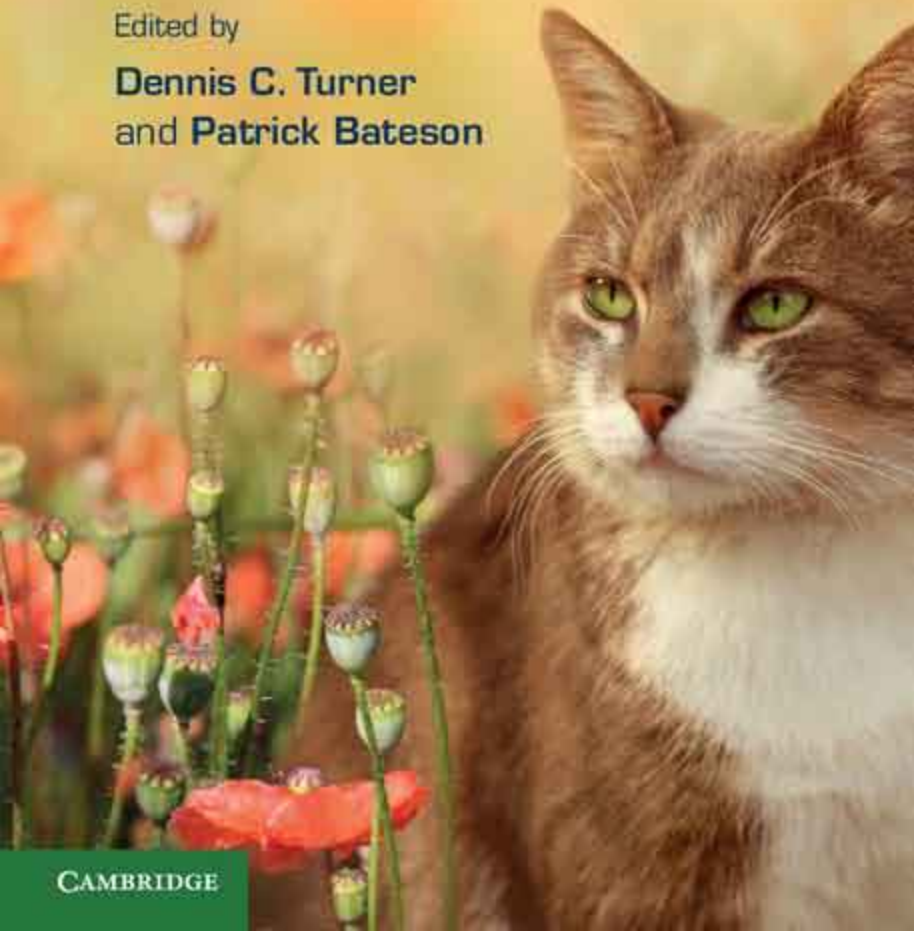
THIRD EDITION

# The Domestic Cat

## The Biology of its Behaviour

Edited by

**Dennis C. Turner**
and **Patrick Bateson**



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## The Domestic Cat

The Biology of its Behaviour

Third Edition

The most commonly kept domestic animal in the developed world, the cat has been a part of human life for thousands of years. Cats have been both worshipped and persecuted over this long period – either loved or hated for their enigmatic self-reliance and the subject of numerous myths and fables.

Highlighting startling discoveries made over the last 10 years, this new edition features contributions from experts in a wide range of fields, providing authoritative accounts of the behaviour of cats and how they interact with people. Thoroughly revised and updated to include information on the basic features of cat development and social life, the history of their relations with humans, health and welfare problems, and the breeding of cats for sale and for show, it is intended for all those, whether specialist or general reader, who love or are simply intrigued by these fascinating animals.

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# Abbreviations

| | |
|---|---|
| AAFP | American Association of Feline Practitioners |
| ACC&D | Alliance for Contraception in Cats and Dogs |
| ACTH | adrenocorticotropic hormone |
| ADCH | Association of Dogs and Cats Homes |
| ASPCA | American Society for the Prevention of Cruelty to Animals |
| BCE | Before the Common Era |
| CAWC | Companion Animal Welfare Council |
| CNR | capture–neuter–release |
| CNS | central nervous system |
| CRF | corticotrophin-releasing factor |
| DEFRA | Department for Environment, Food and Rural Affairs |
| DJD | degenerative joint disease |
| DLH | domestic longhair |
| DSH | domestic shorthair |
| EE | environmental enrichment |
| HPA | hypothalamus–pituitary–adrenal |
| LUTS | lower urinary tract signs |
| MYA | Million Years Ago |
| NCPPSP | National Council on Pet Population Study and Policy |
| NRC | National Research Council |
| PCA | Principal Component Analysis |
| RSPCA | Royal Society for the Prevention of Cruelty to Animals |
| SRS | stress response system |
| TNR | trap–neuter–return |
| TU | tail up |
| VNO | vomeronasal organs |
| WSPA | World Society for the Protection of Animals |

# I

# Introduction

# 1 Why the cat?

Dennis C. Turner and Patrick Bateson

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

The domestic cat is a much-loved and well-known animal. In a number of Western countries it has become even more popular than 'man's best friend', the dog, as is apparent in the pet population statistics presented in Table 1.1. On farms their value as a rodent catcher has been appreciated for centuries. Loved and familiar though they are, cats are still perceived by many people as something of an enigma. They are friendly to people and yet the individual, in Rudyard Kipling's phrase, 'walks by himself', readily accepting the comforts of the human home and yet behaving as though his

**Table 1.1** Cat and dog population figures for Europe[a] and the United States[b] in 2010 and for the United States, Canada, Australia and Japan in 2007[c]

| Country | Cat population in 000s | Dog population in 000s |
|---|---|---|
| Austria | 1744 | 612 |
| Belgium | 1884 | 1330 |
| Czech Republic | 1750 | 3152 |
| Denmark | 673 | 580 |
| Estonia | 244.5 | 174.6 |
| Finland | 665 | 651 |
| France | 10,965 | 7595 |
| Germany | 8200 | 5300 |
| Greece | 595 | 665 |
| Hungary | 2240 | 2856 |
| Ireland | 310 | 425 |
| Italy | 7400 | 7000 |
| Netherlands | 2877 | 1493 |
| Norway | 747 | 452 |
| Latvia | 476 | 269.8 |
| Lithuania | 651.3 | 746.3 |
| Poland | 5550 | 7311 |
| Portugal | 991 | 1940 |
| Romania | 3891 | 4166 |
| Russia | 18,000 | 12,520 |
| Slovakia | 290 | 250 |
| Slovenia | 400 | 240 |
| Spain | 3385 | 4720 |
| Sweden | 1269 | 749 |
| Switzerland | 1507 | 445 |
| United Kingdom | 8000 | 8000 |
| USA[b] | 86,400 | 78,200 |
| USA[c], 2007 | 83,884.3 | 67,085.1 |
| Canada, 2007 | 8300 | 5002 |
| Australia, 2007 | 2450 | 3484 |
| Japan, 2007 | 9788 | 13,179 |

[a] *Source*: FEDIAF, The European Pet Food Industry, Facts & Figures 2010, Brussels.
[b] *Source*: American Pet Products Association, cited on the ASPCA website for owned animals: www.aspca.org/about-us/fay/pet-statistics.aspx.
[c] *Source*: Bateson, A. (2008). *Global Companion Animal Ownership and Trade: Project Summary, June 2008*. London: World Society for the Protection of Animals, WSPA.

independence were total. For many cat owners, their companion animal brings something of the wild into their living rooms. For others, the cat's paradoxical qualities cause mistrust and even hatred. Certainly the cat, more than any other domestic animal, has been as much persecuted as it has been appreciated. It is surrounded by fables and myths. Even many of the people who love cats are inclined to treat them as mysterious. However, in an era in which a great deal has been discovered about the biology of behaviour, many of the cat's former secrets have been uncovered.

While many popular books on cats continue to appear, the accounts of cat behaviour are usually based on the authors' personal experiences with only a few individual animals. Cat owners often make careful observations on their own pets, but most people also appreciate that each cat has a distinct personality and its own idiosyncratic style of behaving. It is difficult and often misleading to make sweeping generalisations about 'The Cat'. Scientists who study larger numbers of animals are also wary of generalising too much. They feel that they must wait until colleagues studying other individuals in other situations also publish their findings. If the results are different (as they often are), the reasons for the discrepancy must be found. However, the body of knowledge has grown sufficiently large in recent years, so that more confident statements can now be made both about the common features of domestic cats and about the origins of their differences.

The first scientific treatise on cat behaviour was published by the late Paul Leyhausen in German in 1956, followed by several editions in that language and partially rewritten for publication in English in 1979. The first review of cat behaviour based fully on the results of many scientific studies and written by the active researchers in the field was the first English edition of this book in 1988, followed by German and Dutch editions. Many of the field studies had not been published previously. We hope and believe that our book awakened the interest of behavioural biologists, ecologists and some veterinarians. Over the following decade, many new studies appeared in scientific journals, and the editors and chapter authors integrated those new studies with those we had included in the first edition into the second edition of *The Domestic Cat* (2000), which also appeared in Japanese in 2006. The present third edition continues to consider the cat in the light of the modern work on its behavioural biology, but we have also included chapters directed at lay people. While the findings and conclusions presented in the first two editions of this book have remained largely valid, we have asked some past authors to update their chapters and solicited a number of new authors who are experts on other topics to join us in preparing this latest edition.

The book begins with a section entitled 'From Kitten- to Adulthood'. Chapter 2 describes the normal pattern of behavioural and physical development, which proceeds in a highly ordered and integrated fashion. Such development is not simply a matter of preparing for adult life, however. The young animal must be able to survive in the year-long period of growth and it must have adaptations for the special conditions it will meet on the way to adulthood. It must also have adaptations for acquiring information and skills that it will need later in its life. Finally, it must be able to cope with variation in the environment. This adaptability is especially important in relation to the development of its predatory behaviour.

