful for addressing unforeseeable issues or questions that may arise, such as new captive management challenges, conservation issues, or emerging diseases. Therefore, when reptile keepers are faced with the daunting question of how much information they should collect, there may be no such thing as too much data, provided that the information collected is accurate, clear, and concise. This point may be especially true given the expansions seen in animal record keeping databases and their improved information retrieval capabilities.

Finally, record keeping is important because it produces information that yields knowledge that can be used to improve animal husbandry and welfare (Braverman 2010). Detailed and accurate records can help eliminate some guesswork in captive management and steer keeping practices away from ‘folklore husbandry’, or those perceptions and practices largely based on anecdote, speculation, or tradition (Arbuckle 2013; Mendyk 2018; Mendyk and Warwick 2023). However, significant

advancements in reptile husbandry are only possible when this knowledge is applied constructively and shared with others.

Many zoological parks, private keepers, and research laboratories keep extensive records on their captive reptiles, yet this information is rarely compiled and disseminated to the herpetological community. Consequently, valuable information that could improve our understanding of captive husbandry or help address specific management challenges may never come to light. Thus, sharing and publishing captive animal data may be essential to help overcome outdated concepts and practices, and for pushing reptile keeping towards improved evidence-based standards of care and welfare. As quoted in Loh et al. (2018), '*Unpublished results are a hobby... published results are what make a difference*'; such a statement has resounding implications for the progression and future of herpetological husbandry.

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Arbitrary Husbandry Practices and Misconceptions

18

Robert W. Mendyk and Clifford Warwick

Abstract

Herpetological husbandry has advanced considerably over the past century as new information on the biology and captive management of reptiles has come to light, leading to greater reproductive success, improved welfare, and increased captive lifespans for many species. Yet, much still remains unknown regarding the biological and husbandry needs for most reptile species maintained in captivity, and even when current information is available for some species, keeping practices may not take into consideration, or operate contrary to, the most current scientific data. Non-evidence-based care practices grounded in personal anecdote, folklore or tradition, and general misconceptions about the biology and husbandry of reptiles, can have direct impacts on the health and welfare of these animals. This chapter seeks to address various common examples of arbitrary husbandry practices and refute general misconceptions that may be impacting the lives of captive reptiles, and the progression of herpetological husbandry as a whole.

Keywords

Herpetological husbandry · Arbitrary husbandry · Folklore husbandry · Misconceptions · Evidence-based husbandry · Welfare

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18.1 Introduction

Herpetological husbandry has advanced considerably over the past century as new information on the biology and captive management of reptiles has come to light, leading to greater reproductive success, improved welfare, and increased captive lifespans for many species. Many advances were made possible through improved understanding of species' biology, particularly concerning physiological needs, environmental tolerances and preferences, behaviour, and ecology, as well as the development of new technologies and specialised husbandry equipment. Yet, many common husbandry practices and claims do not take into consideration, or operate contrary to, the most current scientific data on, and understanding of, species' biologies, indicating that important aspects of reptile husbandry can be largely non-evidence-based and speculative. Arbuckle (2010, 2013) coined the term 'folklore husbandry' to call attention to husbandry practices that are based on trial and error, and lacking in evidential support. Mendyk (2018) explored this idea further, challenging specific examples of folklore reptile husbandry encountered in zoological parks.

In many instances, current husbandry concepts and practices may be products of trial and error founded on a lack of available information or knowledge of key aspects of reptilian biology, especially in understudied taxa. In such cases, assumptions may be made regarding the natural history and essential needs of species in order to develop methods for their captive care. Frequently, such keeping practices may be based solely on tradition—i.e. 'that's what we've always done' or are practiced for no definable or scientifically justifiable reason. Whilst the term 'folklore' draws attention to outdated and potentially harmful husbandry practices, it more importantly illustrates that many aspects of herpetological husbandry remain largely arbitrary. Arbuckle (2010, 2013) also cautiously recognised a place for folklore husbandry, and notes that some practices have persisted because trial and error-based approaches can work. Folklore husbandry and its associated lack of evidence for a particular concept or practice does not necessitate that such an approach is certainly wrong, nor that a supporting evidential basis will remain absent (Arbuckle 2010, 2013). Rather, it implies that the founding basis, being largely assumptive, remains at best scientifically unvalidated and at worst dangerously wrong. Regardless, both of these possibilities constitute common mainstays of historical and current herpetological husbandry.

Within the arbitrary husbandry spectrum, outdated concepts and practices that may impact health and welfare can be influenced by many different phenomena and proliferated amongst all reptile keeping communities from novice private keepers and hobbyists to zoological parks (Mendyk 2018). In situations where information on a species' biology is largely lacking, keepers may continue to make both informed and uninformed assumptions about how animals may live in nature or look to ecologically similar or related taxa as an analogous reference, and in these cases, husbandry practices may or may not agree with a species' biology. In other cases, such as in popular pet reptile hobbyist magazines, books, care sheets, personal websites, forums, message boards, and social networking websites, arbitrary

husbandry is effectively promoted. It is likely that, for the majority of reptile keepers, little information may be acquired through primary, objective scientific literature due to lack of awareness of, or access to, relevant scientific resources, and limited familiarity with its interpretation.

Further exacerbating this situation, now more than ever, is the issue that poor quality information and misinformation can be easily circulated online. Less experienced keepers and those who acquire reptiles impulsively risk gravitating towards readily available, but poor quality, simplistic, handed-down information on husbandry concepts and practices, rather than more advanced resources and methodologies. More experienced and better-informed practitioners could do more to counter arbitrary husbandry practices and raise welfare standards within the herpetological community. For example, Murphy et al. (2020) have proposed standardised educational approaches in herpetological management for zoological establishments that could be adapted to other situations.

Because outdated and inappropriate care practices can have profound impacts on keeping success and welfare, as well as stifle advancement in the field, it is important that husbandry data and experiences are shared, and quality literature is produced and promoted to push back against the onslaught of outdated, inaccurate, and potentially harmful information (Jessop et al. 2023; Mendyk and Block 2023). Building on previous works that have addressed arbitrary husbandry (Arbuckle 2010, 2013; Mendyk 2018), this chapter discusses various relevant examples and general misconceptions across all reptile keeping communities that may be affecting captive management practices and the health and welfare of captive individuals.

18.2 Evidential Assessment

Arbitrary husbandry manifests via liberal dispersion within common literature and word of mouth, thus comprehensive scientific referencing of its underpinnings is vague. Nevertheless, regardless of original or regular sourcing, examples used herein are likely familiar to academic and zoo herpetologists as well as private reptile keepers. Tables 18.1, 18.2, 18.3, and 18.4 provide a concise summary of common arbitrary husbandry claims and misconceptions, sources, and bases pertaining to: general, environmental, nutritional, and behavioural considerations, respectively. Herein, we have highlighted 17 examples of arbitrary claims and misconceptions. However, certain examples are examined in a relatively greater depth due to their nature being particularly illustrative for the messages of this chapter, whereas others are examined in a relatively lesser depth because they are well addressed elsewhere in this volume (e.g. Arena and Warwick 2023; Doody 2023; Font et al. 2023; Gillingham and Clark 2023; Jessop et al. 2023; Lillywhite 2023; Mendyk and Augustine 2023).

18.3 General Misconceptions (See Table 18.1)

Table 18.1 Example common arbitrary husbandry claims, misconceptions, sources and bases: general considerations

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>'Reptiles are 'easy to keep' pets'.</i>	Commercial and hobbyist sectors.	Belief that biological needs are low and minimalistic provisions adequate.	Fails to account for numerous factors including fuller spatial, physiological, environmental, behavioural, and psychological needs.	Reptiles are not 'easy to keep' pets.
<i>'Reptiles live longer in captivity than in the wild'.</i>	Commercial, hobbyist, and zoo sectors.	Belief that accounts of long-lived specimens are generalisable.	Individual 'records' for specimens not representative of captive populations. Longevities of wild specimens frequently unavailable. Captive premature mortality rate high.	Unfounded and speculative.
<i>'Reptiles would not feed, grow & reproduce unless experiencing good welfare'.</i>	Commercial, hobbyist, and zoo sectors.	Belief that 'good' feeding, growth, and reproduction are strong indicators of generalised welfare.	'Good' feeding, growth, and reproduction are unreliable indicators of holistic physiological, behavioural, and psychological condition and welfare.	Unrepresentative and unfounded.
<i>'Reptiles are only active when seeking food or a mate, & if provided nothing else is required'.</i>	Commercial and hobbyist sectors.	Belief that certain specific fundamental physiological and behavioural drivers are strong indicators of generalised welfare.	Minimalistic perception that fails to account for numerous factors including diversity of physiological, behavioural, and psychological needs.	Unrepresentative and unfounded.

Note: See also section: 'Evidential discussion'

18.3.1 'Reptiles are Easy to Keep'

Many reptiles, in particular colubrid and pythonid snakes, certain lizards such as bearded dragons (*Pogona* sp.) and leopard geckos (*Eublepharis* sp.), and some emydid turtles (e.g. *Trachemys scripta elegans*) are commonly promoted as easy to keep—especially as pets in the home. Promotional messages include factors that are technically correct, such as some species' relative docility and 'quietness', and factors that are misleading or incorrect, such as reptiles being low maintenance or (due to their lack of fur or feathers) good pets for people with certain allergies (Diaz-Perales et al. 2013; Warwick et al. 2013, 2019; Valdez 2021).

'Docility' is commonly interpreted to imply lack of 'aggressiveness', and even suggest comfort, for example, when handled. However, apparent docility may also indicate an immobility response among some species, whereas other species may react defensively. Recent research concluded that, for example, bearded dragons (*Pogona* sp.) behaviourally exhibited signs of stress even when gently handled (Stockley et al. 2020). The docility issue does not infer that a species is comfortable with a situation or that its welfare-associated biological needs are being met. 'Quietness' is a characteristic of reptiles because most are biologically mute or their calls are not within human hearing range, and again this does not associate with reduced welfare-associated biological needs. 'Low maintenance' might be interpreted as involving fewer feeding sessions per week or less frequent cleaning schedules (e.g. for snakes versus dogs or cats), but also wrongly infers low-level biological needs or that minimalistic captive environments are generally capable of fulfilling complex biological needs. As postulated by Burghardt (2013) (see also Mendyk and Augustine 2023) even the best captive environments effectively impose controlled deprivation on their inhabitants. Therefore, fulfilling complex biological needs in what are routinely comparatively (with nature) rudimentary enclosed systems may be difficult or unattainable for many and possibly all species; thus, 'low maintenance' may infer *under-maintenance*.

Allergies are very common among humans, and most organic materials (including from reptiles) are capable of causing allergic reactions. However, reptiles have also been identified directly as conduits for human allergic reactions (Kelso et al. 2000; San Miguel-Moncin et al. 2006), and indirectly via their excretion of consumed invertebrate prey matter (Jensen-Jarolim et al. 2015). Also, that humans may or may not experience allergic reactions from keeping reptiles is not an animal welfare consideration.

Moreover, several scientific methods have been proposed that seek to objectively score species (including reptiles) according to how challenging they may be to keep in private homes (e.g. Schuppli and Fraser 2000; Warwick et al. 2013; Schuppli et al. 2014; Koene et al. 2016; EMODE Pet Score 2019), as well as private and professional situations (Jessop et al. 2023). None of these methodologies (which utilise objective criteria concerning animal welfare, public health and safety, and other issues) score or otherwise categorise reptiles as 'easy to keep'. Differences in biological needs and the ability to provide for such needs may be presumed, but the claim that reptiles are 'easy to keep' is misleading.

18.3.2 'Reptiles Live Longer in Captivity than in the Wild'

Several data sets on captive reptile lifespans and record longevity have been compiled (Flower 1925, 1937; Bowler 1977; Slavens 1988; Snider and Bowler 1992; Slavens and Slavens 1994; Mendyk 2015) and are often cited as evidence for captive reptiles living long lives. There is also an abundance of raw life history data from zoos and related institutions archived in animal record databases (e.g. the Zoological Information Management System [ZIMS]) that can be used for comparative studies on captive lifespans, although for the most part these data have yet to be utilised (Mendyk 2015; Mendyk and Block 2023). No such data repositories currently exist for private keepers, and acquiring accurate lifespan data from the commercial (breeders and traders) and hobbyist sectors may not be possible due to limited or poor record keeping (see Mendyk and Block 2023), or due to a general reluctance to acknowledge shorter lifespans and premature deaths in their collections (Bennett unpublished).

Few studies have been conducted on reptilian lifespans in nature. However, it is clear from some in-situ studies of natural populations, and for individuals of many species in captivity, that potential lifespans can be considerable, where ranges of 8–120 years are not unreasonable (Warwick 2014). Whereas issues including predation may account for high mortalities under natural conditions, context is importantly applied, because such attrition factors ought not to occur in 'protected' captive situations (Warwick 2014).