Chapter 3 considers normal reproductive behaviour of adult cats, starting off with maternal behaviour during the gestational phase and birth, but especially while raising the kittens. Already in this chapter it becomes apparent how socially flexible cats can be both in the home setting and in outdoor colonies where mothers can nurse kittens of other females of the group which have given birth at about the same time. However, maternal neglect, even cannibalism of kittens, are also topics of concern, especially to cat breeders, and are considered in this chapter. Normal mating behaviour in the cat is described before the more common problems of breeding males and females are discussed.

Communication in the domestic cat, first with other cats then with humans, is the topic of Chapter 4. Olfactory, auditory, visual and tactile communication are all important. The authors build a strong case for the evolution of one new signal from a non-signalling behaviour in domestic cats. Domestication may also have allowed other signals to diversify or develop a secondary function, e.g. in the context of cat–human interactions.

The second section of the book is entitled 'Social Life and Ecology'. Chapter 5 brings together and updates the findings of several chapters in earlier editions of *The Domestic Cat* on social and spatial organisation of cats with outdoor access, their hunting behaviour and effects on prey species. Clearly food (including prey) abundance and distribution play a major role in domestic cat behavioural ecology. However, outdoor colonies are truly structured and functional social groups rather than loose aggregations of individuals around concentrated abundant sources of food. Chapter 6 considers the social behaviour of cats in the human home, a topic that will interest many readers – even though only a handful of studies have been conducted in the home setting. This chapter also includes basic information about the cat–human relationship and the socialisation of kittens toward both conspecifics and other species.

'Cats and People' is the next section of the book. Chapter 7 traces the origins, domestication and early history of the house cat. Although cats have been terribly persecuted at certain times in history, they were also treated with great affection bordering on reverence from the earliest stages of their domestication. Chapter 8 looks at cultural differences in human attitudes toward cats today in select countries from Asia, the Middle East, Europe and South America with different historical and religious backgrounds. The interplay between human and cat personalities is examined in Chapter 9, in which the authors consider the various factors influencing styles of interaction that make each human–cat relationship unique. They examine the question: Why it is possible to socialise with non-human animals from an evolutionary perspective before presenting latest results from an observational study of owner–cat behaviour and interactions.

The next section of the book is devoted to various aspects of 'Cat Breeding and Cat Welfare'. It begins with a chapter defining animal welfare and quality of life and how these can be assessed (Chapter 10). Particular attention is paid to welfare issues in cat shelters and procedures followed in such shelters, before considering how housing in different situations (boarding and breeding catteries, rescue shelters and sanctuaries, research facilities, veterinary practices and private homes) affects cat welfare. Chapter 11 is about

breed and gender behaviour differences in relation to the ancient history and origin of the domestic cat. Indeed, some breeds have an ancient origin as determined by recent genetic analyses. Results of a new study of 15 popular breeds of cats to determine a genetic basis of behavioural differences between breeds are summarised and differences between intact males and females, independently of breed, are considered. Chapter 12 explains the more recent history of cat breeding and showing of cats, explaining how breed standards have developed, how judges are trained and how titles are awarded. Artificial (human) selection is not without consequences for the health and welfare of the animals, of which the cat fancy is becoming increasingly aware. Health and, in particular, the impact of stress on disease and 'sickness behaviours' are the main topics of Chapter 13. Early life experiences, chronic environmental disturbances and environmental enrichment all play important roles in keeping cats healthy and in a good state of welfare. Cats can also develop behavioural problems, the topic of Chapter 14, which tarnish the relationship of their owners to them. The most common problems – inappropriate urination and defecation, urine marking, various forms of aggression, scratching furniture, and eating grass and plants – are explained and suggestions for solutions are given.

Chapter 15 begins the last section entitled 'The Future'. Given the enormous popularity of cats, i.e. the tremendous increase in owned and, unfortunately, free-ranging unowned cats, 'cat population management' becomes a necessity. After explaining 'why', this chapter informs 'how', based upon years of experience, case studies in different countries and a theoretical population model.

Finally, as a postscript by the editors of the book, Chapter 16 demonstrates that while a lot has been learned in the last few years about the behavioural biology of the cat, a great deal more remains to be discovered in the future. Whether or not cats walk by themselves, they still preserve some of their secrets.

# II

# From Kitten- to Adulthood

# 2 Behavioural development in the cat

Patrick Bateson

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

As a cat grows up, its characteristics and behaviour develop with regularity and consistency. Most kittens open their eyes during their second week, for example, and start to eat their first solid food at around one month of age. Cats are also adaptable and modifiable in their behaviour, responding sensitively to changes in their environments. Moreover, they are highly variable in their habits. Some domestic cats spend much of their time hunting, while others seldom leave the comfort of their owner's armchair. Explaining how and why such consistencies and differences arise during development is the main theme of this chapter.

Biology presents many wonders, but one of the most remarkable is how an animal as complex as a cat grows from a single cell. Until recently, the processes involved seemed largely beyond understanding and, even now, much remains to be discovered. Nevertheless, some factual certainties have been self-evident for a long time. Different species in the cat family share many patterns of behaviour in common. The play of the cheetah cub, for example, is strongly reminiscent of the play of a domestic kitten. These 'robust' constancies of development are profound and real. At the same time, every cat is capable of adapting to many challenges posed by its environment. It can cope with disabilities generated by accidents or disease. It can learn to recognise particular members of its species and acquire preferences for particular foods that are available to it. Above all, it is highly adaptable, readily solving difficult challenges posed for it in its life. The plasticity of the cat is as remarkable as its robustness. Here, however, lies a trap for the unwary. It does not follow that two distinct processes can be cleanly separated, one leading to an invariant outcome and the other generating an individual's distinctiveness due to its previous experience over and above its particular genome. If this were true, it might be appropriate to ask the question how much of behaviour pattern is innate and how much is learned or, more generally, how much is genetic and how much is due to the environment? This dichotomy is, however, neither true nor helpful and confuses the understanding of ill-informed writers for the media with real biology (Bateson & Gluckman, 2011).

## Normal development

The time from conception to birth is usually 63 days in the domestic cat (Hemmer, 1979). This is 3–7 days longer than in its supposed wild ancestor, *Felis sylvestris libyca* (Haltenorth & Diller, 1980). The sensory world of the kitten in the first 2 weeks after birth is dominated by thermal, tactile and olfactory stimuli. Olfaction plays a central role in the orientation of suckling. Newborn kittens with no suckling experience searched for the ventrum of lactating mother cats and attached to nipples within minutes (Raihani *et al*., 2009). They did not behave in the same way towards non-lactating females. Olfaction is more or less fully mature by 3 weeks of age (Villablanca & Olmstead, 1979). One-day-old kittens can detect and attempt to move along a thermal gradient, avoiding cold regions and approaching warmth. They can regulate their body temperature to

some extent by 3 weeks of age (Jensen *et al*., 1980). By 7 weeks of age a fully adult pattern of temperature regulation is attained (Olmstead *et al*., 1979). Hearing is also present early in life and is well developed by one month of age. Definite responses to sounds are seen by day 5, orientation to natural sounds by about 2 weeks, and adult-like orienting responses are found in all kittens by the fourth week after birth (Olmstead & Villablanca, 1980).

Kittens' eyes remain closed until around 7–10 days after birth, although the age at which they open ranges between 2 and 16 days (Villablanca & Olmstead, 1979). When eye-opening starts, 2–3 days usually elapse before both eyes are completely open (Braastad & Heggelund, 1984). Under normal rearing conditions, the time of eye-opening varies considerably between individuals. A considerable amount of this variation is explained by four factors: the father's identity (paternity), exposure to light, the kitten's sex and the age of the mother. Dark-reared kittens open their eyes earlier than normally reared kittens; kittens of young mothers open their eyes earlier than those of older mothers; and female kittens open their eyes earlier than males. Most of the variability in the kittens was explained by paternity, indicating strong inheritance (Braastad & Heggelund, 1984).

Visually guided behaviour develops rapidly in the weeks after the eyes have opened. By the end of the third week, a kitten is able to use visual cues to locate and approach its mother (Rosenblatt, 1976). Its visual acuity has improved markedly by one month after birth (Thorn *et al*., 1976), although the fluids of the eye do not become completely clear until about 5 weeks and some improvement in acuity continues until as late as 3–4 months (Ikeda, 1979).

During the first 2 weeks after birth, kittens are relatively immobile and use a slow, paddling gait. Rudimentary walking appears during the third week, but not until 4 weeks of age can kittens move any distance from the nest (Moelk, 1979). By the fifth week they show brief episodes of running, and by 6–7 weeks they have started to use all of the gaits found in adult locomotion (Peters, 1983). Complex motor abilities, such as walking along and turning around on a narrow plank, may not develop fully until 10–11 weeks after birth. The body-righting reaction is present at birth and fully mature by one month. The ability to right the body in mid-air while falling (the air-righting reaction) starts to appear during the fourth week and develops smoothly over the next 2 weeks (Martin, 1982).

Limb-placing reactions develop progressively over the first 2 months, with internally controlled responses present at birth and visually controlled responses developing later, in parallel with the development of the visual system. Some tactile contact-placing is present at birth, while visually guided paw-placing starts to develop at around 3 weeks and is mature by 5–6 weeks (Villablanca & Olmstead, 1979). Teeth start to erupt shortly before 2 weeks of age, and continue until the fifth week. The change from milk teeth to adult teeth starts at about three and a half months after birth (Hemmer, 1979).

During the first 3 weeks after birth, the kittens depend entirely upon their mother's milk for their nutrition, and episodes of nursing are initiated entirely by the mother, who returns frequently to the nest to nurse her kittens (Martin, 1986; Deag *et al*., 2000). Under free-living conditions, mothers start to bring live prey to their kittens from

4 weeks after birth onwards, and kittens may start to kill mice as early as the fifth week (Baerends-van Roon & Baerends, 1979).

Four weeks is also the age at which kittens normally start to eat some solid food and marks the onset of the weaning period (Martin, 1986). As weaning progresses, the kittens become increasingly responsible for initiating bouts of nursing (Schneirla *et al*., 1963; Deag *et al*., 2000).