Regardless of what examples may exist for certain individual reptiles in particular captive conditions, even where these are claimed to be 'record' ages, the fact remains that without detailed data for both exceptional and general life expectancies in nature, maximum captivity-based lifespans cannot be used to claim that reptiles live longer in captive environments. Indeed, given that potential lifespan is largely influenced by genetic and epigenetic factors (Govindaraju et al. 2015; Mayne et al. 2019), there are no compelling reasons to believe that potential lifespans—all things being equal—should differ between wild or captive animals.

Further, relative to the total number of reptiles traded and kept in captivity, few appear to truly live long lives, although long-term studies detailing the life expectancies of captive reptiles have been scant, and mostly limited to a few species in zoological parks (Mendyk 2015) and research institutions (Braz et al. 2012). Two recent studies have shown that premature mortality can be high among captive reptiles. For example, a six-year study of reptiles in private homes found that 75% did not survive 12 months (Toland et al. 2012). Bennett (unpublished) found that monitor lizards (*V. exanthematicus*) kept in private collections had a mean captive lifespan of just over one year. Mendyk (2015) also reported high levels of early mortality in several species of wild-caught and captive-bred varanid lizards in zoos, and suggested that captives in general were not reaching their lifespan potentials, even though some individual specimens had attained record old ages. Within the commercial supply sector, mortality rates among reptiles are even greater. For example, a detailed study of a US based wholesaler and global buyer and seller found that 42% of reptiles died within 10 days of their arrival at the facility (Ashley

et al. 2014). Whilst some of those mortalities may have involved problematic trauma and morbidity pre-arrival, poor health conditions nevertheless reflect substantial supply chain and wholesaler hub welfare failings.

Species-specific data on premature mortality in captive reptiles are lacking, and needed for gauging the success of many current husbandry practices. Captive lifespans will likely continue to increase with improved husbandry practices as keepers seek to address deprivations (Mendyk and Augustine 2023). However, intuitively, the ‘big picture’ informs us that a vast number of reptiles enter the human domain annually; and were the greater portion of these to survive, then all captive sectors would likely be saturated with living healthy individuals. Instead, there is a great ongoing annual supply and turnover of reptiles, which infers that these animals experience high premature mortality in captivity. Given the known long potential lifespans for many reptile species, and the short lifespans observed in captivity, it may instead be the case that most captive reptiles are not currently living longer in captivity than in the wild.

18.3.3 ‘Reptiles Would Not Feed, Grow and Reproduce Unless Experiencing Good Welfare’

Feeding, growth, and reproduction reflect certain aspects of physiological states. These states are influenced by certain environmental triggers, an organism’s physical resources, and behavioural opportunities within a narrow context. Accordingly, many animals across numerous taxonomic groups are known to feed, grow, and reproduce not only under conditions of major stress (e.g. broiler chickens, farmed crocodylians, and other intensively reared animals), but also in circumstances calculated to inflict pain (e.g. laboratory research protocols). In addition, reptiles are known to exhibit numerous recognised stress-related behaviours whilst also manifesting good feeding, growth, and reproduction (see Warwick 2023).

Stress and other factors of poor health in certain contexts can result in reduced appetite, growth, and fecundity, particularly where chronic corticosterone disturbance is involved (see Gangloff and Greenberg 2023). However, research has also shown that such physiological considerations are not generalisable across all stress contexts or taxa; although stress—both in nature (e.g. seasonal mating competition) and in captivity (e.g. environmental deprivational factors) may each occupy certain roles in stimulating reproduction (Broom & Johnson 1993; Warwick et al. 2013; Martinez-Silvestre 2014; Gangloff and Greenberg 2023).

18.3.4 ‘Reptiles are Only Active When Seeking Food or a Mate, and If These Features are Provided, Nothing Else is Required’

In nature, many reptiles occupy and navigate extensive home ranges against which typical captive enclosures are extremely diminutive (see Arena and Warwick 2023). Locating food and mates, as well as other resources such as shelter and basking zones, feature among natural space-utilising behaviours that can—at least

theoretically—be provided within the context of conscientious husbandry. However, these features are far from the only drivers of space-utilisation. Other drivers may include novel or alternative habitat searches, specific food searches, inherited transientism, microhabitat selection, extended sociality, and seasonal stimuli. Apart from the commonly vast areas over which these space-drivers are typically performed, they are also fundamentally and/or spontaneously determined for reasons, and at times, particularly identifiable by the individual reptile; thus, they cannot be reliably predicted by keepers.

At its simplest, one might appreciate the notion that even if—hypothetically—reptiles favoured ‘sheltered’ or ‘small’ areas, then such areas are only arguably appropriate when they are bordered or surrounded by larger or open spaces; otherwise those areas are not ‘sheltered’ or ‘small’, but rather non-contextualised, confined spaces where animals are effectively trapped. Moreover, the innate drives that are strongly fundamental to reptilian biology are instilled constants within their behavioural and psychological makeup, and this infers that both drives and target states require fulfilment. Accordingly, regardless of whether or not the keeper is aware of, and aims to provide for the array of space-utilising needs of reptiles, almost without exception, neither the degree of space nor the predictability of need can be fully met in captive conditions.

18.4 Environmental Considerations (See Table 18.2)

Table 18.2 Example common arbitrary husbandry claims, misconceptions, sources and bases: environmental considerations

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>‘UV is unnecessary for many commonly kept reptiles’.</i>	Commercial, hobbyist, and zoo sectors.	Belief that dietary vitamin D ₃ is sufficient for normal physiological needs.	Not generalisable to reptiles, and where most commonly directed—snakes—evidentially speculative. Precautionary principle advises naturalistic UV provision.	Speculative and unfounded.
<i>‘Arbitrary or single thermal conditions are acceptable as long as some heat source is provided/all’</i>	Commercial, hobbyist, and zoo sectors.	Belief that simple temperature provision, thermal environments, and thermoregulatory changes are unimportant and adequate for	Gross and subtle variation in environmental temperatures are fundamental to reptilian biology and to the normal regulation of physiological and behavioural states	Exaggerated, unrepresentative, and unfounded.

(continued)

Table 18.2 (continued)

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>heat is the same</i> .		general thermoregulatory needs.	and condition. Reptile biology includes both hard-wired behaviour and interaction with specific heat sources (e.g. thigmotherms, heliotherms) and other factors that require naturalistic thermal provisions.	
<i>'Adequate thermal gradients are possible in small enclosures</i> .'	Commercial, hobbyist, and zoo sectors.	Belief that narrow range thermal gradients are adequate for general thermoregulatory needs.	Wide ranging temperatures across multiple thermal zones that accommodate full body thermoregulation are biologically important for reptilian health and welfare and provision of such zones is incompatible with small enclosures.	Unrepresentative and unfounded.
<i>'Arbitrary or single, constant humidity level is sufficient</i> .'	Commercial, hobbyist, and zoo sectors.	Belief that a simple humidity provision is adequate for general humidity needs.	Gross and subtle variation in environmental humidity are fundamental to reptilian biology and to the normal regulation of health-states.	Unrepresentative and unfounded.

Note: See also section: 'Evidential discussion'

18.4.1 'UV is Unnecessary for Many Commonly Kept Reptiles'

In many if not most reptiles, ultraviolet radiation (UV-B) plays an important role in the synthesis of vitamin D₃, which is essential for the absorption of dietary calcium (see also Lillywhite 2023; Mancera and Phillips 2023; Maslanka et al. 2023). Without access to UV-B, many reptiles may be unable to produce sufficient levels of vitamin D₃ from dietary sources alone (Oonincx et al. 2010), which can contribute to a cascade of health issues and physical and physiological impairments (see also Maslanka et al. 2023). Some reptile groups, particularly snakes, varanid lizards, and nocturnal taxa, are less likely than others to be provisioned with UV light in

captivity, due largely to preconceptions that they may not need or benefit from it—despite clear evidence to the contrary (Carman et al. 2000; Gillespie et al. 2000; Gyimesi and Bums 2002; Acierno et al. 2008; Ferguson et al. 2009, 2010; Bos et al. 2018). A further important point, even for species that may not utilise UV-B towards the production of vitamin D metabolites (Hedley and Eatwell 2013), is that the benefits of ultraviolet light also include positive effects on behaviour, and as a potential topical microbial suppressant or disinfectant (McGuigan et al. 1974; Baines et al. 2016).

Even when supplemental UV light is provisioned for captive reptiles, there may be little or no consideration of its actual intensity or justification for a particular intensity, or variation in UV levels within enclosures. Such arbitrary provisioning ignores key aspects of species' natural history with regard to the UV levels present in their environments (see Ferguson et al. 2010; Baines et al. 2016) as well as normal variations in intensity within these habitats (e.g. shade), that can be used by individuals to behaviourally photo-regulate exposure based on physiological needs (Ferguson et al. 1998, 2003). Such practices can result in under- or overexposure to UV; both of which can have serious health consequences.

18.4.2 'Arbitrary or Single Thermal Conditions are Acceptable as Long as Some Heat Source is Provided: All Heat is the Same'

Most reptile keepers are probably aware that reptiles behaviourally regulate their body temperatures by seeking out different thermal conditions within their environment (see also Arena and Warwick 2023; Gillingham and Clark 2023; Lillywhite 2023). However, there can be a disconnect when applying this concept to captive husbandry practices, where specific temperature ranges and thermoregulatory options may be overlooked, misinterpreted, or not considered at all, leading to stress and poor welfare (Mendyk et al. 2014, 2016; see also Arena and Warwick 2023; Gillingham and Clark 2023; Jessop et al. 2023; Lillywhite 2023).

Why do reptile keepers provide the thermal conditions they do? In some cases, keepers may be unaware of the actual temperature ranges they are providing but consider these conditions to be sufficient simply because some arbitrary heat source (e.g. a heat lamp) is provided. In other cases, the same or similar thermal conditions may be applied to a wide range of species regardless of their own specific thermal tolerances, needs, and preferences. For example, among North American reptile keepers, surface basking temperatures of 95–100 °F (35.0–37.8 °C) are frequently recommended in the general literature for a wide range of taxa (e.g. Mendyk et al. 2014, 2016), which appears to have little to do with the actual thermal biology of each species, and more to do with the convenience of working with round numbers. In reality, these arbitrary temperatures may be very different from the conditions available to, sought out, and utilised by, species in nature, and may fail to provide the thermal conditions needed to ensure good health and welfare.

As poikilothermic ectotherms, the practice of maintaining reptiles at a single (e.g. constant room) temperature without access to supplemental thermal conditions contradicts fundamental aspects of their biology. Such practice assumes that there is a single 'perfect' body temperature for an individual that can be provided continuously, when in fact reptiles select different temperatures situationally depending on changing behavioural and physiological needs (e.g. digestion, immune response, energy conservation, sleep). Compelling captives to remain at a constant body temperature may have unintended health consequences as well as a cascade of other physiological effects, such as being unable to reduce metabolism to achieve rest, or an inability to behaviourally induce fever to fight infection (see Arena and Warwick 2023; Gillingham and Clark 2023; Lillywhite 2023).

Some of the greatest technological advancements in herpetological husbandry over the past several decades have been the development of many different specialised forms of lighting and heat sources. Whilst reptile keepers now have access to more options for equipment, the importance of one particular type of lighting or heating provision over another for a given species may not be recognised due to the misconception that all heat sources (e.g. halogen lamps, heat pads, ceramic heat emitters) are the same in effect, and thus are interchangeable between species despite differences in thermoregulatory habits and preferences (heliothermy, thigmothermy) (Arena and Warwick 2023). Related to this issue are fundamental misunderstandings about the physical properties of light (e.g. the differences between short-, mid-, and long-wave infrared [IR] radiation), how reptiles utilise different IR wavelengths for thermoregulation, as well as the different IR wavelengths emitted by each type of lamp or heating element (see Muryn 2019; Mancera and Phillips 2023). Pairing of a species with incorrect light or heat sources may fail to provide the appropriate cues and conditions needed by that species to adequately thermoregulate. This issue in turn could cause thermoregulatory 'confusion' or uneven heat distribution throughout the body, which can have physiological consequences or even lead to thermal burns.

18.4.3 'Adequate Thermal Gradients are Possible in Small Enclosures'

Smaller environments possess inherently reduced capacities for thermal gradation, implying minimal and/or inadequate temperature range differences across and within an enclosure. Given that reptiles may require their entire bodies to be warmed (notably during basking activity) or cooled, captive environments require a multi-incremental and wholly occupiable mosaic of 'thermal zones' so that all individuals can thermoregulate normally (see Arena and Warwick 2023; Gillingham and Clark 2023; Lillywhite 2023; Warwick 2023).

18.4.4 ‘Single, Constant Humidity Levels are Acceptable’

Under natural conditions, most reptiles inhabit complex environments that offer broad variations in environmental factors such as temperature, humidity, and substrate moisture levels (Mendyk and Augustine 2023). Species may seek out different microhabitats with specific humidity and/or moisture levels depending on their physiological and physical needs at the time, such as during ecdysis or to help limit evaporative water loss. Therefore, the common practice of maintaining a single, uniform humidity level in an enclosure may not provide the range of conditions needed by an individual to fully satisfy all of its needs in a manner familiar to it, which can lead to chronic dehydration and associated health issues (e.g. dysecdysis, renal disease, and gout).