## How does weaning occur in the cat?

Weaning in the domestic cat is characterised by a gradual reduction in the ease with which kittens can obtain maternal care, rather than by overt maternal rejection. Weaning may be described as the period during which the rate of parental investment drops most sharply (see Chapter 3). Starting at about 4 weeks after birth, mothers make suckling more and more difficult for their kittens, both by avoiding them and by progressively adopting body postures in which their nipples are less accessible. By about 7 weeks after birth, suckling frequencies have generally dropped to a low level, kittens are usually obtaining most of their nutrition in the form of solid food, and weaning may be considered to have finished.

Weaning in the domestic cat is not usually accompanied by aggressiveness on the part of the mother (Bateson, 1994). Nonetheless, the normally tranquil weaning process may sometimes be markedly disrupted if conditions are adverse – for example, if the mother's food supply is inadequate (Martin, 1986).

A number of questions concerning weaning – none of which has yet been fully answered for any species, let alone the domestic cat – therefore arise. What genetic and environmental factors affect the timing and nature of the weaning process? Is it the case, for example, that mothers whose food supply is limited, or who are nursing many kittens, wean their kittens earlier than normal? Under adverse conditions, mothers might curtail investment in current offspring, by weaning them early, in order to preserve themselves for future reproduction (Bateson, 1994). However, the opposite prediction is equally plausible: mothers with large litters or poor food supplies may have to nurse their kittens longer in order to get them to the minimum size and weight at which they can become independent. Or possibly, as conditions become more adverse mothers wean their offspring later, but at a certain point food is so restricted that they abruptly cease caring for their offspring and abandon them, so that they themselves can survive and reproduce later when conditions may have improved. At present, though, all this remains conjecture and badly needs investigation in free-living conditions.

Whatever the precise nature of their effects, naturally varying factors such as the mother's nutrition and the number of kittens she is nursing are likely to have systematic effects on the timing of weaning and its abruptness. The weaning period is a time of major changes for the developing kitten, during which it must make the transition from complete dependence on maternal care to partial or complete independence. If weaning occurs much earlier than normal, how does the kitten adapt, both in behavioural and physiological terms, and what are the long-term consequences? Is it the case that kittens

which are forced to grow up more rapidly than normal, perhaps because their mother's food supply was poor, pay a cost in terms of later behavioural abilities? Here again much remains to be discovered.

By 5–6 weeks of age, voluntary elimination has developed, and kittens are no longer dependent on their mother to lick their perineum in order to stimulate urination (Fox, 1970). Many kittens when placed for the first time on loose earth or the commercially available material used in litter trays will dig a shallow hole, squat, urinate and then cover up the hole (pers. obs.). Weaning is largely completed by 7 weeks after birth (Martin, 1986), although intermittent suckling – without, necessarily, any milk transfer – may continue for several months, particularly if the mother has only one kitten (Leyhausen, 1979).

Many major changes in behaviour have been recorded between 1 and 2 months of age. One month is also said to be about the earliest age at which learned performance based on purely visual cues is possible (Bloch & Martinoya, 1981). However, conditioned responses to sounds are seen by 10 days of age (Ehret & Romand, 1981), and kittens show specific forms of learning – such as forming nipple preferences – shortly after birth (Ewer, 1961; Hudson *et al*., 2009). A predisposition to respond defensively towards large and difficult prey such as rats – a defensive 'personality' – develops during the second month (Adamec *et al*., 1983). By 6–8 weeks of age, kittens have begun to show adult-like responses to threatening social stimuli, both visual and olfactory (Kolb & Nonneman, 1975).

Adult-like sleep patterns have also developed by 7–8 weeks after birth (McGinty *et al*., 1977). Females become sexually mature at between 7 and 12 months of age (Hemmer, 1979). Males usually reach sexual maturity between 9 and 12 months. However, purebred cats of both sexes can become sexually active much earlier. Brain weight at birth is about 20% of adult weight, and reaches the adult level by about 3 months of age (Smith & Jansen, 1977a).

Social play becomes prevalent by 4 weeks after birth (West, 1974; Barrett & Bateson, 1978). In the fifth and sixth weeks, kittens start to crouch while moving towards another kitten and to search for an object that has disappeared; in the seventh week such behaviour is integrated into playful social interaction (Dumas & Dore, 1991). Social play, involving much chasing, continues at a high level until 12–14 weeks, when it begins to decline slowly (West, 1974; Caro, 1981b). Correlations between different measures of social play also break down at the end of weaning, as do correlations between some measures of predatory behaviour (Caro, 1981a). Social play-fighting can sometimes escalate into serious incidents, especially during the third month (Voith, 1980). Certain measures of social play become increasingly associated with some measures of predatory behaviour during the third month. This might indicate that motor patterns come under the control of new motivational systems as the kitten develops, some becoming controlled by the same factors that control predatory behaviour, and others by the factors controlling agonistic behaviour.

Play with objects develops slightly later than social play, as kittens start to develop the eye–paw coordination that enables them to deal with small, moving objects, and its incidence rises markedly at around 7–8 weeks after birth (Barrett & Bateson, 1978), while locomotor play also develops rapidly at around this age (Martin & Bateson, 1985b).

## The social environment

Under natural and semi-natural conditions, cats will form strong social relationships with familiar individuals, usually close kin. From an early age, the mother is recognised and greatly preferred to unfamiliar females. The young also recognise other adults in their own group and readily accept care from them (see Chapter 5). In groups of feral cats and those reared in large outdoor enclosures, the kittens are often allowed to suckle from females other than their own mother (Feldman, 1993). Social relationships such as these, which depend so much on familiarity, are most readily formed in the first 2 months after birth in domestic cats. When the process by which strong social attachments are formed was first described in precocious birds, it was called 'imprinting' because it happens quickly and leaves a long-lasting effect on social preferences. Cats are much less well developed at birth and form social attachments more slowly than do geese or ducklings.

Humans and members of other species may also be incorporated into the social group and responded to with affection if they were encountered by the cat when it was young. Despite a basic ability to respond socially towards people, adult cats and kittens show considerable individual variation in their friendliness towards humans, whether familiar or unfamiliar, and even kittens from the same litter can differ considerably in their friendliness (Turner, 1985).

The mother–kitten relationship is crucial to the kitten's development, particularly in view of the domestic cat's relatively slow development and long period of dependence on maternal care (Deag *et al*., 2000). From the outset, interactions between mother and kittens regulate suckling. During the first 3 weeks after birth, the mother initiates suckling by approaching her kittens and adopting a characteristic nursing posture in which her nipples are easily accessible. At this stage, kittens can orient towards the nest, using olfactory and, to a lesser extent, thermal cues (Luschekin & Shuleikina, 1989). Nest orientation starts to decline during the third week, following eye-opening and the development of visually guided behaviour (Rosenblatt, 1976).

Kittens will suckle from a non-lactating female in the same way as from a lactating female until about 3 weeks of age, which means that milk reward is not necessary for either the initiation or maintenance of suckling. After 3 weeks of age, an absence of milk reward leads to a reduction in the duration of suckling, although the frequency with which suckling is initiated remains unaffected (Koepke & Pribram, 1971). In the absence of their mother, kittens of 12 weeks will suckle from the teats of intact adult males (personal observation). Clearly, suckling is a rewarding activity in its own right, irrespective of whether the kitten obtains milk from so doing.

Later, as the kittens become more mobile, they become increasingly responsible for approaching the mother and initiating suckling. In the later stages of the weaning period, towards the end of the second month, the kittens become almost wholly responsible for initiating suckling and the mother may actively impede their efforts by blocking access to her nipples or by removing herself from the kittens' proximity (Martin, 1986; Deag *et al*., 2000). The increasing role of the kitten in initiating suckling develops in close parallel to the kitten's improving sensory and motor abilities.

Kittens which have been reared since birth on an artificial brooder are perfectly capable of suckling from a brooder nipple, but fail to suckle when given access to a lactating female because they show inappropriate social responses to her (Rosenblatt *et al*., 1961). Kittens which are artificially separated from their mother much earlier than normal (at 2 weeks of age) subsequently develop a variety of behavioural, emotional and physical abnormalities (Seitz, 1959). They become unusually fearful and aggressive towards other cats and people, show large amounts of random and undirected locomotor activity, and learn less well.

The importance of social relationships in the behavioural development of cats is likely to have a considerable effect on their personalities (Hudson *et al*., 2011; see also Chapter 9). It is clearly seen in the development of predatory behaviour. Under natural conditions, cat mothers gradually introduce their young to prey, providing them with a series of situations in which their developing predatory skills can be expressed. Early on, the mother will bring dead prey to her young; later she will bring live prey and release the prey near the kittens, intervening only if the kitten starts to lose control (Leyhausen, 1979). Rather than 'teaching' her kittens to catch prey, the mother creates situations in which their own responses will lead them to acquire behaviour that serves to increase their chances of survival and reproduce successfully.

The predatory behaviour of cat mothers is beautifully meshed with the improving capabilities of her developing kittens and, as their predatory behaviour develops, so hers declines. In the short term, the mother's responses to prey which she has brought back to the nest are finely tuned to her kittens' responses. The longer the kittens pause before interacting with the prey, the more likely the mother is to attack the prey, for example. Kittens show increased rates of predatory behaviour in the presence of their mother, and the mother's behaviour tends to lead the kittens to interact with prey (Caro, 1980c). When dealing with live prey, laboratory studies suggest that kittens tend to follow their mother's choice. For example, kittens usually killed the same strain of rat that they had seen their mother kill (Kuo, 1930).

Social experience when young plays an important role in determining the range of stimuli eliciting predatory, as opposed to social or fearful, behaviour. In a pioneering set of experiments, Kuo (1930) raised kittens and rats together in the same cages. Kittens raised with rats never killed rats of the same strain when they grew up, although some would kill rats of a different appearance. The implication of Kuo's results was that kittens whose social companions during early life were rats formed social attachments to rats, inhibiting later predatory responses to them. However, when given the opportunity to form social attachments to other kittens as well as rats, other kittens were preferred. Kittens raised both with siblings and rats formed clear social attachments to their siblings. Nonetheless, these kittens did show a distinct tolerance of rats and a reduced predatory response towards them, although some eventually became rat-killers (Kuo, 1938).