Several pertinent questions can be raised in relation to arbitrary environmental moisturisation (such as misting enclosures). For example, what is the specific purpose? Is applied moisturisation actually providing animals with the ability to sufficiently drink, and is the applied duration adequate for its purpose? If there is substantial ventilation (e.g. certain screen tops, air vents), does daily moisturisation significantly contribute to greater humidity levels inside an enclosure? Because the ambient humidity levels in zoo facilities and private homes where reptiles are kept may be lower than those of the environments from which many species originate, elevated humidity levels from misting can quickly equalise with the drier ambient conditions if there is a strong diffusion gradient, and may not actually offer the intended benefits, or if so, only briefly. Even if elevated humidity levels within an enclosure could be retained for extended periods, would a single high ambient humidity level be appropriate for xeric or temperate species that normally seek out temporary refuge in burrows and other areas with higher humidity levels?

18.5 Nutritional Considerations (See Table 18.3)

Table 18.3 Example common arbitrary husbandry claims, misconceptions, sources and bases: nutritional considerations

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>‘Food is food whatever its origins’.</i>	Commercial, hobbyist, and zoo sectors.	Belief that current feeding regimes approximate wild diets and energetic needs.	Lack of detailed evidential basis for many species’ natural diets and available evidential basis for dietary diversity for numerous species indicate that diets in nature involve greater variation than diets in captivity.	Unfounded and speculative.

(continued)

Table 18.3 (continued)

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>'Arbitrary feeding quantities & frequencies are acceptable'.</i>	Commercial, hobbyist, and zoo sectors.	Belief that ad hoc provisioning of food is adequate.	Under natural conditions, animals acquire food volume and type according to availability, opportunity, physiological need, and often require natural foraging and food handling behaviours. These dynamics are not accounted for in arbitrary diets.	Unfounded and speculative.
<i>'Standing water should not be provided for xeric habitat species'.</i>	Commercial, hobbyist, and zoo sectors.	Belief that xeric habitat species only obtain dietary moisture via food or imbibe via condensed aerosolised droplets.	Some species typically obtain moisture via diet but drinking from standing water remains a general opportunistic activity requiring some such provision.	Unrepresentative and unfounded.
<i>'Arbitrary provisioning of water is acceptable'.</i>	Commercial, hobbyist, and zoo sectors.	Belief that a water bowl placed anywhere in an enclosure will be located and utilised by a species.	Species differ in how they source water depending on habitat usage (e.g. arboreal vs terrestrial sources); water provisioning in captivity should reflect the habits of a species.	Unrepresentative and unfounded.

Note: See also section: 'Evidential discussion'

18.5.1 'Food is Food Whatever its Origins'

Few, if any, captive reptile diets approach replicating those of wild individuals, but does regular captivity-based nutrition at least reasonably approximate the compositions, sizes, shapes, tastes, and textures of natural items, or accommodate normal foraging, food handling, and ingestion behaviours? Disparities between wild and captive diets stem largely from the lack of commercial or local availability of natural food items, as well as keeper convenience, where food items are selected simply because of their ease or general availability.

Incorrect anthropomorphic assumptions about the properties of wild food items can also impact the appropriateness of captive diets (see Maslanka et al. 2023). For example, to humans, ‘fruit’ typically references soft, sugary, cultivated foods, whereas fruits consumed by wild reptiles may be hard and fibrous with very different nutritional values (Schwitzer et al. 2008; Sweeney et al. 2017). Many other examples exist, including the types of vertebrate and invertebrate prey or plant matter offered to captives. Whilst a comprehensive understanding of the effects of unnatural captive diets on reptile health and welfare has yet to emerge, there are many documented examples of nutritional deficiencies and other health issues related to captive diets (Mans and Braun 2014; Boyer and Scott 2019). Yet to be explored in any depth are the impacts of captive diets on other essential biological functions besides nutritional status and growth, such as skeletomuscular development, reproduction, and cognitive development (Mendyk and Augustine 2023).

18.5.2 ‘Arbitrary Feeding Quantities and Frequencies are Acceptable’

Field metabolic rates are one way in which the energetic needs and food requirements of a species can be approximated (Nagy et al. 1999; Nagy 2005; Maslanka et al. 2023). However, because such values are lacking for the vast majority of reptile species maintained in captivity, what is the factual basis for captive feeding quantities and frequencies? For instance, generally speaking, most snakes tend to be fed weekly or bi-weekly in captivity, but are these frequencies based on the feeding habits and energetic demands of wild individuals for each species, or regimens that contribute to better growth rates in captivity (e.g. Hill et al. 2019)?

The paucity of data from wild populations makes determining the energetic needs of captive reptiles difficult. Nevertheless, it is not unreasonable to presume that many reptiles have lower energetic requirements in captivity than in the wild—free-living reptiles travel long distances to patrol territories or seek out food, water, mates, or other resources (see also Arena and Warwick 2023). Obesity is a major health issue among captive reptiles that is related to excessive diets and insufficient activity (Mans and Braun 2014; Boyer and Scott 2019; see also Lillywhite 2023), as is excessive fecundity (e.g. Mendyk 2012). Thus, current feeding concepts and practices require refocused attention away from how much an individual can or will eat, and towards how much they truly need to carry out all biological functions and live healthy lives.

18.5.3 ‘Standing Water Should Not be Provided for Xeric Habitat Species’

Many reptile species occupy xeric environments and acquire moisture via dietary sources and imbibition of condensed aerosolised droplets (see Lillywhite 2023; Maslanka et al. 2023). However, opportunistic moisture supplementation may also occur where animals drink from standing water pools. Given the possibility that such opportunities may present in nature, it follows that captive environments ought to

assume potential value in providing some standing water in order to accommodate possible preference or biological need. More importantly, supplemental water provisioning can also provide opportunities for hydration when other essential elements of a species' biology related to water conservation may be unknown, overlooked, or not provided (e.g. the use of cool, humid burrows for relevant species).

18.5.4 'Arbitrary Placement of Water Sources is Acceptable'

Reptiles vary widely in their habits, with species ranging across a spectrum from strictly fossorial to exclusively arboreal. Thus, species may be accessing water differently within their respective environments based on their unique habits and habitat usage. For example, strictly arboreal species may not recognise or descend from trees to access pools of water located on the forest floor, just as terrestrial species may not source or utilise water collected in epiphytic plants or the concavities of trees. In captivity, the practice of arbitrarily providing a water bowl on the floor of an enclosure—regardless of the species and its habits, may not be offering the same features or cues that may be familiar to a species for sourcing water, which could lead to chronic dehydration, associated health issues, and death. Providing multiple water sources in different locations can offer captives options for water provisioning and better meet the features and cues with which species may be adapted or familiar.

18.6 Behavioural Considerations (See Table 18.4)

Table 18.4 Example common arbitrary husbandry claims, misconceptions, sources and bases: behavioural considerations

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>'Reptiles are not social'.</i>	Commercial, hobbyist, and zoo sectors.	Belief that innate high level precocity and independence infer asociality.	Evidence of sociality is increasingly accumulated and social needs are widely recognised across many species.	Unrepresentative and unfounded.
<i>'Snakes thrive in small enclosures'.</i>	Commercial and hobbyist sectors.	Belief that biological needs are low and minimalistic provisions adequate.	Perception of 'thrive' commonly taken to imply feeding, growth, and reproduction, which are unreliable or false indicators of welfare.	Unrepresentative and unfounded.

(continued)

Table 18.4 (continued)

Claim	Common source	Arbitrary basis	Scientific comment	Conclusion
<i>‘Reptiles (especially snakes) are sedentary, do not use space, suffer from insecurity & agoraphobia or become anorexic in large environments’.</i>	Commercial and hobbyist sectors.	Belief that biological needs are low and minimalistic provisions adequate, and that snakes are hard-wired to fear open spaces.	Evidence from wild and captive home range studies confirms that snakes (including commonly perceived ‘sedentary’ species) are regularly active and occupy large areas. Agoraphobia is a human anxiety condition not known in reptiles. Preferences for closed habitat spaces do not indicate ‘fear’ of open spaces. Insufficient hiding spaces, shade, and thigmotactic surfaces. Seasonal or acclimation anorexia is not an indicator of stress related to open spaces.	Unrepresentative and unfounded.
<i>‘Snakes do not need to stretch out’.</i>	Commercial and hobbyist sectors.	Belief that rectilinear posturing in snakes uncommon and unnecessary.	Evidence from wild and captive snakes confirms regularity of rectilinear posturing when possible and deleterious health effects when prevented.	Unrepresentative and unfounded.

Note: See also section: ‘Evidential discussion’

18.6.1 ‘Reptiles are Not Social’

Perceptions that reptiles are not social animals may derive from long-standing assumptions within both the herpetological and herpetocultural communities. All studied reptiles exhibit some degree of sociality, with many species now being recognised as highly social (see also Doody [2023](#); Gillingham and Clark [2023](#)).

Captive environments inherently limit an individual's spatial, habitat, and conspecific interactions, and these constraints on normal sociality could result in both social under-stimulation and/or co-occupant conflict. Accordingly, whether deprivation of normal social behaviours or promulgation of problematic co-occupant aggression, both issues arise from the nature of captivity and do not indicate asociality in reptiles.

18.6.2 'Snakes Thrive in Small Enclosures'

A common perception among reptile keepers that a snake is 'thriving' relates to whether the animal feeds, grows, and reproduces. Snakes, as with many other animals, are well-known to naturally seek refuge in burrows, crevices, or similar such spaces. However, as stated below, occupation of small areas is not an indicator that such environments positively represent broader activity budgets, and therefore should not be interpreted as wholly acceptable conditions. Feeding, growth rates, and reproduction, as stated elsewhere, are not necessarily genuine indicators of good welfare (see also Warwick et al. 2019; Arena and Warwick 2023; Jessop et al. 2023). Furthermore, many reptiles that are claimed to be thriving also exhibit significant signs of stress and compromised welfare, thus the belief-based claim is incorrect (Warwick 1990, 2023).

18.6.3 'Reptiles (Especially Snakes) are Sedentary and Do Not Use Space'

Many reptiles (including snakes) naturally occupy extensive home ranges or those that are nevertheless substantially greater than spaces available in captivity. Even the so-called sedentary species are frequently active within ranges considerably greater than typical captive environments (Warwick et al. 2019; Arena and Warwick 2023). Furthermore, both large and small individuals manifest extensive space-utilisation budgets because whereas larger animals may traverse considerable distances (e.g. Burmese pythons [*Python molurus bivittatus*] and Komodo dragons [*Varanus komodoensis*]), many diminutive reptiles necessarily pursue highly active invertebrate prey and engage in considerable predator avoidance and thermoregulatory behaviours that require significant activity levels (see Warwick 2023).

18.6.4 'Snakes Suffer from Insecurity, Agoraphobia or Anorexia in Large Environments'

Agoraphobia is a human anxiety disorder, and in this context is an example of irrational anthropomorphism; the condition is unknown in snakes (Warwick et al. 2013, 2019; Arena and Warwick 2023; Jessop et al. 2023). Like many animals, whether resulting from potential predatory factors, shelter from environmental challenges, prey location, normal microhabitat occupation, or various other factors,

snakes may for varying periods occupy secluded areas. However, such habitat selection preferences form only part of overall activity budgets, and do not infer a generalised fear or disuse of open spaces (see also Gillingham and Clark 2023). Relevantly, just as diminutive ‘well-furnished’ enclosures imply spatial deprivation, large poorly furnished enclosures imply habitat deprivation—thus both space and the quality of space are fundamentally important and can impact an animal’s ability or willingness to carry out essential behaviours such as feeding and thermoregulation.

18.6.5 ‘Snakes Do Not Need to Stretch Out’

Rectilinear behaviour, or straight-line—‘stretched out’—posturing, occurs across all main types of snake movement (rectilinear or creeping motion, concertina locomotion, sliding behaviour, serpentine lateral undulation, sidewinding), and is common among both mobile and stationary snakes (Warwick et al. 2019; Arena and Warwick 2023; Jessop et al. 2023). A recent study identified at least 24 negative clinical and behavioural conditions associated with snakes housed in small enclosures, such as racks and other facilities, that prevented straight-line body postures (Warwick et al. 2019). Other recent studies have shown that recommendations for small snake enclosures are not evidence-based, whereas recommendations for larger and more enriched enclosures are strongly evidence-based and essentially now mainstream guidance (Warwick et al. 2021; Hollandt et al. 2021). Enclosures that deprive snakes of the ability to fully stretch are associated with convenient captive housing, and have no rational welfare basis.

18.7 Animal Welfare Conclusions

Many current herpetological husbandry concepts and practices are unquestionably inconsistent with objective evidence and wrong. Other concepts and principles remain open to validation. However, this situation implies that many of these approaches cannot be reliably recommended or must be treated with caution. The evolution and advancement of herpetological husbandry requires enduring scientific evaluation and validation and the realisation that captive environments and management practices can always be improved (Mendyk and Augustine 2023). Such evaluation and validation demand objective scrutiny using the best scientific evidence, and the avoidance of anything that falls short—with little room for guesswork or handed-down information. Accordingly, beyond regular self-evaluation and assessment of husbandry practices (see Jessop et al. 2023), proper scrutiny of all husbandry issues can benefit from independent insight from impartial observers, who are immune to confirmatory biases.

The environmental, physiological, behavioural, and psychological needs of reptiles demand highly specific conditions that must be comprehensively met to aspire to fulfil good welfare. In reality, the basic and minimalistic husbandry

experienced by many reptiles in captivity may only be meeting a very low-quality care threshold. Yet, rather than emphasise knowledge deficiencies in accordance with a precautionary principle, erroneous and uncertain information with potentially negative animal welfare implications has been, and continues to be, largely overlooked by some keeping sectors.

Many herpetological husbandry concepts and principles require re-evaluation from the ground up. Amongst the various scientific, practical, and ethical considerations that ought to underpin ‘herpetoculture’ and its re-evaluation, animal welfare should constitute the overriding issue of relevance and concern. Good animal welfare has been postulated as the primary indicator that ‘all is well’—i.e. if an animal genuinely is able to experience the normal and positive elements of its evolved lifestyle and has no ‘wants or needs’ that are unmet, then its welfare is good and that state becomes a vice-versa indicator of life quality. Thus, fully meeting all reptile welfare needs signals both essential care for the individual animal, as well as success for the keeper in whom its well-being is entrusted.

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Abstract

Captive animal welfare has benefited from various new technologies and a new generation of welfare-minded and better-informed individuals adopting more welfare-oriented practices. However, for captive reptiles, there remain many aspects that are grounded in and reflect a long history of arbitrary or folklore husbandry and advice, and reptile-keeping continues to be compromised by practices that benefit the keeper rather than the animal that is kept. This second edition of *Health and Welfare of Captive Reptiles*, like the first volume, contains a diversity of primary classical subjects, each hopefully constituting an advancement in our understanding of reptilian biology and meeting the associated needs

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of these animals in captivity. Some subjects, comprise miscellaneous considerations that, directly or indirectly, will have a significant bearing on reptile health and welfare. It is these factors that form the basis of this chapter. It is hoped that, at the very least, their inclusion may create or stimulate an awareness of other potential issues that may affect the well-being of captive reptiles.

Keywords

Animal welfare · Reptile husbandry · Stress · Pain · Sensitivity · Environment · Euthanasia · Killing · Ethics

19.1 Introduction

Research into captive animal welfare has benefited from various new technologies and a new generation of welfare-minded and better-informed individuals adopting more welfare-oriented practices. However, in regards to captive reptiles, there remain many aspects that are grounded in and reflect a long history of folklore husbandry and advice (see Mendyk and Warwick 2023). In addition, the welfare of captive reptiles continues to be compromised by practices that benefit the keeper rather than the animal that is kept. It is thus not unexpected that with the adoption of any new approach to housing reptiles, particularly those that contradict basic principles of reptile biology, for example, snake rack systems (see Arena and Warwick 2023), we will also continue to face new challenges in addressing their health and welfare. Furthermore, as the original version of this chapter described, there will always remain a number of miscellaneous considerations that, directly or indirectly, will have a significant bearing on reptile health and welfare. It is these factors, some of which have been addressed within the first edition of this volume (and other chapters within this current volume), that form the basis of this chapter. It is hoped that, at the very least, their inclusion may create or stimulate an awareness of other issues that may affect the well-being of captive reptiles.

19.2 Stress, Pain and Sensitivity

The very nature of conditions of captivity and the necessity to display reptiles to the public in an educational setting imposes risks of maladaptation and injury. Furthermore, the very fact of confinement creates a variable degree of stress, which often leads to behavioural alterations with serious consequences (Frye 1991a, b, 2015; Divers and Stahl 2019). For many years, reptiles have been maintained in captivity for display, research, culinary, fashion, curio and pet purposes. The consideration of these vertebrates in both nature and captivity has suffered from two basic undesirable attributes. First, until recently, they have had little intrinsic appeal to the public and researchers alike; and second, certain anatomical and physiological differences between reptiles and, for example, mammals, have inclined them to be distanced

from the more popular and well-studied endothermic vertebrates. With respect to both of these points, a factor most often misunderstood and neglected is the reptilian response to the multi-faceted stresses that are imposed by conditions of captivity. Non-scientific herpetologists and pet keepers in particular too often associate perceived ‘stoicism’ in reptiles as indicative of a low sensitivity/high tolerance to abnormal conditions, stress and pain. Such misconceptions have often resulted in reptiles being mismanaged, neglected and abused.

19.2.1 Stress

The stress response and associated distress can be divided into several key categories: acute, chronic, psychological (including emotional) and physiological. Inevitably there is overlap between and complex associations within these divisions. Also, although some associations may be relatively straightforward, in that a predatory threat stressor may initiate a psychological-physiological stress sequence, other less obvious considerations also arise. For example, whilst acute and chronic stress may sometimes manifest as independent phenomena, the two can occur simultaneously, such as when a chronically stressed animal is captured and handled and where acute stress episodes cumulatively flow into chronic stress situations. The assessment and proper management of stress in captive reptiles, as for other captive animals, is essential for optimal health and welfare (Martínez-Silvestre 2014). However, the entire stress issue is by no means straightforward. In this section, we will explore additional, and perhaps less tangible, concepts that may contribute significantly to the issue of stress in wild and captive reptiles.

19.2.2 Natural Versus Captivity-Related Stressors and Stress

Acute and chronic stressors that, in nature, might present essential exercise for an organism’s biological attributes, include physiological response mechanisms and these are part of experiential learning for survival. In captivity, acute and chronic stressors can be negative and highly destructive. Thus, in nature, stressors and stress may constitute a normal part of an evolved holistic system, whereas in captivity, stressors and stress likely occupy dysfunctional roles. At what point potentially valuable stress becomes a totally negative experience is difficult to define. Being able to determine the level at which a noxious influence loses any natural value and becomes adverse, has obvious welfare implications. Psychological consequences of acute stress may occur for periods of some seconds to several minutes (it is also conceivable that residual effects may last for some hours or longer) and it is worth bearing in mind that even a single acute stress occurrence, whether physical (e.g. thermal), psychological (e.g. perceived threat) or physiological (e.g. adrenal response), may have long-term adverse consequences (see Gangloff and Greenberg 2023; Greenberg 2023). Furthermore, social stress (demonstrated in rodents to be the most potent stressor—Koolhaas 1997) is remembered via individual recognition for

up to a week in the lizard *Anolis carolinensis*, but not for 10 days (see Forster et al. 2005; Korzan et al. 2007).

Various forms of chronic stressor exist in nature. Drought, climate extremes, hibernation, aestivation, food deprivation, and other factors certainly contribute to long-term pressures with possibly fatal consequences. However, these factors are in natural concert with the normal psychological and physiological coping mechanisms of the individual. Such stressors challenge the individual or population, but within parameters for which they have evolved.

19.2.3 Stressors and Stress in Nature and in Captivity

There is at least one fundamental difference between, in particular, chronic stress in nature and chronic stress in captivity. Nature provides various stimuli that contribute continually to an animal's awareness of its surroundings. These stimuli are not necessarily stressful in a negative manner and include essential factors such as inter- and intraspecific interaction, food and shelter searches and predator avoidance. In addition, there exists a multitude of chaotic influences that may be very subtle. It is probable that these activities and stimuli are significantly positive, even if they serve merely to occupy animals as they endeavour to survive. Thus, natural conditions offer greater holistic stimulation of a reptile's perceptive capabilities than conditions presented by artificial, relatively sparse, sealed and inactive (biologically and climatically) enclosures of captivity. Also, in nature, animals have a variety of choices to escape from stressors, whereas in captivity, these options are denied; thus, certain situations can result in quite varied responses even when the same stressor is faced in either setting (Wielebnowski 2003). For example, in the wild, male-to-male combat behaviour during breeding seasons, which is frequently described among lizards and snakes, has a valuable role in mate selection and success; and unwilling combatants and losers can easily avoid confrontation with their victors. However, in captivity, unwilling combatants cannot avoid others, and losers and victors must co-mingle, which may result in social stress.

Bearing this in mind, a reptile that has encountered a stressor in nature may be psychologically better able to contend with the situation than a stressed captive reptile that is presented with little option but to be enveloped by its stressor. Also, despite the occurrence of sometimes severe pressures (for example, drought and starvation), the natural environment possesses a degree of non-stressing normality and familiarity (such as the diverse stimuli mentioned previously) that provides an important component of security to an animal. A major stressor in nature, regardless of intensity, may be viewed as a single aberrant event in an otherwise stable scheme, which is arguably very different from a captive environment where the various inputs may be completely inadequate, incorrect and essentially intolerable. In other words, in the wild, enough of life is 'going right' to keep stressors in context and to alleviate distress. An important exception involves anthropogenic invasion of natural environments, which can impose extraneous stressors into otherwise normal

systems, including those where animals are bound by specific resources and thus cannot relocate.

19.2.4 Stress and Natural Rhythms

Reptilian life in nature, as with all animals, is strongly influenced by solar, lunar and other environmental cycles. It is conceivable that there exists particular sensitivities in the context of a circadian rhythm that are of special importance in the issue of stressors and stress in nature and in captivity. In nature, an animal may experience a number of acute stressors; for example, a predatory conflict or occasional fall during the course of its daily activity pattern (Oliveira et al. 2010). Indeed, several such events could occur in a single day. In these situations, exposure to individual stressors probably lasts only a few seconds or minutes. In predatory encounters, the victim either is killed or escapes and, in serious falls, an animal either soon dies of its injuries or may be met by scavengers. The chances are, though, that one way or another, an acute stress experience will cease within a day. Where stressors (or perhaps just certain types of stressor) and stresses persist over much longer time periods, then the factor arguably becomes an extra-routine pressure, and potentially it is biologically perceived by the organism that the challenge is more involved than a daily problem and so has inherently different demands. Some activities, such as seasonal male-to-male combat, may incorporate prolonged, repeated stressors. However, associated stress, being largely part of voluntary actions, presumably occupies a contextual position, i.e. subject to hormonal-related drives that balance favourably against pressures of combat.

No matter how stressful, the end of an animal's day is usually concluded with a period of necessary quiescence and sleep, and the individual probably moves into the next day in a more or less unstressed state. Sleep (and rest) may be a major part of such stabilisation (Warwick 2023) and to date, the relatively few studies of sleep in reptiles indicate that these animals do indeed sleep (Libourel and Herrell 2015; Shein-Idelson et al. 2016). However, in captivity, it is conceivable that disturbance of rest and sleep may compound the already compromising effects of captivity-related stressors (Mancera and Phillips 2023; Warwick 2023).

In captivity, diverse stressors are present that simply do not fit in with either acute or chronic stressor patterns occurring in nature. For example, a victim of a predatory encounter will not be held captive in highly restrictive conditions for days; whereas for transportation, storage, sometimes display, and even prior to research processing, captive reptiles are often confined in cloth bags or small containers, and the stressful episode may be drawn out beyond a daily rhythm. These sorts of stressors are very common and present a worrying problem in the captive environment. Apart from facing artificial, multi-faceted and possibly abnormally severe stressors in captivity, the cage environment usually lacks opportunities for normal interactions that, in nature, may reduce potential impacts of stressors and stress.

It could be argued that animals which, for example, sustain painful injuries from a predatory encounter but nevertheless escape may suffer negative physical or

psychological effects lasting more than a day. However, either the consequences will quickly be fatal or the victim will be able to return to normality because its environment remains viable for normal interaction. There are some situations in nature where an acute stress problem exceeds beyond the day and prevents animals from returning to their normal patterns (e.g. shelter places, feeding routines and so on). An animal that falls into a crevice or trap may face this situation. Studies of such unfortunate problems appear elusive, but from personal observations and some anecdotal accounts of captive animals, trapped reptiles often battle for extended periods of time trying to free themselves. This comparison and analogy may offer a perspective on the searching behaviour seen in caged reptiles—animals that are literally trapped and confined, behaving as they might had they fallen into a ditch except that, instead of either escaping or deteriorating and dying due to dehydration or starvation, in captivity, they are caught half-way between the two.

Consequently, it is possible that periods of stress that persist beyond one day may dramatically affect the way in which stressors are perceived by animals and impact accordingly on stress effects. Extra-circadian stress may form a marker between acute and chronic stress and pose a particularly significant threat to wild or captive reptiles. Of course, circadian rhythms in captivity are not usually compatible with those in nature. The issue has various connotations in husbandry, but in this stress context, it obviously interferes greatly with estimating the start and finish of a reptile's normal day, and so the establishment of any pattern of extra-circadian stress.

19.2.5 Stress Measurement Through Disease and Mortality Data

There are various ways of recognising and assessing stressors and stress. These may be physiological (see Gangloff and Greenberg 2023; Greenberg 2023) or behavioural (for example, Warwick 1990a; Martínez-Silvestre 2014; Mendyk and Augustine 2023; Warwick 2023). However, whilst observations and evaluations of stressors and stress are possible using these approaches, analyses of historically collated data are generally not possible because records of, for example, abnormal captivity-stress-related behaviours are not regularly gathered. More routine collations of data are maintained in veterinary documentation associated in particular with formal zoological and laboratory facilities. These data might add a useful, although not necessarily comprehensive, measurement for maladaptation and stress in animals based on the type and frequency of disease outbreaks.