Willingness to try new foods, and preferences for particular types of food, also appear to be strongly influenced by the mother. Kittens that were presented daily with a novel food, tuna or cereal, while their mother was present started to eat the new food on the first or second day of exposure (Wyrwicka & Long, 1980). However, kittens which were presented with the novel food while on their own did not start to eat it until about

the fifth day of exposure. The readiness of a kitten to take novel food is, of course, likely to depend on how long it has been deprived of food as well as on the range of its previous experience.

Mother cats were trained to eat banana or mashed potato and their kittens' food preferences were tested (Wyrwicka, 1978). When offered a normally preferred food (meat pellets) and an unusual food (banana or mashed potato), most of the kittens followed the example of their mother and ate the unusual food rather than meat pellets. The kittens' preference for the unusual food persisted even when the kittens were tested on their own. The kittens started to share their mother's food choices soon after weaning commenced (at about 5 weeks of age), and the effect was most marked towards the end of the weaning period (7–8 weeks). Young cats are clearly well adapted to learning from their mother, and show a strong interest in, and ability to learn from, the behaviour of other cats. This general phenomenon, of being able to benefit from observing a conspecific's experiences, is found in many species and is referred to as social learning (Heyes & Galef, 1996).

Kittens that were allowed to watch their mother perform an operant response (pressing a lever to obtain food) were able to acquire the response quickly, whereas kittens who were given the opportunity to acquire the response by trial and error never did so (Chesler, 1969). Moreover, kittens that watched their own mother acquired the response sooner than kittens who observed a strange female, suggesting that social learning is facilitated if the 'model' cat is familiar to the observer.

Adult cats also show social learning. Anecdotal observations of cats letting themselves out of rooms by jumping up at door handles might be explained as simple trial-and-error learning when the door handle is a lever because their response is rewarded by release from the room. However, such an explanation is much less plausible when the handle is a knob which the cat cannot turn and, therefore, their response cannot be rewarded. In such cases, it seems more likely that the cat has observed the actions of humans leaving the room (pers. obs.). Systematic experiments have demonstrated that cats can acquire some learned responses faster by observing another cat perform them than by conventional conditioning procedures (John *et al*., 1968). Observing another cat acquire the response is important, and has a more beneficial effect than watching another cat perform a skilled response that has already been learned (Herbert & Harsh, 1944).

The mother is, of course, not the only source of social experience during a kitten's development, and increasing evidence indicates that siblings play an important role in social development. During the early suckling period, for example, competition between littermates for access to nipples can be an important regulator of suckling (Rosenblatt, 1971). Kittens establish distinct and consistent preferences for suckling from a particular teat during the first few days and are more likely to displace another kitten from their most favoured nipple than from another nipple (Hudson *et al*., 2009). The establishment of teat preference is one of the earliest forms of learning shown by kittens.

Social experience with siblings also seems to play at least a facilitating role in the development of later social skills. Kittens which have been reared on an artificial brooder, with no experience of siblings when young, do eventually form social

attachments, but are generally slower to learn social skills than normally reared kittens. Brooder-reared kittens do not appear to form substitute social attachments to their brooder (Guyot *et al*., 1983). However, the mother may provide a substitute source of social experience for single kittens raised without littermates (Mendl, 1988). She plays much more when she has a single kitten than she does when she has two kittens which play with each other. She acts as a substitute sibling. The presence of siblings encourages young kittens to interact with prey. Pre-weaning kittens are more likely to watch prey if their siblings are also watching the prey (Caro, 1980c). Social experience with littermates is, therefore, yet another factor influencing behavioural development.

## Discontinuities and continuities in development

Attempts to trace particular patterns of behaviour back to the early action of certain genes, or to particular kinds of early experience, are often misconceived because of profound changes that occur at certain stages in development. Early influences may not necessarily exert detectable long-term effects on behaviour because of major changes in the organisation of behaviour that have occurred in between (Bateson & Martin, 1999). Such a possibility is, of course, in stark contrast to traditional views of development, which tended to emphasise the important and far-reaching consequences of all events that occurred early in life.

The control of behaviour patterns and their biological functions are likely to change as development proceeds. The time a kitten spends in contact with its mother, for example, is influenced primarily by its need for milk early in life and by its need for comfort later. Some activities, such as suckling, are special adaptations to an early phase and drop out of the repertoire as the individual becomes nutritionally independent of its mother. Similarly, certain motor patterns and reflex responses that are present at birth have disappeared from the behavioural repertoire by the time the cat is a few weeks old (Villablanca & Olmstead, 1979).

Cats are, of course, formidable hunters and many of the motor patterns that appear in play resemble those used in catching and killing prey. Not surprisingly, many hypotheses about the function of play in cats have invoked links between play and later predatory behaviour, with play seen as a form of practice for adult predatory skills (Moelk, 1979). However, little hard evidence has yet been produced to support this view (Martin & Caro, 1985; Bateson & Martin, 2013). Play experience is most certainly not necessary for at least the basic elements of predatory behaviour to develop (Baerends-van Roon & Baerends, 1979). For example, 'Kaspar Hauser' cats which were reared in social isolation and without opportunities for visual experience, let alone play behaviour, nonetheless showed 'normal' predatory responses when presented with a prey-like moving dummy at 11 weeks of age (Thomas & Schaller, 1954).

However, the possibility remains that play may have subtle beneficial effects on predatory skills. The one experimental test of this hypothesis so far carried out failed to find any relations between early object play experience and later predatory skills in domestic cats. Cats which had no opportunities for playing with small, inanimate

objects when growing up did not subsequently differ from kittens which had regularly played with objects, when their predatory skills were measured at 6 months of age (Caro, 1980b). This failure to find an effect might have been due to insufficient differences in the experience of the normal and the deprived groups of cats, or to measures of predatory behaviour that were insufficiently fine-grained to pick up genuine differences in skill. Furthermore, the benefits of play may be missed because a single experience of catching and eating a mouse can be enough to make a kitten a skilled mouse-killer thereafter. For all of these reasons, the role of play in behavioural development continues to generate much discussion (Bateson & Martin, 2013).

Despite these indications that not all aspects of development are continuous, it is clear that many types of early experience can be related to what happens later in ontogeny. For instance, many measures of predatory behaviour at 1–3 months of age are positively correlated with the same measures taken at 6 months (Caro, 1979). Individual differences in behaviour early in development can, to some extent, predict individual differences later in life.

Laboratory studies suggest that cats' choice of prey and their adult food preferences are strongly influenced by experience with their mothers when young. For example, cats are more likely to kill prey species with which they are familiar from experience as kittens (Caro, 1980a). Similarly, cats with experience of a particular type of prey when young are more skilful at catching and killing the same type of prey when adult. This effect of early experience appears to be specific, in that early experience with one type of prey does not produce a general improvement in predatory skills when other prey species are considered (Caro, 1980a).

Most cats eventually become reasonably competent predators, for example, almost irrespective of the type of experiences they have as young kittens.

In reaching an understanding of these sorts of effects, one useful principle is the system theory concept of 'equifinality'. In an open system, such as a living organism, the same steady state at the end of development may be reached from different starting conditions and by different developmental routes (see Bateson, 1976; Martin & Caro, 1985). In behavioural terms, this principle suggests that the same skill might be achieved as the result of quite different developmental histories.

The cat's predatory skills provide a particularly good example of the same set of behaviour patterns developing via different routes. Individuals differ considerably in their predatory behaviour during early development – particularly during the second and third months. This variation lies not so much in the basic predatory motor patterns, which virtually all individuals express, but in their integration, in the assessment of whether a prey can be caught, and in choosing the appropriate tactics (Baerends-van Roon & Baerends, 1979). Despite this individual variation among young cats, however, most eventually become competent predators, albeit with different preferences and specialisations for particular types of prey. At the crude level of overall predatory competence, much of the early individual variation in predatory skill disappears by adulthood. Some measures of predatory skills made before 3 months of age are not related to those made at 6 months, because individuals who were poor predators as kittens have usually caught up by the time they are fully grown (Caro, 1979).

These fascinating and almost uncanny aspects of development make sense in the light of the very different kinds of early experience that can enhance predatory skills. Adult predatory skills are improved by experience with prey when young, by watching the mother dealing with prey when young and, possibly, by the effects of competition between littermates in the presence of prey (Caro, 1980a). Kittens that have never killed a rat, for example, can become rat-killers merely by watching another cat kill a rat (Kuo, 1930). In addition, experience of prey when adult may also improve adult skills, which means that adults which have lacked early experience with prey can, to some extent, catch up later in ontogeny (Caro, 1980b).

The main point here is that a given set of adult behaviour patterns – in this case predatory behaviour – is affected by several different types of experience. Lack of one type of experience – say, experience of dealing with prey when young – may be compensated for by other forms of experience, such as watching the mother deal with prey when young, or experience with prey when adult. Thus, a given developmental outcome – competence as a predator – might be attained via many different types of developmental history. In functional terms, this type of process would clearly be of benefit to the individual, in that it allows the same type of behaviour to develop in a variable environment where individuals might have quite different types of early experience.

Of course, other processes may lead to apparently similar results. The effects of trauma or injury may disappear as the result of normal repair mechanisms. Where certain types of experience exert a facilitatory effect on development, it is also possible that considerable individual variation early in life will have disappeared by adulthood. In this case, though, the same developmental end-point is reached via the same developmental route, but at different rates. For example, exposing kittens to a cool environment during the first few days after birth hastens the development of temperature regulation. At 2 weeks of age, therefore, individuals may differ considerably as a result of differences in their exposure to low temperatures, but by 4 weeks of age they no longer differ (Jensen *et al*., 1980).

## Why are cats so different from each other?

For those who know cats well, they seem as different from each other as do humans. Why should this be? If they were adapted in the past to a common set of conditions, should they not all be alike? The answer may be 'no' for several reasons. First, if one member of a social group behaves in a particular way it may be advantageous to other individuals to behave differently. An obvious case would be when a dominant animal is monopolising a limited source of food. Second, climate and habitat are not uniform and specialisations for one set of environmental conditions might be quite inappropriate in another. The same applies to social conditions. Finally, some of the variation seen in cats may be the product of artificial selection.