Abnormally high incidence of disease, pathological conditions associated with normally innocuous sources, and non-specific degenerative manifestations may be related to captivity stresses and a compromised immune response. This would seem to be the case with crocodylians (P.C. Arena, pers. obs.). Indeed, this perspective is related to Cowan's (1980) evaluation of 1200 captive reptile mortalities. Other studies have been conducted that collate results of necropsies in captive reptiles and examine the aetiologies of mortalities. For example, Bosch and Frank (1983) analysed post-mortem data for 6591 reptiles (and 583 amphibians) and concluded

that significant pathological changes were found in the liver and intestine in reptiles other than snakes. In snakes, the intestinal tract was most frequently affected. Bacteria were important direct or indirect contributors to disease and fatalities. Parasites played a less significant role, but were present in 30–50% of cases. Although a large number of the instances of disease and death were probably attributable to particularly poor husbandry, many were implied as occurring in reputable establishments. Scheinert et al. (1992) analysed 307 reptile cases and concluded that the most common causes of mortality were pneumonia, parasites and overall poor husbandry. Interestingly an investigation of the intestinal microbiota of farmed Australian saltwater crocodiles (*Crocodylus porosus*) detected high levels of pathogenic bacteria that had no apparent impact on the host's health, although the authors concluded that this required further investigation (Willson et al. 2019). Whilst it is not possible to draw stringent conclusions from these data, which are based on diverse and often highly specific histories, findings of these studies are largely consistent with opportunistic microorganism and parasite infections, and therefore, suppressed immune competence is implicated.

19.2.6 Emotional Stress

Some methods of stress assessment offer strong indicators of a particular state—for example, measurement of the adrenal response in a physiological approach, hyperactivity in a behavioural approach, or by examining physical condition and growth. It is also worth considering that animals showing neither physiological nor behavioural indicators of stress and normal growth may still be experiencing distress (see Gangloff and Greenberg 2023; Greenberg 2023; Warwick 2023). Numerous studies have shown that the reptilian neuroendocrine system is essentially similar to mechanisms within other vertebrates (see Gangloff and Greenberg 2023; Greenberg 2023), and indeed, behavioural indicators of stress in reptiles often appear to approximate signs in mammals and birds (see Gangloff and Greenberg 2023; Greenberg 2023; Warwick 2023).

To these examples one could add a human dimension because we share familiar categories of stress response and distress. In anthropomorphic terms, most of us probably realise that humans may endure chronic stress related to poor environments and unsatisfactory lifestyles for much of their existence, and similarly so, where incarcerated in prisons. It might be appropriate to regard such states as also involving emotional stress. Despite such unfortunate states, people feed regularly, grow well, interact diversely, and often apparently normally and, where relevant, reproduce successfully, activities that are frequently perceived as signs of an absence of significant stressors, and often the mere presence of one of these signs is thought a significant indicator that all is well. However, in reality, this is routinely far from the case and it is reasonable to assume that, whilst the variable may be difficult to trace, reptiles also suffer emotional stress, an indicator of which is acutely elevated body temperature, manifested through basking behaviour (Cabanac and Gosseli, 1993;

Kreger 1993; Cabanac and Bernieri, 2000). Among current tools proposed to assess such scenarios is Benn et al.'s (2019) 'Welfare Quality® Protocol'.

19.3 Pain Perception and Assessment Sensitivity

Reptiles have the capability to detect and respond to painful stimuli and appear to possess established mechanisms by which this may be achieved (Loew 1987; Liang and Terashima 1993; Crowe-Riddell and Lillywhite 2023; Lillywhite 2023). In humans, pain assessment can be aided by verbal communication. However, because this is not possible in most animals, it is their behavioural reactions to pain that must be used (Carstens 1987). Pain-related behaviour is often easily recognised in domesticated animals, but subtle pain-related signs may become increasingly difficult to recognise and routinely evaluate as one examines non-domesticated animals related more distantly to mammals. With this in mind, it is even more crucial to practise preventive care, in particular through observational vigilance for genuinely normal behaviour and physical condition, because it may be unclear when an animal is experiencing harmful and potentially damaging conditions. Although this approach is common sense, too often it is not common practice.

19.3.1 Stress-Induced Analgesia

Stress-induced analgesia may function to reduce pain sensation and motor responses in injured animals that use behavioural strategies such as tonic immobility or death feigning (voluntary thanatosis) (Purkayastha and Das 2010; Sannolo et al. 2014; Castro-Exposito et al. 2017) to escape predators. It may also function to prevent further damage during recovery from injury (Carstens 1987). During predator/prey or aggressive conspecific interactions, stress-induced analgesia may be employed to reduce pain from injury and thus allow the animal to recover and act to continue or engage in appropriate attack, defence or escape behaviour (Butler and Finn 2009; Madin and Madin 2011; Breuning 2018; Gentsch et al. 2018; Van Waeyenberge et al. 2018; Warwick 2019a, b). This issue has been demonstrated in rats (*Rattus* spp.) and, given the similarity in neurogenic response, other vertebrates, including reptiles may have the ability to self-induce analgesia in the presence of noxious stimuli. However, the possibility of self-induced pain suppression should not be readily interpreted as a product of conscious convenience in the animal; rather, it is most likely a complex and variable holistic response. Whilst it is believed that some behaviours (e.g. maladaptive stereotypies and related forms) may occur as moderators of stress and pain (Hediger 1964; Broom 1991; Garner 2005), there are no confirmed cases of such stereotypies in reptiles (see Warwick 2023). Furthermore, manifestation of (theoretically) stress-moderating stereotypies should anyway be regarded as biologically desperate responses to human-generated environmental deficiencies that constitute a grave sign of poor husbandry.

19.4 Thermal Factors, Thermoregulation and Light

Temperature is one of the most important factors governing the biology of reptiles (Heatwole and Taylor 1987) (see also Arena and Warwick 2023; Gillingham and Clark 2023; Lillywhite 2023). Although this issue has long been recognised as crucial to the maintenance of reptiles in captivity, it is surprisingly poorly understood. Unlike the thermoregulatory opportunities afforded free-ranging animals, captive reptiles are presented with a narrow and often inadequate range of thermal parameters based very largely on human-estimated requirements. This almost certainly results in reptiles adopting considerable modifications in behavioural routines to attempt to satisfy their thermal needs. Consequently, provision of thermal environments should be appropriately compatible with those in nature to accommodate physiological and behavioural aspects. Inadequacies in artificial temperature regimes probably present significant adaptational problems and undesirable demands on an animal. Here we outline some of the key considerations.

19.4.1 Captive Reptiles and the Thermal Environment

Too often, reptile keepers have not considered the natural thermal behaviour of reptiles when designing artificial conditions and, just as importantly, the thermal properties of the natural environment itself (Avery 1991; Cabanac and Gosselin 1993). Data are needed regarding the type, thermal attributes and position of heat sources in captive situations (see also Arena and Warwick 2023). In artificial conditions, a form of ‘thermal confusion’ may arise because environments rarely provide the diversity and range of micro-climates and microhabitats required for adequate site selection and temperature exchange. Although numerous heat sources are available nowadays, these are almost certainly incompatible with the natural thermal environment and provide only elementary temperature variation. Small enclosures present particularly poor thermal ranges, and it seems reasonable that artificial environments that are incapable of allowing proper thermal gradation should not be used, even for short-term instances. Furthermore, species-specific seasonal changes in thermoregulatory requirements are rarely taken into consideration, particularly with captive individuals that are perpetually on display to satisfy exhibitory requirements. These seasonal requirements should also take into account the provision of adequate cover and substrate depth, because many heliothermic lizards (e.g. *Tiliqua* spp.) will regularly seek shelters or burrows in response to varying ambient temperatures and activity levels (Kerr et al. 2003; Kerr and Bull 2004; Mendyk and Warwick 2023).

Also, in the case of heliotherms in particular, the common thermal gradient design may have to be replaced by cages of a greater magnitude with heat sources that will allow the entire body to be bathed by heat (directly via radiation and reflection and also via conduction and convection) and additional cooler areas for shuttling between, including between land and water (Terpin et al. 1979), and between surface and shelter (exposed and unexposed) (see also Arena and Warwick 2023). Thermal

matters are complicated further because there may not be a clear distinction between the various thermal requirements of reptiles, and they may utilise a combination of methods of regulating heat depending on a variety of factors. For example, it has been shown that large reptiles depend primarily on radiant sources of heat for thermoregulation, whereas smaller species tend to rely on convective ones (Porter and Gates 1969; Terpin et al. 1979). In addition, larger individuals and species can take advantage of greater thermal inertia, which consequently can have a major impact on heating and cooling rates. The impact of body size on thermoregulatory requirements has been investigated further in some of the largest reptiles (crocodiles), where large size tends to render typical reptilian shuttling behaviour ineffective as a means of making rapid changes in body temperature (Grigg et al. 1998). Instead, certainly in *Crocodylus porosus*, daily temperature variability decreased with increasing body mass (Grigg et al. 1998; Seebacher et al. 1999).

Basking periods may be important indicators of thermal provisions; if an animal remains in a heating or cooling phase for prolonged periods, this may indicate difficulties in thermoregulation and maintaining a preferred temperature. Furthermore, thermal extremes or sudden temperature changes (even a single event) may be deleterious to health, although adverse consequences may not become apparent until perhaps days or weeks after its occurrence (Lance 1992). This thermal shock factor has very important implications for reptiles that are transported in the cargo holds of aircraft and indeed, many storage, transport and other situations where species-specific temperature requirements may not be met precisely.

In conclusion, the subtleties of natural thermal factors and thermoregulation have great implications and consequences for reptile husbandry, not only for long-term captives in zoos and elsewhere, but also for animals under short- and medium-term conditions where naturalistic ranges of temperature and corresponding behaviours are not available or permitted.

19.4.2 Thermal Burns

An example of apparent, but almost certainly misunderstood, physical insensitivity and poor thermal environments concerns thermal burns, which are common in captive reptiles (Gartrell et al. 2019), and which occur when animals come into direct contact with heat sources whilst attempting to raise their body temperature to preferred levels. The general problem may be exacerbated somewhat by ambient temperatures that are too low, and which result in animals being forced to raise their body temperature through extreme proximity to heat sources (J.B. Murphy, pers. comm.). Thermal burns may also result from inappropriate heat sources or exposure to high-intensity/inappropriate wavelengths of ultraviolet radiation (Hellebuyck et al. 2012).

Damage from thermal burns ranges from minor lesions and scarring of the skin to extensive injury such as fusion of the eyelids or burns that extend deep into the body tissues (Frye 1991a). In addition, thermal burns may result in erythema, necrosis, delayed healing, and may become secondarily infected with pathogenic bacteria or

fungi (Gardiner et al. 2009; Baines 2010; Hellebuyck et al. 2012). The first report of damage to the eyes of captive reptiles linked the appearance of lesions on the eye spectacles of gold-striped geckos (*Woodworthia chrysosiretica*) with the placement of ceramic heating bulbs (Gartrell et al. 2019). In this study, the integrity of the spectacles was damaged in terms of ulceration, perforation and mycotic dermatitis (the latter possibly due to inadequate maintenance of temperature and humidity) (Frye 1991a; Warwick et al. 2013; Gartrell et al. 2019; Hollwarth 2019).

These injuries and their resulting complications may lead to permanent defacement, disability or death. In addition, although light and heat sources are available that approximate the range of spectra present in solar radiation, the mere proximity of the source to the reptile may be damaging to ocular tissue, particularly in the case of fossorial, crepuscular and nocturnal species (which are likely to be thigmotherms—see Arena and Warwick 2023). Indeed, ultraviolet b (UV-B) lamps of inappropriate wavelengths have been associated with major eye and skin damage and even death in reptiles (Gardiner et al. 2009). These lamps are commonly employed to raise level of vitamin D3 and stimulate metabolism and reproduction in reptiles (Burger et al. 2007), yet there exists little empirical data on the natural UV exposure of reptiles and consequently, guidance on adequate provision of UV requirements in captivity are sparse (Baines et al. 2016). However, a recent study determined that UV-B lamps are hazardous for reptiles and ineffective in achieving plasma levels of vitamin D comparable to free-living bearded dragons (*Python molurus bivittatus*) (Diehl et al. 2018). On the other hand, Bos et al. (2018) used UV-B radiation to raise levels of plasma vitamin D in Burmese pythons (*Python molurus bivittatus*), but stated that further investigations are required in order to determine whether these raised levels have health benefits to these and other species of snake.

The point of particular interest here is that when it comes to thermal burns, individuals may appear to be oblivious to gross trauma during the period of damaging injury, and in fact, insensitive to pain. One current view is that these burns arise after an animal has rested against an inactive heat source, which is then activated and heats up rapidly, causing tissue and presumably local neural damage (Frye 1991a). Anecdotal accounts suggest that reptiles also settle on already active heat sources and then suffer burns. We propose that a major reason for this behaviour is threefold. First, a large reptile may not be able to attain an optimal body temperature from a small intense heat source such as a lamp. Second, thermal provisions in captivity fail to simulate adequately the thermal diversity of the natural environment. Finally, a contributory factor may be the variation in the thermal perception of different areas of the reptile body. For example, recent investigations of nociception capabilities in reptiles using thermal stimuli demonstrated that the dorsal integument was less sensitive to temperature detection than the ventral surfaces of the feet and that reptiles may vary in their responses between thermal and other noxious stimuli (Sladky et al. 2009; Couture et al. 2017).

In nature, the thermal requirements of, for example, heliotherms are satisfied by a radiant solar source, which bathes the entire animal with heat. However, the efficiency with which a body absorbs warmth depends on not only its own properties,

but also other factors, including the intensity of the heat source, the position of the body with respect to the heat source and the proximity and properties of other reflective surfaces (Geiger 1959). Thus, a thermally receptive body is subject to thermal inputs of a multidimensional and heterogeneous nature. Different regions of a reptile's body have different absorbency spectra and thus different heating rates (Heatwole and Taylor 1987). In captivity, often the only source of heat available is one or two small, and usually intense, heat lamps or floor heaters. In order to raise their body temperature, reptiles move toward a heat source and bask. Especially where large reptile species and individuals are involved, with associated slower blood circulation (Coulson and Coulson 1986), and thus heat dispersal, these animals must attempt to raise the temperature of the entire body using primarily diminutive heat sources. Thermal absorption is attempted whilst continually losing warmth from body surfaces that are not exposed to the heat source and that may, indeed, be in contact with cooler surfaces that conduct heat away from the animal (see also Arena and Warwick 2023).

Compensatory behaviour may include moving closer to the heat source, whereupon the peripheral nerve endings are damaged and desensitised. Once this occurs, the reptile moves closer still and eventually contacts the heat source in an attempt to raise its body temperature to an optimal level, a point it may never achieve. Thus, an unnatural thermal environment and related 'biological confusion' (analogous to an ecological trap, whereby the reptile's natural ability to assess the quality of its environment become compromised by novel conditions [Dwernychuk and Boag 1972]) may result in thermal burns. Clearly, more data are needed to clarify the reasons behind this aberrant behaviour, especially in consideration of body size and the associated heating requirements of reptiles. If this hypothesis were supported, heliotherms of a small body size in particular, would be less likely to suffer thermal burns because a heat lamp is, to them, a relatively expansive source that may more effectively saturate their bodies entirely. Related considerations include the fact that large lizards are more reflective of solar radiation than smaller individuals (Norris 1967), and that they heat and cool at a slower rate as a result of a low ratio of surface area to volume. Snakes, by the very nature of their morphology, may be compromised by inadequate thermal provision.

Of key interest is that thermal burns in snakes are commonly seen in immunosuppressed pythons (A. Martínez-Silvestre, pers. obs.). An interesting clue is that the ventral skin may be contaminated with the animal's own faeces, which consequentially causes infection, with or without high temperatures. Such immunosuppression can be related to poor husbandry, including high temperatures that—although insufficient to burn the skin—may leave the skin at greater exposure to infection. Thus, in these cases, although the skin may bear the appearance of a thermal burn, the sign may actually be an indicator of husbandry-associated stress.

19.4.3 Light and Photo-Invasive Environments

Because photoperiods are integral cyclic influences on the biological responses of an animal these, to an extent, control various physiological and behavioural parameters. In many captive situations, reptiles are provided with a single combined source of heat and light. These may be operated manually or automatically set to particular light and thermal periods—which may not correspond with natural conditions. Unfortunately, in the captive environment, photoperiods are often based around convenience for keepers rather than natural patterns for the reptiles.

Apart from obvious physiological and behavioural disruptions brought about by unnatural photo and thermal periods, it is also suggested that incompatible periods, and especially prolonged exposures to light, are probably a significant stressor for captive reptiles (Warwick et al. 2018a). Photo-invasive environments may also be highly disruptive on rest and sleep quality (see Arena and Warwick 2023; Mancera and Phillips 2023). Consequently, it is imperative that animals are always provided with suitable hiding places where individuals may avoid light at any time, as well as ensuring normal periods of light and dark.

19.5 Circadian Rhythms and Nocturnalism

Circadian rhythms are highly conserved biological phenomena with a circa-24-hour period. These phenomena allow organisms to adapt to the 24-hour light-dark cycle on earth and control a variety of physiological and biochemical processes in life forms as diverse as vertebrates, plants and cyanobacteria (Sun et al. 2019). There are broad similarities between the circadian clocks of vertebrate classes, and the genes regulating this process are remarkably conserved (Sun et al. 2019). Reptiles exhibit circadian rhythms of feeding, metabolism, egg hatching, sleep and thermoregulation, as well as locomotor and burrowing behaviour (Norris and Kavanau 1966; Heckrotte 1975; Blem and Killeen 1993, Lutterschmidt et al. 2002; Roe et al. 2004; Nash et al. 2015; Ping et al. 2016). The circadian clock of reptiles is contained within the retina, pineal and parietal eye and is multioscillatory in nature (Tosini et al. 2001). Unlike mammals, the pineal gland is a key part of the circadian system of reptiles (Tosini et al. 2001).

Although there has been little research on the effects of circadian disturbance in reptiles, there is a large body of evidence from a range of species showing that organisms undergoing experimental disruption of circadian rhythms show impaired biological functioning, increased levels of disease and decreased life spans (Martino et al. 2008; Evans and Davidson 2013). For example, mice housed on a 20 h light/dark cycle underwent changes to metabolic hormones leading to obesity, and a rearrangement of neural architecture leading to reduced executive function and cognitive flexibility (Karatsoreos et al. 2011). In humans and rodent models (where most research has been performed), circadian disruption has been implicated in deregulation of inflammatory responses, increased oxidative stress, immune

suppression, insulin resistance, cancer, mood disorders (including depression-like symptoms) and premature death (Martino et al. 2008; Evans and Davidson 2013).

Circadian disruption in captivity is likely to have a greater impact on nocturnal species whose rhythms are at odds with those of their diurnal human keepers. For example, many snake species are nocturnal, although others are able to exhibit some plasticity in their circadian systems (Degregorio et al. 2014). Nocturnal reptiles, in particular, are often subjected to shifts or reversals in circadian rhythms in captive environments (see also Warwick 2023; Arena and Warwick 2023). Most zoos use reverse light schedules for the exhibition of nocturnal animals, but the effects of this on the physiology, welfare and long-term health of the animals is unknown because virtually no literature exists. However, such practices are likely to be detrimental (McWilliams and Atkinson 1999). As well as a physiologically appropriate light/dark schedule, animals need a gradual shift from light to dark analogous with dawn and dusk to allow physiological processes to adapt; this is also missing even in many interior zoo enclosures (McWilliams and Atkinson 1999). In pet shops and private collections, the lighting schedule is likely to be arranged primarily for the convenience of the keepers, meaning nocturnal reptiles are probably disturbed during the daytime for cleaning and feeding purposes, as well as transfer between enclosures. Very little is known about the effects of circadian disruption and reverse light/dark cycles on reptiles, and, given the prevalence of nocturnal reptiles such as snakes kept in zoos and other collections, this is an area that warrants urgent investigation.

19.6 Growth

Growth often is regarded as a definite indicator of good physical and mental health. However, although a popular perception among many amateur and some professional herpetologists, growth as a positive health sign per se is a gross over-interpretation of condition and overlooks important biological aspects. Often, estimates of optimal growth are based on continuous, fast development. However, optimal growth rates should mean normal growth rates, compatible with conspecifics in nature that have access to appropriate sustenance in the context of evolved energetic considerations. Normal growth may, therefore, be slow and erratic and very different from patterns in captive animals (see Gangloff and Greenberg 2023; Greenberg 2023; Warwick 2023). Indeed, what many keepers view to be good growth may actually be excessive and create pathological conditions (Frye 1991a, b; Mendyk and Warwick 2023; Warwick 2023). Thus, a growing animal may be promulgating disease because of its growth rate.

Even reptiles that do appear to be exhibiting reasonably normal growth rates develop and harbour a diversity of diseases (Frye 1991a). Further, behavioural signs of psychological stress are often identified in reptiles showing apparently normal growth (Warwick 1990a, 2023), and studies involving domesticated animals have drawn similar conclusions (Fox 1984; Broom 1986, 1988; Broom and Johnson 1993). Consequently, the absence of good growth or the presence of abnormal growth may offer reasonable indication of physical and psychological problems,

but, importantly, the presence of even normal growth rates does not confirm an absence of psychological or physical distress. Growth rates, like other potential indicators of condition, should be considered in association with a variety of physical and behavioural signs and not as an independent indicator of holistic health.

19.7 Electromagnetism in the Artificial Environment

Environmental electromagnetism (EEM) is occasionally suggested as a potential interference with an organism's own electromagnetic field (EMF). Mostly, this relates to popular concerns regarding perceived human health hazards from powerful electricity sources such as overhead mains cables, but sometimes reference is also made to domestic convenience facilities. Despite the widespread nature of electromagnetism, data appear to be in short supply and inconclusive, but the issue has attracted some scientific interest and there is now growing evidence of the impact of EEM on wildlife and various ecosystems (Balmori 2009, 2010; Sun et al. 2019).

Reptiles (particularly in the case of intensive collections) are often housed in close proximity to a myriad of electrical maintenance devices, including air, substrata and aquatic radiators, heat lamps, cables, tapes, pumps, filters and other electrical and electronic equipment. Furthermore, since the first edition of this volume, there has been a dramatic increase in the adoption of mobile and wireless technologies, not only for the purposes of mobile communications, but for various forms of temperature and humidity sensors. The impact of EEM on human health still remains contested and controversial (D'Angelo et al. 2015). However, there is a growing body of evidence relating to the effects of EEM on animal tissues from nematodes (Sun et al. 2019) to rats (EL-Naggar et al. 2019). Long-term exposure to EEM has also been linked to the variation in abundance of bird populations adjacent to EEM emitting base stations (Everaert and Bauwens 2007). In addition, Nishimura et al. (2010) found that the agamid lizard *Pogona vitticeps* displayed behavioural changes in response to extremely low-frequency electromagnetic fields (ELF). Individual lizards exposed to ELF for extended periods raised their tails significantly more than individuals in a control group. Because tail-lifting in lizards has been linked to predator defence postures, and intraspecific agonistic behaviours (Cooper 2001; Sherbrooke and Middendorf 2004), the study by Nishimura et al. provided evidence that reptiles may be sensitive to electromagnetic fields.

Interestingly Everaert and Bauwen (2007) proposed that because EEM may also have an impact on invertebrate species, this, indirectly, may lead to reduced numbers in bird species that feed on insects. If this interaction was valid and there is growing evidence that various species of insects are negatively affected by EEM (Balmori 2009), then it can be extrapolated that many wireless emitting repellent devices used in homes and other facilities that house reptiles may have an impact beyond the control of invertebrate pests. Information regarding potential impact of EEM on wildlife is still in its infancy. However, given the evidence to date, and the increasing adoption of, at times, intensive housing conditions of reptiles, there is a need to

investigate the true impact of EEM on the welfare of captive reptiles (see also Mancera and Phillips 2023).

19.8 Reintroductions to Nature

Occasionally, captive reptiles are released or considered for release into nature following either short-term studies, wherein wild animals are held temporarily captive, or where a few formal zoological establishments work toward reintroducing reptiles as a measure to populate an area for perceived conservation purposes. Deliberate releases of, for example, unwanted pets also occur, as do accidental escapes from formal and private collections; a case in point is the Burmese python (*Python molurus bivittatus*), which has successfully invaded ecosystems in the southern US (Engeman et al. 2011). Because the latter of these introductions are already discouraged or guarded against, little further needs to be said here apart from reiterating the importance of minimising wherever possible the chances of such events occurring. In the former categories, and especially zoological establishment projects, species reintroductions have become increasingly popular as a prospect for formal facilities to demonstrate some practical application to conservation endeavours. Whilst protection of biodiversity is not of direct relevance to this volume, the actual and potential impact of captive animal release projects has relevance for the welfare of both of those set free and of those animals in nature with which introduced individuals may come into contact. Thus, not only is the concept of a reintroduction idea of direct significance to the welfare of animals, but also the welfare and success of those released is of direct significance to the validity and success of reintroduction ventures.