As far as scientific investigation is concerned, the extent to which individual differences can be induced by the conditions of early life is an active area of research at the moment. A fruitful area that is ripe for exploration is the study of behavioural genetics

in the domestic cat. Much, of course, is known about genetic influences on morphological characters of the cat, such as the length and coloration of the coat. However, relatively little attention has been paid to the role of genetic factors in the development of individual differences in behaviour (see Chapter 11). Cats are particularly suitable subjects for such analysis because kittens are easily cross-fostered to another mother. So, it would not be difficult to investigate the extent to which differences in kittens' friendliness to humans are affected by the genes they inherit from their true mothers and how much their personalities were affected by the temperaments of their foster mothers. In practice, of course, such questions rarely reduce to simple answers and what happens to an individual depends on an interplay between its own behaviour and that of its caregiver. Nonetheless, such matters should not be prejudged and some personality characteristics may be expressed in a very wide variety of care-giving conditions.

Alternative routes in development may also lead to different outcomes for adaptive reasons. In the domestic cat, weaning is a gradual process during which the mother progressively reduces the rate at which she is giving care and resources (notably milk) to her offspring. Under favourable laboratory conditions, weaning commences at about 4 weeks after birth and is largely completed by 7 weeks (Martin, 1986).

Weaning represents a period of major transition for young mammals, marking a change from complete dependence on parental care to partial or complete independence. This transition, which is shown most obviously by the change in food source, involves a whole range of behavioural and physiological changes on the part of both mother and offspring (Martin, 1986). If, as is likely for a variety of reasons, the time of weaning may vary according to factors such as maternal food supply, then the developing offspring must be able to adapt by altering its behaviour accordingly (Bateson, 1981).

Evidence that kittens may alter their development in response to changes in weaning time comes from two sources. Early-weaned kittens developed predatory behaviour sooner than normally weaned kittens and were more likely to become mouse-killers (Tan & Counsilman, 1985). Conversely, late weaning was associated with delayed development of predatory behaviour and a reduced propensity to kill mice, although these effects might have been due to non-specific debilitating effects of delayed weaning. In general, these results fit with the notion that the development of predatory behaviour is linked in an adaptive way to the time of weaning; in other words, it develops when it is needed.

A series of studies has shown that the development of play behaviour is markedly influenced by the time of weaning. Under normal laboratory conditions, kittens' play behaviour undergoes a number of major changes towards the end of the second month, most notably by showing a large increase in the frequency of object play (Barrett & Bateson, 1978). This change in play coincides with the end of the weaning period, suggesting that the change from social to object play occurs in response to the kitten's increasing independence from the social environment of the nest.

To test this hypothesis, early weaning – or, more specifically, a reduction in maternal care – was simulated in a variety of different ways: by gradual separation from the mother starting at 5 weeks (Bateson & Young, 1981); by interrupting the maternal milk supply with the lactation-blocking drug bromocriptine starting at 4 weeks (Martin &

Bateson, 1985a) or 5 weeks (Bateson *et al*., 1981); or by slightly reducing mothers' food supply (Bateson *et al*., 1990). In all cases, the experimental manipulation led to an increase in the frequency of certain types of play. A higher rate of play after early weaning may mark a conditional response by the kitten to enforced early independence, by boosting the benefits of play before complete independence.

## Processes of development

Cat breeders regard temperament as important and have successfully selected for good nature in a relatively small number of generations (see Chapter 9). Friendliness to humans is affected in part by the characteristics of the father, whom the kittens may never encounter (Turner *et al*., 1986; Reisner *et al*., 1994; McCune, 1995). This aspect of their behaviour must, therefore, be inherited, but further details of the mechanism have not yet been worked out. Friendliness to humans is also greatly affected by early socialisation (McCune, 1995).

Early handling of kittens by humans has a number of effects on the behavioural and physical development of cats, the handled animals tending on the whole to develop more rapidly. In one study, Siamese kittens that were held and lightly stroked daily for the first few weeks of life were precocious in their physical and behavioural development compared with unhandled littermates (Meier, 1961). They opened their eyes earlier, emerged from their nest box for the first time earlier and even developed the characteristic Siamese coat coloration earlier than their littermates. In another study, kittens handled for 5 min per day from birth to 45 days of age approached strange toys and humans more readily, but were slower to learn an avoidance task than unhandled kittens (Wilson *et al*., 1965). Both results were attributed to a general reduction in fearfulness resulting from the early handling. The precise effects of early handling on kittens' development are likely to depend on a variety of factors, including the number of different people who handle the kitten, and the frequency and duration of handling.

The quality of the kitten's early nutrition is another factor with general effects on development. Several studies have found that kittens of undernourished mothers subsequently exhibit a variety of behavioural and growth abnormalities (Simonson, 1979). In one case, mother cats were fed 50% of their *ad libitum* intake during the second half of the gestation period and the first 6 weeks after birth (Smith & Jansen, 1977a,b). These undernourished mothers showed less active mothering than normal and were more irritable towards their kittens. Their kittens showed growth deficits in some brain regions (cerebrum, cerebellum and brain stem), although their overall brain composition was not affected. The undernourished kittens were 'rehabilitated' with *ad libitum* access to food from 6 weeks of age onwards and eventually achieved normal body size. However, they showed a number of behavioural abnormalities and differences in brain development later in ontogeny. At 4 months, for example, they had more accidents during free play and performed poorly on several behavioural tests. Males showed more aggressive social play than controls, while females did less climbing and more random running (Smith & Jansen, 1977a).

Although gross undernourishment of the pregnant mother or of the kittens after birth leads to many abnormalities in the young, much more subtle effects which are almost certainly adaptive can be produced by relatively minor reduction in the nutritional state of the mother. Early-weaned domestic cats play more than later-weaned animals (Tan & Counsilman, 1985). In one study, two kittens from litters of four were separated gradually from their mothers, starting at 5 weeks after birth, while the remaining pairs were left with their mothers (Bateson & Young, 1981). Two weeks after the beginning of separation these separated kittens showed significantly higher rates of object contact while playing than did their littermates left with their mothers. In a second study, cat mothers were given a single dose of bromocriptine when their kittens were 5 weeks old (Bateson *et al*., 1981). The drug suppressed lactation for about 24 h, thereby removing the kittens' milk supply without removing the mother. Once again, object play of the kittens whose mothers' lactation had been suppressed was significantly greater than in a control group 2 weeks after administration of the drug. In both these experiments the reduction in parental care was simulated when social play was well developed and the major influence was on object play that was not fully expressed for another 2 weeks. In a third study (Martin & Bateson, 1985a), three doses of bromocriptine were given to the mothers, starting when the kittens were 4 weeks old, i.e. a week earlier than in the previous experiment. In this case, cat contacts during social play were significantly greater in the kittens of mothers with blocked lactation than in those of the control group.

The general finding of these studies on the cat do not contradict the findings of other studies where low food availability results in a decrease in levels of play. The early-weaned kittens were neither stressed nor seriously food-deprived. Direct interference with the mother–offspring relationship, designed to promote early weaning, is not equivalent to the whole family experiencing low food availability. In addition, in all the laboratory studies of early-weaned kittens, kittens had access to *ad libitum* food supplies after they were weaned, an unlikely event when food is limited in the wild.

Several strands of evidence suggest that in the domestic cat, mothers will generally wean their young early when the energy loss during lactation is heavy. For instance, kittens in larger litters showed a sharper decline in the rate at which they put on weight at an earlier age than those in smaller litters, suggesting earlier weaning onto solid food when the load on the mother is greater (Deag *et al*., 2000). Moreover, mothers that had been ill and eating less than usual weaned their young earlier (see Bateson & Young, 1981; Martin, 1986). When cats were given a rationed diet after the birth of their kittens so that they received approximately 80% of the energy intake when given *ad libitum* food, their kittens played with objects significantly more than when the mothers received *ad libitum* food (Bateson *et al*., 1990). This was a specific effect and was not due to a general increase in the activity of the rationed kittens. Over the first 18 days after birth the extent to which mothers were unavailable to their kittens when rationed was strongly correlated with the object play of their kittens 70–84 days after birth. While the kittens in the rationed condition were well buffered from the effects of rationing, they nuzzled significantly more than those in the *ad libitum* condition in apparent attempts to reach their mothers' nipples.

## General issues about development

The development of behaviour clearly depends both on inherited factors (primarily genes) and non-inherited factors (primarily environmental influences). However, to look at a cat's behaviour and ask: 'Is it genetic or is it learned?' is to ask the wrong question. All behaviour patterns require both genes and an environment in order to develop. They emerge as a result of a regulated interplay between the developing cat and the conditions in which it lives. Moreover, like the records in a juke box, different genes may be expressed in different environmental conditions. For that reason, the cat's behaviour cannot be divided into two types – those patterns caused by internal factors (often referred to as 'genetic' or 'innate' behaviour) and those caused by external factors ('acquired' behaviour). Many actions, such as suckling, are clearly present at birth (the strict meaning of 'innate') and many other behaviour patterns, such as some of the motor patterns used by the cat for catching prey, appear without opportunities for practice or for copying from other individuals. Nonetheless, even such spontaneously expressed patterns of behaviour are often modified by learning and by other forms of experience later in development. And other environmental factors, such as the quantity and quality of nutrition, can have general effects on behavioural development.

Modern understanding of an individual's development goes well beyond accepting that interactions between the organism and its environment are crucial. The conditional character of an individual's development and its implications for post-natal health and survival emphasises the need to understand the processes of development that underlie these subsequent interactions. This is what Waddington (1957) termed 'epigenetics' more than half a century ago. More recently, epigenetics has become narrowly and mechanistically defined as the molecular processes by which traits defined by a given profile of gene expression can persist across mitotic cell division, but which do not involve changes in the nucleotide sequence of the DNA (Felsenfeld, 2007). The term has come to describe those molecular mechanisms through which both dynamic and stable changes in gene expression are achieved, and ultimately how variations in environmental experiences can modify this regulation of DNA. Epigenetically mediated variation in the context of the specific expression of genes is critical in shaping individual differences in phenotype. This is not to say that differences in the copy number or nucleotide polymorphisms leading to altered sequences of particular genes between individuals do not contribute to phenotypic differences, but rather that individuals carrying identical genotypes can diverge in phenotype if they experience separate environmental experiences that differentially and potentially permanently alter gene expression (Fraga *et al*., 2005). The molecular processes involved in phenotypic development were initially worked out for the regulation of cellular differentiation and proliferation. All cells within the body contain the same genetic sequence information, yet each cell lineage has undergone specialisations to become a skin cell, hair cell, heart cell and so forth. These phenotypic differences are inherited from mother cells to daughter cells. The process of differentiation involves the expression of particular genes for each cell type in response to cues from neighbouring cells and the extracellular environment, and the suppression of others. Genes that have been

silenced at an earlier stage remain silent after each cell division. Such gene silencing provides each cell lineage with its characteristic pattern of gene expression. Because these epigenetic marks are faithfully duplicated across cell division, stable cell differentiation results (Mohn & Schübeler, 2009). In recent years epigenetic changes to DNA have been found to transmit across from one generation to the next, but such changes may not persist for very long (Gissis & Jablonka, 2011).

## Concluding remarks

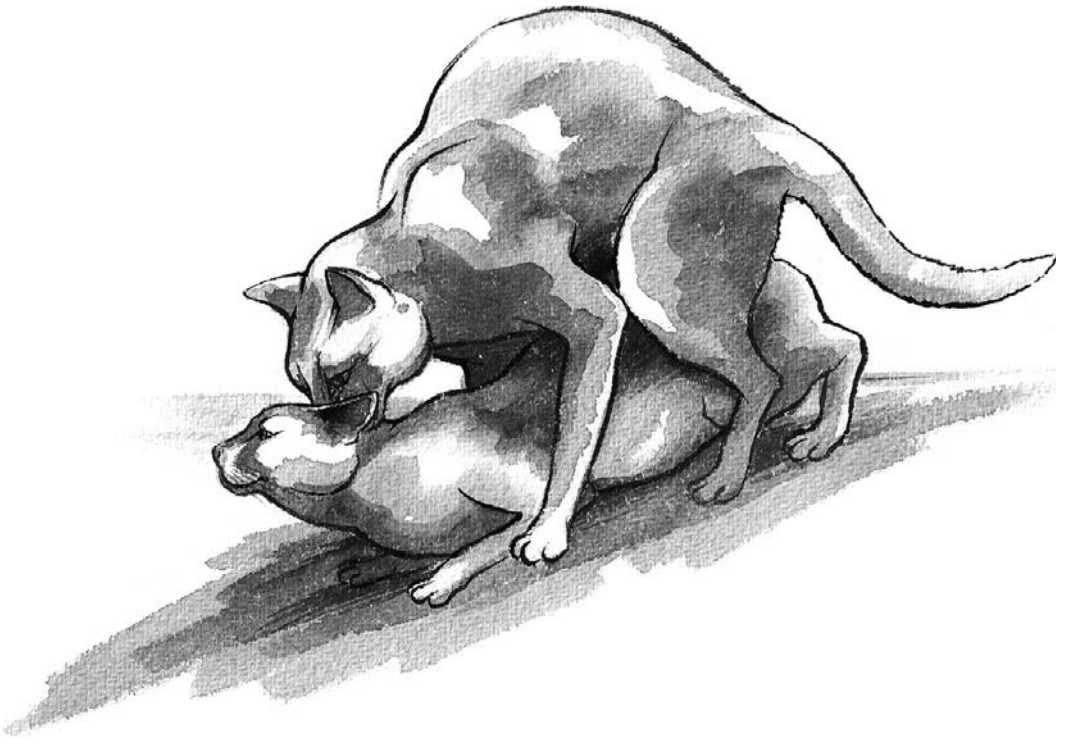
Development is not merely preparation for adult life, as the young animal has to survive. Some behaviour seen in early life is an adaptation to the conditions in which the kitten is living at the time, the most obvious example being suckling – a specialised means of obtaining nutrition from its mother. As some patterns of behaviour drop out of the kitten's repertoire, others come in. The changes are almost like those seen in the metamorphosis of a caterpillar into a butterfly.

The dynamics of the developmental processes generate behaviour in the individual cat which sometimes remains unchanged once formed and sometimes changes a great deal. These processes may often seem complicated, but it is becoming apparent that relatively simple rules for development can generate the variability found at the surface. For instance, at a particular stage in its development the kitten has something almost equivalent to a hunger for learning about certain kinds of things. However, once the knowledge is acquired, the kitten is resistant to further change. The most striking example of this is the way preferences are formed for social companions. Once formed, their preferences can be hard to change.

While cat owners tend to focus on how different individuals are from each other, development is such that cats end up behaving in similar ways despite remarkably different histories. The same skills found in adults have often developed in distinctive ways. The example considered at some length in this chapter was predatory behaviour. While cats show many of the components of stalking and catching prey without obvious previous experience of doing such things, they also greatly improve these skills. They may do so as a result of play or as a result of watching their mother. But if all else fails, they may become as good as other cats with plenty of early experience as the result of catching prey when they are forced to fend for themselves. Examples of versatility such as these demonstrate adaptability of the cat and how able it is to thrive in different environments. They serve to explain the similarities as well as the differences that are found in cats living in utterly different climates and conditions.

# 3 Normal and problematic reproductive behaviour in the domestic cat

Benjamin L. Hart and Lynette A. Hart



*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

Of all domestic animals, cats are the most capable of breeding, giving birth to offspring and raising their young without human care or intervention. In the classic example, a mother cat that has secretly gone through parturition in some obscure location reveals a litter of perfectly healthy kittens to the human family members after the kittens have been born. This romanticised view of feline motherhood has given way to the more formalised cattery operation, or the family breeder where a mother cat may give birth to her litter of kittens in the midst of an overly concerned family audience.

In this chapter, following some general information about parturition and the care of newborn, normal maternal behaviour is discussed along with comments about problems with various aspects of maternal behaviour. Problems with maternal behaviour manifest themselves primarily as either lack of proper attention to the kittens, resulting in inadequate care and nutrition, or cannibalism of the kittens. Of course, a necessary aspect of reproduction is the mating, which in this chapter is dealt with mostly in the context of intentional mating of females with selected males, in a home or cat-breeding facility.

## Maternal behaviour

Under our watch, when disturbances in maternal care occur, such as inadequate nursing of the kittens, we step in and supplement or take over. If a mother just refuses to groom or look after her newborn we may bottle-rear the whole litter. Because reproduction is the keystone of natural selection, various aspects of maternal behaviour in nature are controlled genetically within rather tight limits, which is sometimes called maternal instinct. The genetic link does have some variability, and when a mother exhibits inadequate mothering, or neglect of newborn, she leaves behind few or no offspring. Her genetic line with the imperfect genetic basis for mothering dies off. Hence poor mothering is rarely seen in nature. In our homes or in the breeding colony, however, where kittens have a monetary and emotional value, our intervention in helping kittens survive does not filter out the ‘bad apples’ for poor mothering from the domestic cat gene pool. Because good mothering genes are not filtered out, the result is considerable variability in the behavioural patterns that were previously under natural selection (Price, 1984). Within a breed or breed type, many cats are normal attentive mothers, while others appear just uninterested in their own kittens. While a promising new mother can make a bit of a mess while going through the experience in the first litter, it is generally true that mothering does not improve in poor mothers even after several litters, revealing that good mothering does not develop through experience.

### Gestational phase

As the time of parturition nears, pregnant females become less active. A female’s grooming starts to focus on the mammary and genital areas. The explanation for this is that the first surfaces outside the uterine environment with which the newborn comes in contact are the anogenital and abdominal areas, and soon afterwards, initial suckling

attempts are made. Newborn kittens have a vulnerable intestinal tract that is penetrable by bacteria that are taken into the mouth and consumed. The mother cat, by the frequent licking and cleaning of the abdomen, mammary area and teats, well before parturition, probably saves her newborn from an overdose of bacteria. The mother not only physically cleanses these areas, but she applies antibacterial saliva as well (Hart & Powell, 1990), and thus helps the young avoid disease (Hart, 1990).

As with other mammals giving birth to litters, delivery of the newborn proceeds through the contraction process, delivery of the foetus, and delivery of the placenta followed by an interval before the next delivery starts. Delivery, of course, involves a good deal of straining and cats usually lie down. They may sit up to change positions. An interesting, and now classical, observation made decades ago was the prominence of purring in some cats during delivery, up until contractions began, and then again following the contractions (Cooper, 1944). Another set of observations revealed that if a person in the family was present during delivery, crying by the mother was reduced and she purred instead (Moelk, 1979). A recent and intriguing perspective on purring that relates to the birth process is that the vibrational frequency of purring is 25 Hz, which is the frequency applied to the surface area by physical therapists on humans to promote wound healing, relieve pain and help in the repair of tendons and muscles (von Muggenthaler & Wright, 2003). It is postulated that the same effects on muscles and bones can occur in cats during purring. The purring of mothers while giving birth and afterwards likely helps her to recover from the trauma, while at the same time helping the kittens grow stronger bones. The same process might apply to purring seen while cats are lying around after going all out in the chase for a dinner, coming back with sore muscles and stretched tendons; purring is healing. More on purring in this light is discussed elsewhere (Hart & Hart, 2013).

Contractions become more intense as the foetus moves rather rapidly through the birth canal. At this time, the female often chews and breaks the foetal membranes as the foetus appears. In fact, she may tug on the membranes, pulling the foetus through the birth canal. After the newborn has passed through the birth canal, the mother generally consumes the foetal membranes and begins licking the newborn rather vigorously, which stimulates the initial respiration.