Several aspects require consideration in the reintroduction issue. These can be categorised as ontogenetic modification, the consequences of artificial selection, pathological threats and inheritance of acquired characteristics. Associations between these matters, welfare and the integrity of natural populations may be obvious in some cases, and highly obscure in others, but all are important academic, practical, scientific, and ethical considerations. Ontogenetic modification and artificial selection, and related matters of individual competence and potential impacts on nature, have received attention elsewhere in this volume (see also Chiszar et al. 1993; Burghardt and Layne-Colon 2023; Warwick 2023). Some interest is at last being directed towards wider education concerning potential variables in the evaluation of animal competence and minimising the risks of introducing potentially pathogenic microorganisms and parasites into free-living populations (Burke 1991; Dodd and Seigel 1991; Chiszar et al. 1993; Jacobson 1993, 1994; Lepeigneul et al. 2014; Ferrell 2019; Martínez-Silvestre and Franklin 2019). However, we feel that pathological threats are worth re-emphasising here and that the possibility of inheritance of acquired characteristics, whilst often controversial and seldom discussed, merits attention.

The concept of releasing reptiles maintained previously in captive conditions, may involve either ‘soft releases’—where acclimation is provided via in situ

enclosures, or 'hard releases' without acclimation, directly into the target habitat. Soft releases, perhaps due to low-stress conditions, have resulted in greater survival and site fidelity than hard releases. However, one study found no difference in survival between soft release and hard release in terrestrial tortoises (Radzio et al. 2019). Another release strategy, known as 'head-starting', is designed to accelerate growth rate, increase body size and eventually improve survival of individuals from species with an otherwise high juvenile mortality. However, in pursuing these objectives, individuals may be subjected to: *first*, chronic stress during the first months of life (e.g. unnatural diets, absence of brumation period, clinical husbandry conditions); and *second*, acute stress at the time of release (e.g. deprivation of shelter, problems locating water supplies, incorrect identification of conspecifics, the establishment of atypical hierarchies, difficulty identifying prey or predators). Therefore, techniques should be performed according to perceived pros and cons that may beneficially affect the survival of the released reptiles.

Stress under natural conditions can also have evolutionary consequences. For example, the symmetry of turtle shells can develop in ways that allow individuals to self-right more easily if turned upside-down, as has been observed in Herman's tortoises (*Testudo hermanni*) with right-side directional asymmetry (Parés-Casanova et al. 2019). Applied consideration of such developmental factors, for example, through selective breeding for known favourable morphologies, could theoretically increase the survival chances of individuals in release programmes.

Pathological threats to wildlife from organisms carried by former captives present a prospect so serious that we find it incomprehensible that release programmes, without appropriate screening (see below), can be contemplated, let alone considered scientifically and ethically justifiable. Not only is the system through which potentially pathogenic organisms in captivity may infect natural populations well understood, but there already exist cases where captive releases are implicated in wildlife disease (Frye 1991a; Jacobson et al. 1991; Viggers et al. 1993; Cunningham 1996; Kuehler et al. 1996; Martínez-Silvestre and Franklin 2019). Further, it is known that whilst it is technologically possible to screen captive animals for several suspected potential pathogens and possibly their identification, it may not be possible either to establish the presence of latent target organisms and particles or to examine comprehensively for non-target organisms and particles that might be present.

The effect that stress plays on the appearance of diseases in released reptiles after periods of captivity is important; stress and immune status may affect the presence of pathogens in rehabilitated reptiles. Under stressful conditions, shedding of pathogens, including zoonotic agents, may be enhanced (Martínez-Silvestre and Franklin 2019). Applying diagnostic techniques for isolation or detection of specific microorganisms is important and useful prior to considering the release of a reptile. These techniques may include bacterial and fungal cultures, polymerase-chain-reaction (PCR) testing, and antibody testing for reptilian pathogens such as *Mycoplasma* sp., *Mycobacterium*, *Brucella*, *Salmonella* and viruses including ranaviruses, picornavirus, herpesvirus, or paramyxoviruses.

Consequently, it may or may not be possible to establish the presence of some potential pathogens, but it is not possible to conclude that pathogens are absent.

Therefore, any animal released into nature is a potential vector for infection of natural populations. Indeed, there is a worrying chance of introducing non-indigenous (captive-related) morbidities and it is conceivable that the development of microorganism infection and parasitic infestation in screened animals may be prompted by possible physical stress and/or trauma associated with the captivity-wild relocation process itself. Considering the number of actually and potentially pathogenic organisms and particles known to be in circulation among captive reptiles, and the frequency with which animals are exchanged between collections, countries and continents, the risks of infecting wildlife is particularly disturbing. Finally, there is the issue of zoos performing these releases where they are obliged by law to conduct conservation-related activities, but the institution may not actually know how to do this nor have the required budget to conduct appropriate screening (Stagegaard et al. 2018).

19.9 Euthanasia and Killing

Reptiles are euthanised and killed for various reasons, including commercial, research, education and humane issues. From a welfare perspective, considerations for improved quality of life among captivity animals should not overlook the quality of death. Paradoxically, although we have mentioned elsewhere similarities in (for example) neural responses among vertebrates, reptiles possess anatomical, physiological, and behavioural attributes that can make the establishment of consciousness or death difficult, and render some of the typical methods of killing inhumane.

19.9.1 Problems in Establishing Signs of Life and Death

From anecdotal accounts and personal experiences with these animals, attempts to ascertain the point of death by, for example, observations of pupillary responses seem to have variable results. Blink reflexes (corneal and palpebral) are often unreliable indicators of death or even unconsciousness; Warwick has observed situations where freshwater turtles, following partial drownings, showed no pupillary or blink reflexes, but were otherwise relatively well coordinated. Respiration rates are difficult to monitor due to the variability in breathing modes shown by reptiles and the ability of many animals to cease breathing for extended periods with no apparent ill effects. Although the use of electroencephalograph (EEG) or electrocardiograph (ECG) devices to monitor fundamental signs of life, and thus death, have been postulated widely, many situations (particularly commercial) often make their use impracticable. Also, such approaches must be considered guardedly. For instance, anecdotal accounts suggest that EEG devices frequently give inconclusive results in reptiles, due in part to poor electrode connections because of thick integument and bony masses, and to problems of identifying potential residual activity in the brain stem. Because reptiles often continue to show coordinated reactions and behaviours with their hearts removed (as in some live animal commercial and marketplace

settings), cardiac monitoring is clearly not an ideal option for measuring signs of life. Therefore, short of complete destruction of the central nervous system or the clear onset of post-mortem changes, it seems that no completely reliable method of assessment currently exists for determining the occurrence of death. Relatedly, a recently discovered and apparently lifeless animal presents similar considerations for establishing the presence of life or death.

19.9.2 Euthanasia and Killing Methods

It is not possible to provide here detailed recommendations on methods of euthanasia and killing. Instead, the reader is referred to Cooper et al. (1989) and OIE (2019) for a review and recommendations on this issue. However, generally speaking, the preferred chemical means of killing reptiles appear to be pentobarbitone sodium via intravenous or intracoelomic injection (with the animal maintained at an active rate body temperature). The favoured physical means seems to be complete and rapid destruction of the central nervous system. There are certain considerations relevant to this subject that do not appear to have been widely discussed and that we feel should be given particular attention.

19.9.3 Decapitation and Spinal Cord Severance

For many years, decapitation was widely recommended as a ‘humane’ physical method for killing reptiles. However, this technique has been identified as inhumane largely because coordinated signs of consciousness in severed heads often continue for long periods after decapitation (e.g. Cooper et al. 1989; Warwick 1991). This situation probably arises due to the resilience of the reptilian nervous system to conditions of hypoxia and anoxia (Belkin 1963; Cooper et al. 1989), which allows prolonged post-decapitation neural function (Cooper et al. 1989; Warwick 1990b, 1991; OIE 2019). Spinal cord severance (e.g. often used on crocodylian ranches) has also been investigated and is similarly associated with long periods of post-severance consciousness (Warwick 1990b). Thus, spinal cord severance is not considered a humane method of killing alligators (Warwick 1990b; Nevarez et al. 2014; OIE 2019).

Some commentators appear to regard decapitation preceded by anaesthesia as an acceptably humane method, based on the assumption that animals should be completely oblivious to the physical trauma. However, evidence derived from EEG evaluation of rodents (Klemm 1987) suggests that this may not be a reliable assumption because decapitated heads from pre-anaesthetised animals showed signs of regaining consciousness. It is suggested that the massive afferent bombardment resulting from the physical severance provides sufficient stimulus to overpower the effects of chemical agents. It is not unreasonable to suggest that this same situation might apply to reptiles, especially in view of the potential for long periods of post-

decapitation consciousness. Consequently, decapitation, even with pre-anaesthesia cannot be regarded as a reliably humane method of euthanasia or killing.

19.9.4 Hypothermia in Relation to Anaesthesia, Euthanasia and Killing

The issue of whether hypothermia (cooling and/or freezing) in reptiles as part or whole procedures relating to their anaesthesia, euthanasia and killing has been discussed for some considerable time. Early assessments recommended against the use of hypothermia due to raised concerns regarding lack of genuine desensitisation attributable to cold and ice-crystal formation causing pain (Cooper et al. 1989). Subsequent similar guidance has followed (e.g. AVMA 2013; OIE 2019). It has also been reasoned that hypothermia may be acceptable in some artificial situations based on its natural seasonal and apparently normal healthy occurrence among certain species (Shine et al. 2015; Lillywhite et al. 2017; Nevarez 2019). Others have reasoned that the evidence for cold endurance among certain species in nature is poorly understood and should not be regarded as broadly relevant to practices in captivity (Warwick et al. 2018b), thus recommending against hypothermia for sedation or anaesthesia. Furthermore, not only is it difficult to accurately monitor for signs of consciousness versus unconsciousness in reptiles, but this would be even more true of determinations of nociceptor function (Warwick et al. 2018b). Currently, primary guidance bodies do not recommend hypothermia for general use in reptiles (AVMA 2013; OIE 2019). Arguably, approaches to anaesthesia, euthanasia, and killing that utilise carefully targeted, natural and evolved or holistic principles theoretically offer potentially rational ways to address what are often difficult applied questions. However, it is also important that the line of relevant reasoning develops in which animal welfare resides centrally to it, and protocols do not emerge in which practical convenience overrides meticulous contextualisation of biology and welfare need.

19.10 Occupancy and Post-Occupancy Evaluation

Occupancy and post-occupancy evaluation (O/POE) refer to the observable forensic assessment of (in particular) an enclosure or area in which animals live, or recently occupied, in order to gain insight into relevant activities, such as visible tracks or indentations in substrate that may indicate behaviour patterns. The term stems from ‘post-occupancy evaluation’, which has long been used in zoos and other major facilities (Shettel-Neuber 1986; Maple and Finlay 1987; Wilson et al. 2003; Kelling and Gaalema 2011; Tingey 2012). Occupancy/post-occupancy evaluation is potentially helpful in determining what facilities in an environment are or are not being used, and generally, what levels of activity may be present when continuous observation is impractical. Therefore, O/POE can be a valuable tool in animal welfare.

In reptiles, key O/POE signs are detritus on transparent boundaries—indicating potentially problematic and stress-related interaction with transparent boundaries (ITB) behaviour; substrate depressions or disturbances adjacent to boundaries—indicating exploratory and escape attempts; substrate depressions adjacent to air vents—possibly indicating poor ventilation; substrate depressions adjacent to shaded areas—possibly indicating photo-invasive environments; excessive liberal dispersal of senescent skin or faeces—indicating poor hygiene management; absence of substrate tracks or disturbance of furnishings (e.g. foliage)—indicating disuse of provisions, sedentarism or hypoactivity; excessive markers of activity proximal to a heat source—indicating a poor thermal environment or hyperbasking and excessive markers of activity proximal to a cool area—indicating a poor thermal environment (see Arena and Warwick 2023; Warwick 2023).

19.11 Human–Animal Interactions and Relationships

Claxton (2011) suggested that all animals begin with a fear of humans, and an individual's interactions with humans can exacerbate or mitigate this fear. For livestock, gentle handling is widely considered a positive stimulus (de Passille et al. 1996; Hosey 2008), and positive human-animal relationships have been described as crucial for good welfare (Hemsworth 2002). Positive human-animal interactions have also been reported to improve the welfare of birds, as well as primates and other mammals living in zoos (for review, see Hosey 2008). However, there is less consensus that human-animal interactions are beneficial for reptiles (Warwick et al. 2011).

A few studies have revealed responses suggesting that handling interactions can be neutral for—or even improve—welfare. For example, holding and manipulating bearded dragons (*Pogona vitticeps*) resulted in decreased hiding (Cannon et al. 2002) and gentle handling of leopard geckos (*Eublepharis macularius*) increased exploration behaviours and behavioural diversity (Bashaw 2017). However, most studies find human handling of reptiles results in physiological (e.g. Bailey et al. 2009) and behavioural (e.g. Agha et al. 2015; Acaralp-Rehnberg 2020) changes indicative of stress, even for normally docile species. For example, Stockley et al. (2020) found handling of bearded dragons increased tongue-flick rate, suggesting stress. Also, it is worth bearing in mind that handling by humans is widely used as a stressor for reptiles in ecological and physiological studies (Broom and Johnson 1993; Stockley et al. 2020).