During delivery of the placenta, the mother often continues to lick the newborn and eats the placenta as it is passed. At this time she generally bites off the umbilical cord. The stretching involved in eating the placenta seems to cause blood vessel constriction in the umbilical cord, and little bleeding occurs. There are times when the umbilical cord does not get chewed off or broken. Then, human attendants at the birth commonly intervene and tie off the cord. Between deliveries the mother continues to lick the newborn along with her own genital region. Taking a page from *Good Housekeeping*, the new mother even cleans the bedding soiled with amniotic fluids.

The duration of the birth process normally varies considerably, with delivery running from 30 to 60 min (Schneirla *et al*., 1963). The contraction phase that precedes the delivery ranges from a few seconds to an hour or so. Interestingly, there are relatively minor differences in the duration of the birth process from the first birth process a mother experiences and after giving birth a few times. What has been noticed is that

the experienced mothers seem to be less disturbed by the whole process and respond more efficiently to the neonates in licking and retrieving those that wander off. Newborn kittens typically begin to suckle within an hour or two after the last foetus is delivered, as the mother lies continuously with her neonates for at least 12 h.

## Post-parturient phase

For the first 2 days or so the mother lies fairly continuously with her litter, leaving for brief breaks to eliminate and feed. These breaks become more frequent over time. The amount of time the mother spends nursing depends on the size of the litter, taking up to 70% of her time if the litter is large, say, six kittens. There is some adjustment while the mother and kittens settle into a routine, and the kittens commonly lose some weight in the first day or so.

For the first few weeks, nursing sessions are initiated by the mother lying near the kittens, with nipples exposed, and licking the kittens, if need be, to arouse them to nurse. Some kittens seem to not prefer a particular nipple, while others in the same litter regularly take specific nipple positions (but see Chapter 2). The attachment to nipples is not all that orderly in that kittens have well-developed outward thrusting movements with their forepaws and often knock a littermate off an adjacent nipple.

During the first 3 weeks after birth, the mother licks the newborns' bodies extensively. In addition to keeping the pelage in good shape, in nature, this maternal grooming removes ectoparasites such as fleas that would have come from flea pupae in the nest (Eckstein & Hart, 2000). Eye infections in the newborn, such as conjunctivitis, may be controlled by the mother's licking and an application of antibacterial saliva. At the other end of the newborns' bodies, anogenital licking evokes elimination; urine and faecal material are consumed by the mother. A reflex in the newborn allows release of urine and faeces by the mother's licking which is otherwise retained by the newborn. This coordinated mother–young interaction keeps the nest clean. As the young begin leaving the nest, maternal anogenital licking stops and the young deposit faeces and urine away from the nest, not infrequently in another part of the room if a kitten-style litter box is not available. When eliminations do occur, mothers will usually continue to keep at least the nest area clean.

As the young become capable of taking adult food at about 30 days after birth, mothers may continue suckling, but become increasingly less available, and weaning becomes complete. It is during this period when mothers with outdoor access start to provision their young, typically with rodents brought back to the nest area.

Mothers moving their kittens from one location to another in the home is rather classic; so classic that at least one furniture moving company has adopted the logo of a mother cat carrying a kitten in the classic curled up posture. This kitten posture is a reflexive response to the kitten being grasped by the nape of the neck by the mother. Humans can elicit the same reflex. Along with assuming the posture, kittens become relatively inactive, which makes the transport system work. This tendency for a mother cat to shift the location of her litter in the home seems to occur in response to environmental disturbances, and is reportedly most likely from 3 weeks after birth, extending

to 5 weeks (Schneirla *et al*., 1963). Although it might be hard to imagine that in nature a mother would move a litter often, the ingrained reflex in the kittens to being grasped by the nape of the neck suggests that moving a litter has survival or fitness value. Several causes for a cat living in nature to move a litter come to mind. If she sees a strange male a mother may quickly move the litter because he might kill the kittens, which could induce the mother to come into oestrus again and raise kittens he has sired. Another possible cause could be the build-up of nest-borne ectoparasites as the young become more difficult to keep groomed; moving to a new parasite-free location could be very beneficial to fast-growing young that need all the nutrition they can get. The predisposition to move a litter must be quite strong and easily triggered in some mothers because human caregivers often see a mother moving her litter even in a strange-male- and parasite-free home.

One other rather interesting aspect of cat maternal behaviour is the ease with which some mothers readily adopt and nurse not only strange kittens but other mammals such as puppies. Not much can be said about any adaptive aspect of this behaviour because in nature, strange kittens or other mammals are virtually never present in the nest and natural selection did not occur to produce a rejection of other kittens. Hence, a default situation continued where good mothers take care of all young things presented.

Another aspect of maternal behaviour that would never seem to occur in nature is seen when several mothers in the same house have given birth to kittens around the same time. The mothers may steal kittens back and forth, even harassing the other mother for each other's kittens. This behaviour can even progress to the point that all of the kittens are piled together and the mothers trade off caring for them. It would be interesting to determine whether the mothers which do this are more closely related to each other than those which do not.

Group rearing of kittens by more than one lactating queen is also observed in groups of feral cats (Macdonald *et al*., 1987). While feral cats – the domesticated cat living unattached to a home – have been observed to communally raise their kittens, the occurrence of this behaviour would seem to be the result of relaxation of strict selection for appropriate maternal behaviour in just expending resources for their own offspring, and the emergence of non-adaptive flexibility in extending the expenditure of maternal resources to offspring other than their own. But again, these mothers might be fairly closely related and the phenomenon explicable through inclusive fitness. Further, this might occur more frequently when food resources are plentiful and clumped in space, allowing the relaxation of selection pressure on the individual mother to feed just her own offspring (see Chapter 5).

## Understanding deviations in normal maternal behaviour

### Maternal neglect

Behaviours of mothers that create problems in the home or breeding colony fall between two extremes, ranging from ignoring the kittens and allowing them to die to killing and eating newborn kittens. One factor playing into the array of problems is the tendency of

cat owners to intervene and help mothers showing inadequate maternal behaviour, to save the litter. In introducing this chapter, we emphasised that aiding the survival of young from mothers that provide inadequate care removes the selection pressures against the genetic basis of poor mothering. This increases the extent to which the mothering instinct is perpetuated in the offspring of poor mothers, who then live to reproduce at almost the same rate as the offspring of exemplary mothers.

Kittens may die of hypothermia, for example, if a mother does not remove the foetal membranes and dry the kittens. Tangled umbilical cords may occur if kittens arrive quickly and the mother is not highly predisposed to clean off the foetal membranes. If a kitten leaves the nest and the mother fails to retrieve it, fatal hypothermia may occur. If a mother does not stay with the litter as described above, hypothermia frequently occurs. Stranded kittens can be warmed gently and presented to the mother again, but sometimes the kittens may not be accepted, even if repeatedly presented to her.

## Maternal cannibalism

This is a rather horrifying, if not troubling, occurrence to most people that is not uncommon. Most confusing seems to be the observation that if one kitten is killed and eaten, the mother may appear normal and attentive to the remaining kittens. While often there seems to be no precipitating event, some instances that have been reported include having a litter larger than usual, and the presence of one or more kittens that are ill or deformed. Previous experience in being a mother does not, however, appear to be related to cannibalism.

The most plausible explanation for cannibalism by mother cats is that killing and eating an offspring might be adaptive under certain circumstances in nature. If a kitten is sick from reduced resistance to a pathogen and shows signs of an infection, such as hyperthermia and inactivity, the mother, by killing and eating it, keeps the pathogen from building up to the point that even somewhat resistant littermates could become sick. For this disease-control system to work, the mother must promptly remove a sick kitten before it is incubating billions of potential pathogens (Hart, 1990, 2011). In this way she protects the rest of the litter. Rather than just depositing the dead kitten outside, the mother gains some additional nutrition, and will need to be gone from the nest one less time. Because a mother's cannibalism, to be effective, must be triggered by the first sign of illness, even a non-infectious disturbance of the kitten or novel odour, noise or vibration might also trigger cannibalism.

Newborn cannibalism may also occur if a mother detects a congenital deformity. While it is not the risk of a pathogen building up in a susceptible newborn, a behaviour that removes a newborn that is unlikely to reproduce later in life – and be of no fitness consequence to the mother – is an adaptive strategy. Cannibalism of the deformed kitten conserves otherwise wasted resources for the remaining normal kittens.

To bring the father, or sire, of the litter into the picture raises the issue that in some wild felids, and domestic cats, infanticide by males may occur. This is true when males have taken over a territory in which there is a female and her litter. Such males rather indiscriminately kill the kittens. This act, in turn, may cause the females to come into

oestrus again and the male can sire the next round of offspring. As mentioned above, if a mother sees a strange male around, one way of avoiding this tragedy for the mother is for her to carry the litter of kittens to a new, more hidden location. On the domestic scene there is, therefore, a logical reason to keep strange tomcats away from lactating female cats. On the other hand, the tomcat which is familiar with the female, and has sired the kittens, is not likely to kill the kittens. While this is what some breeders have found, a good recommendation is to be watchful when a tomcat is around. Even without any parental care by the male, the personality of kittens can often be related to the personality of the tomcat (Turner *et al*., 1986; Reisner *et al*., 1994).

## Sexual behaviour

This is an aspect of reproductive behaviour that gets less attention in the literature than maternal behaviour, probably reflecting fewer problems in this area. We will first discuss some major aspects of male and female sexual behaviour and then deal with problems.

In nature and in our neighbourhoods, much of the general activity of cats takes place at night, including interactions with the opposite sex. A female cat in oestrus shows a heightened activity level and her distinct mating calls often attract breeding males from near and far. Sex attractants in her urine may provoke visiting male cats to stay around and unfamiliar males to appear on the doorstep. In the presence of a male, females that are in oestrus are likely to assume a receptive posture – elevation of the pelvic region, deviation of the tail to one side, and treading of the back legs. As the male cat investigates, these responses become more intense. The receptive posture is, at times, so uninhibited that this behaviour can be displayed to the pet owner or induced by stroking the female on her back and touching the perineal region. The response can be enhanced by grasping the skin over the back of the neck while stroking the perineal region.