For mammals, the sex of the handler (Sorge et al. 2014), the type and consistency of handling (Gourkow and Fraser 2006), and the individual animal's previous experience with handling (Hosey 2008) can all affect the animals' perception of handling, and therefore its welfare (Waiblinger et al. 2006; Whitham and Wielebnowski 2013). Reptile handling procedures can be deconstructed into a variety of elements that may or may not be present in any particular handling protocol, including exploring a novel environment (as in Hoopes et al. 2000), enclosure in a bag or bucket (as in Lance et al. 2004), physical restraint or

immobilisation (as in Kalliokoski et al. 2012), repeated blood sampling (as in Wack et al. 2008), forced exercise (as in Trompeter and Langkilde 2011), and inversion (as in Cabanac and Bernieri 2000). Each of these elements likely has a different potential for causing a stress response. For example, inverting sheep for shearing is more aversive than shearing them whilst restrained upright (Rushen 1996). Work is underway in the laboratory of the author (MJB) to identify which elements most reliably predict stress responses and provide guidance on how to most efficiently produce or avoid handling stress in reptiles. Interactions with humans may also provoke different reactions in different individuals. Indeed, several studies (Bowers and Burghardt 1992; Mehrkam and Dorey 2014; Gibson 2015) have identified individual differences in reptiles' responses to human interactions, and Bashaw and McMillan (2018) found that some leopard geckos actively avoided opportunities for gentle handling whilst other individuals did not.

Repeated interactions with humans are an inevitable consequence of captivity. Hosey and Melfi (2014) explained how human–animal relationships develop based on the history of these interactions. The form of these relationships will depend on whether the animal perceives the interactions as positive, neutral, or negative and to what extent the animal can differentiate individual humans. As an illustration, Wielebnowski et al. (2002) found that having fewer keepers who each spent more time with clouded leopards (*Neofelis nebulosa*) was associated with lower faecal glucocorticoid hormone metabolites; they suggested the formation of relationships with keepers reduced stress. Whilst human–animal relationships have not been well studied in reptiles, Burghardt and colleagues described how captive Aldabra (*Aldabrachelys* spp.) and Galapagos (*Chelonoidis* spp.) tortoises (*Chelonoidis carbonaria*; Bowers and Burghardt 1992), green iguanas (*Iguana iguana*; Bowers and Burghardt 1992), and monitor lizards (Burghardt 2013) differentiated among individual humans, seeking interactions with familiar people and exhibiting fear-related behaviours to unfamiliar ones.

Although the World Association of Zoos and Aquariums (WAZA) places choice for animals at the top of its welfare pyramid (Mellor et al. 2015), and the opportunity to make meaningful choices is a critical contributor to welfare (Boissy et al. 2007; Whitham and Wielebnowski 2013), captive animals rarely have a choice about whether or how to engage with humans. Hosey (2008) predicted that animals who have some control over their interactions with humans are likely to perceive the interactions as more positive. For example, adding a retreat space where petting zoo mammals could escape from contact with unfamiliar people improved their welfare and reduced human-directed aggression (Anderson et al. 2002). Similarly, positive reinforcement training (PRT), where animals are given a request for a behaviour and desirable responses produce a reinforcer, has been associated with improved welfare in nonhuman primates (Bassett et al. 2003; Laule et al. 2003; Schapiro et al. 2003) and other laboratory animals (Bayne 2002). Paralleling the proliferation of PRT, captive animal facilities are also increasingly moving to 'protected contact' systems in which animals and humans interact only through a barrier and no punishment is used (Desmond and Laule 1991). These systems are perceived as desirable in part because they give the animal greater control over its interactions with humans by allowing choice of whether or not to participate in husbandry activities (Clubb and

Mason 2003; Desmond and Laule 1994). Positive reinforcement training, especially target training, is increasingly being used with reptiles and successful techniques are being shared among reptile enthusiasts through informal means (for example, in social media groups such as Facebook's 'Reptelligence'). However, to date, little published scientific research has explored the effects of PRT on reptile welfare.

19.11.1 Changing Human Behaviour to Improve Captive Welfare

Captive reptiles are, by definition, under the care of humans and are therefore wholly reliant on humans to meet their welfare needs. Whilst there has been some argument that it would be impossible to provide a captive environment that provides sufficient enrichment and stimulation to approximate a reptile's natural habitat (Warwick 2023), it is imperative that reptile handlers endeavour to meet the needs of the animals in their care. There is a wealth of evidence-based advice available on how to better manage captive reptiles, including in this book. Nonetheless, many carers, especially private individuals, may not be engaging in husbandry practices to ensure optimum feasible welfare for their animals, as evidenced by self-reported husbandry conditions (Howell and Bennett 2017; see also Jessop et al. 2023; Mendyk and Warwick 2023), and concerns by veterinarians (Loeb 2018; Whitehead 2018). Educating people by providing factual information alone can have limited success in changing longstanding behaviour (Kelly and Barker 2016; Warner and Forward 2016), so it is necessary to first consider the barriers to behaviour change, and, subsequently, ways to effectively get around them.

Previous research into captive reptile management behaviours has determined an over-reliance on arbitrary or folklore husbandry by reptile keepers (Arbuckle 2013; Mendyk 2018; Mendyk and Warwick 2023). Arbitrary or folklore husbandry is the tendency to engage in a management practice simply because 'it has always been done that way' (Mendyk and Warwick 2023). This approach is perhaps understandable in cases where scientific evidence for appropriate management does not exist, but it is problematic when available evidence suggests that existing practices are potentially harmful. When reptile keepers learn that their current management practices are lacking, and that available scientific evidence suggests changing these practices, not all keepers make these changes, thus poor husbandry persists.

So why do some keepers resist making positive changes? At times, people engage in behaviours that are not consistent with their existing beliefs and attitudes (Festinger 1962; Bennett and Perini 2003). For example, private lizard keepers indicated that taking care of their reptile was one of their highest priorities and that they felt confident in their ability to care for their lizard (Howell and Bennett 2017). In principle, therefore, they should be open to making any necessary changes that would benefit the animal. However, the extent of arbitrary or folklore husbandry present in reptile care suggests that, for some reptile carers, their beliefs and attitudes about the importance of looking after their reptile does not accord with their actual behaviours, which could be detrimental to the animal. There are several possible

reasons for this situation, such as having a lazy attitude towards behaviour change, or the inconvenience associated with learning how to manage a captive animal more appropriately. However, neither of these reasons seem likely in the case of reptile carers who claim to prioritise animal welfare and feel confident to meet their reptile's needs. Instead, other factors may be involved.

According to the theory of cognitive dissonance, when people experience a disconnect between their attitudes and their behaviour, this causes a sense of discomfort (Festinger 1962). In order to alleviate this discomfort, people can either choose to change their behaviour to bring it more in line with their attitudes and beliefs or they can try to justify their existing behaviour (Festinger 1962). When people have already engaged in a dissonant behaviour, they are more likely to justify it, rather than change, because changing would require them to acknowledge that their earlier behaviours were not ideal (Bennett and Perini 2003). In other animal contexts, this dissonance has been found in dedicated, affectionate dog breeders who engaged in painful, medically unnecessary tail-docking procedures on puppies, arguing that it reduced the likelihood of tail injuries in adult dogs (Bennett and Perini 2003). It is possible that many reptile carers who engage in potentially damaging husbandry practices simply struggle to accept that they could be doing more harm than good, especially if they consider themselves to be confident, capable carers, such as those reported in Howell and Bennett (2017).

Even though cognitive dissonance is a barrier to behaviour change, it is possible to implement programs that can effectively change behaviour. According to the theory of planned behaviour, the factors that most influence the intention to perform a behaviour are pre-existing attitudes towards the behaviour, what people believe their friends and family would think of them engaging in the behaviour (i.e. subjective norms), and how difficult they believe it would be to engage in the behaviour (Ajzen 1991). The normalisation of poor husbandry practices mentioned earlier in this chapter may be explained by the subjective norms highlighted in the theory. Perceived difficulty can also influence the intention to engage in recommended companion animal management behaviours (e.g. cat containment indoors; McLeod et al. 2015), and this may be the case for reptile keeping, which requires a great deal of equipment and resources. It is possible that some management practices are perceived as too difficult to realistically implement. For example, snake owners may agree with the requirement for minimum enclosure dimensions which posits that a snake's cage should be at least as long as the full length of the snake (Warwick et al. 2019; Arena and Warwick 2023), but they may lack the space to accommodate a larger enclosure.

The theory of planned behaviour has been used as a basis for programs designed to effect behaviour change (Coleman et al. 2000; Hemsworth et al. 2002), but its success in other animal husbandry contexts appears to depend partially on how intensively the program is managed. A successful program has been ProHand, which aims to change livestock handler behaviour in order to improve welfare outcomes for livestock, by changing the negative attitudes that often underlie negative behaviours towards livestock (Coleman et al. 2000). The program includes a 60–90 minute online or face-to-face course with facilitated discussion (Coleman et al. 2000), and

sometimes includes monthly newsletters and a follow-up visit by the researchers between 1 and 3 months after the online course (Hemsworth et al. 2002). The more intensive follow-up showed improved outcomes for stockperson behaviour, as well as livestock welfare and production (Hemsworth et al. 2002). The course without substantial follow-up showed fewer improvements over the long term, although there was a reduction in the proportion of negative behaviours towards the animals (Coleman et al. 2000).

Effecting behaviour change in reptile keepers is not impossible, but it will take more than simply supplying factual information, and may even require generational change in the case of recalcitrant carers who refuse to accept that their practices may be deficient or defective. Effective strategies should focus on improving attitudes towards evidence-based practices, and helping people understand the ways in which they can realistically implement any desired changes.

19.12 Ethical Considerations

Aside from the occasional gecko that wanders freely in to and out of someone's home, reptiles are generally forcibly confined in captivity for whatever purpose appeals to their human captors and rarely for the benefit of the animal. This somewhat blunt description of a common human-reptile relationship underscores the keeper's responsibility to ensure that the best efforts are employed to secure an animal's well-being. Keeper responsibilities also extend beyond reptile welfare to conscientiously prevent harm relating to various matters allied to keeping captive animals, including live prey food welfare, species conservation, ecological protection, invasive alien introductions, and public health and safety (Warwick 2014; Mendyk and Warwick 2023).

A concluding feature of Warwick's (2014) essay on the ethics of reptile keeping asks whether people would accept confining a dog to a vivarium in the home? Most likely, such confinement would not happen, and the captors may face prosecution were they to do so. The common position among reptile keepers that such confinement is acceptable does not reflect lesser biological and welfare needs for reptiles—whether for space, environmental or other provisions and complexities. Rather, it reflects normalisation of certain practices (Mendyk and Warwick 2023) and reflects a widespread erroneous belief that reptiles lack intelligence and emotions, highlighting an anthropomorphic perspective that has been discussed elsewhere in this book (see Doody 2023). It is arguably a most unfortunate scenario that those reptile keepers or enthusiasts and biologists who are, on the one hand, such admirers and advocates of their characteristics are, on the other hand, also their greatest deprivors of freedom and holistic well-being. Good ethics demand that people do the right thing. Therefore, it is imperative that reptile keepers (having incarcerated these animals in their restricted position) continuously question themselves about the welfare of their charges and the rightfulness of their dominion over them.

19.13 Animal Welfare Conclusions

Reptiles, as a result of their unique anatomical and physiological attributes, are one of the most popular vertebrate groups held in captivity. The fact that these vertebrates may remain alive to endure atrocious conditions of captivity, often for comparatively long periods, has led to them being diversely exploited in such phenomena as rattlesnake round-ups, crocodylian ranching, turtle ranching, culinary situations, zoos and other exhibition halls, and museums and research establishments, but perhaps most detrimentally by the pet trade.

When reptile curators and scientists fail to recognise or understand factors affecting the well-being of their charges, they seem unable to presume the benefit of any doubt in favour of animal welfare. For example, the belief that reptiles did not feel or express pain, as at one time viewed, led to them being (and remaining) poorly understood and mistreated. At least as unfortunate is the ingrained perspective, held by many proponents of animal-keeping, that their practices are justified until proven otherwise. Not only is this view imbalanced, but it is also unscientific and unethical. Those who promote matters as serious as confining life forms for their own non-essential purposes can reasonably be requested to justify their position, scientifically and ethically, ahead of their practices. Where welfare is concerned, anything less than this is unwise and unfair.

Our ability to exercise the benefit of the doubt is perhaps the most important consideration for animal health and welfare. Practically, this could mean not participating in or otherwise condoning situations wherein reptiles are kept and where any doubt exists over associated well-being. Arguably, this is not only the most ethical approach, but also the most scientific approach. Scientists, curators and others, particularly those in positions of influence and responsibility, could do far more to increase the acceptability of the individual animal's welfare as being paramount. However, rooting this philosophy in educators is largely dependent on the prospective welfare proponents themselves becoming properly motivated in the first place. We feel that it is reasonable, from both a comparative biological perspective and a necessary ethical perspective, to suggest that one of the most important steps toward greater sensitivity to reptiles and other animals is simply to focus on our many similarities rather than differences and to put ourselves in the position of the utilised subject. With our existing biological knowledge, and with the benefit of the doubt placed on the side of non-human animals, we are then qualified to ask the question: how would we like life in their position?

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