Whether in the back yard or the home den area, if a male is comfortable with the surroundings, he will approach the female, and do a genital investigation. The investigation often evokes a gape or flehmen by the male. Flehmen presumably allows the male to confirm the markers of oestrus in genital secretions and urine. The male next takes a neck grip on the female, mounts and usually engages in alternate stepping of the back legs. (This neck grip usually immobilises the female, just as it does when a mother cat moves her kittens while carrying them in her mouth.) Mounting is fairly far forward on the female and he then slides backward while continuing the leg stepping until he gains intromission. The simultaneous leg treading helps the process along.

Pelvic thrusting begins at the time of intromission and soon there is a deep pelvic thrust, where the male remains motionless for a few seconds. At this time, emotional activation seems to build up in the female, as indicated by her eyes dilating. Ejaculation occurs after a few seconds and the female rather suddenly pulls away, typically emitting a loud cry. She often turns as if to try to hit at the male, as he springs back. She then begins the feline signature, copulatory after-reaction, licking her genitalia and rolling and rubbing on the floor. The male engages in his own bit of genital licking. The genital licking behaviour is more than just surface hygiene as the male is physically cleansing

the penis and then applying antibacterial saliva. Cats seem to be afflicted with few sexually transmitted diseases, one of the reasons being that the transmission of genital diseases is broken by the genital licking (Hart, 1990, 2011).

When a female cat is mated, whether she becomes pregnant or not, her oestrus lasts for 4–6 days, and she does not come back into oestrus for that season. However, if she is not mated, the oestrous period may last for as long as 10 days and she recycles at intervals of 2 or 3 weeks. This pattern reflects the fact that ovulation in the female domestic cat is induced by copulation – so-called reflex ovulation. Once mated, the female does not have to put up with any more courtship attempts or matings.

Cat breeders often understand this system of reflex ovulation and when they desire not to have a female bred, or not to have the female repeatedly come into oestrus, they can evoke ovulation by probing the vagina with a smooth blunt instrument such as a glass rod. Several insertions of 10 s, about 5 min apart, for a couple days are usually sufficient to induce ovulation (Diakow, 1971). Females may even display the copulatory after-reactions to these insertions.

In the wild, i.e. among cats with outdoor access or living in outdoor colonies, only a few studies of the mating system of domestic cats have been conducted and these were summarised by Liberg *et al*. (2000) in the second edition of this book. Most of those studies concerned group-living populations. At lower cat densities in rural areas, a dominant 'breeder-class' male's range covered the home ranges of several females, but the ranges of breeder-class males overlapped even during the mating season. (The socio-spatial organisation of domestic cats with outdoor access is related to food abundance and dispersion – see Chapter 5.) In this study, females in oestrus were often courted by more than one male, especially at higher cat densities such as that reported from a central Roman colony, where up to 20 males were seen to court the same oestrous female (16 simultaneously). Nevertheless, the authors concluded that male cats compete for females singularly and mating success is strongly correlated with dominance, which in turn is correlated with age and body weight. The authors also concluded that more field research is needed to determine if female cats actually 'choose' their mates in such systems and mention several hypotheses on how this might occur.

## Problems with males

In the home or breeding facility setting, failure of a male to show interest in females or their discomfort with the breeding environment may be reflected in an absence of mating. Sometimes even a highly motivated male may fail to copulate because of physical interference with intromission.

The first of these problems, an apparent lack of sexual prowess, can be addressed by giving the male sufficient time to acclimate to the breeding area even before the receptive female is placed with him. The pair should be allowed to mate several times in succession. For regular breeders, if a specific area is reserved for breeding, the male, who is usually the one that needs acclimation to the room, may come to anticipate copulation when placed in that area. The most wary male may wait a few hours before copulating, but after a series of matings, he will usually copulate within 15 min or so.

One problem seen in long-haired cats is that a hair ring may develop around the base of the penis, actually preventing intromission (Hart & Peterson, 1970). The hairs may come from the preputial sheath of the male, or with frequent mating, from the fur of the female when the penis is rubbed over the back of the female. While the hair ring is often removed by the males themselves, the owner can also remove the ring by gently sliding it over the penis. Males are usually able to mate immediately after removal of the hair ring.

The problem of lack of interest by a male could be due to low levels of testosterone. The blood testosterone levels can be analysed, compared to a normal range, providing several blood samples have been taken throughout the day, as blood testosterone concentrations fluctuate. Normal copulatory activity can occur with half of the usual level of testosterone, so testosterone levels would have to be quite depressed to account for a male's lack of sexual interest.

The occurrence of a painful or fear-eliciting event during the mating encounter may result in a male showing no interest in mating. In this case, the event that caused the male to be fearful should be removed or the breeding moved to another area. If a general high level of anxiety seems to be the cause, this behaviour could be passed onto the progeny.

### Problems with females

These problems are primarily difficulties with oestrus detection and the rejection of a male's sexual advances even though the female shows signs of sexual receptivity. As described above, the signs associated with sexual receptivity can be evoked by petting on the back or even rubbing the perineal region while holding onto the skin over the back of the neck – more or less as a male cat would do. However, these responses cannot be elicited in all females at the time of oestrus. Placing the female near a sexually active male may be necessary, even if not the intended sire.

A female that is in oestrus but will not accept the male is another, but not uncommon, problem. By gently restraining the female, some males that are experienced might be accepted. A male and female can be left overnight or at least for several hours, hoping for the best. The drawback here is that you cannot know whether mating has occurred. If the female has not been induced to ovulate she will be in oestrus again a week or more later. One particular male might be accepted by a female but not others. A simple solution would be to present the female a different stud male. One other thing that can interrupt breeding harmony is the occurrence of a painful and fear-eliciting event, just as with males. Removing the objects causing the reactions or moving the breeding area could be attempted.

## Concluding comment

Reproduction in cats has several aspects unique to domestic animals. For one thing, reproductive behaviour in both sexes is fraught with individual idiosyncrasies and special sensitivities, especially in the home or breeding cattery. Fortunately, cat breeders

seem to understand that the management of this aspect of a cat's life in a human environment is a place where persistence and patience are invaluable.

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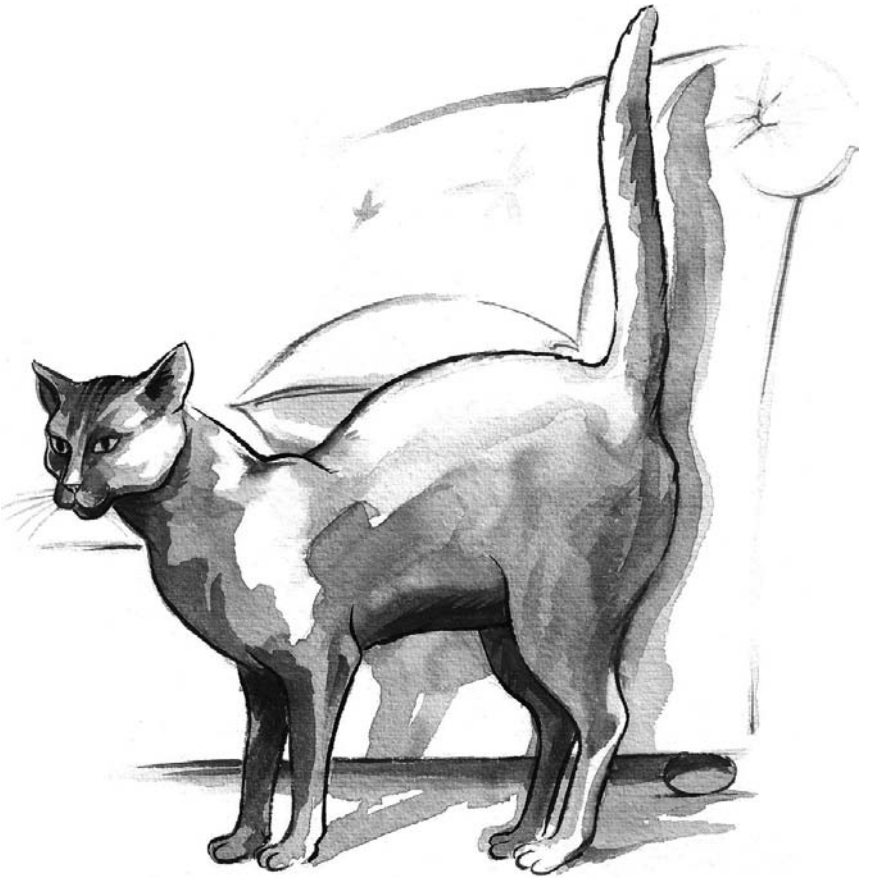
# 4 Communication in the domestic cat: within- and between-species

Sarah L. Brown and John W. S. Bradshaw



*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

Many previous accounts of communication between domestic cats have been largely based on a traditional ethological approach. The signals and the context in which they occur have been described and related to the kind of environment signaller and receiver can expect to find themselves in, and to the sensory capabilities of the receiver. For example, this approach explains the use of scent signals by domestic cats as products of both their acute sense of smell, which probably evolved primarily in relation to detection of food, and also their origin as territorial animals which needed to communicate with neighbours that they might rarely encounter face to face. However, the domestic cat is the product of two distinctly different phases of evolution, the first as a wild, largely solitary, predator, and the second as a commensal and then semi-domesticated social species, living in an increasingly dependent relationship with humans. There are few studies of the communicative repertoire of the ancestral species, *Felis silvestris libyca*, and it is now clear from the distribution of *libyca* DNA that many wild cats, including those from Africa and the Middle East, are, in varying proportions, hybrids between wild *F. silvestris* subspecies and domesticated *F. s. catus* (Driscoll *et al*., 2007). Commensalism will have brought with it new selection pressures on communication, largely intraspecific and resulting from the higher density at which these cats live, by comparison with that of their solitary ancestors.

Thus the influence of commensalism on signalling adds a further dimension to the explanation of why signals take the form they do. In the case of the cat, the ancestral species *F. s. libyca* is thought to be exclusively territorial, and so its signalling repertoire must presumably have changed as it evolved to live at high densities and to become facultatively sociable. When individual animals live close together, and benefit by cooperation, they need the ability to resolve conflicts without resorting to physical violence, particularly when both protagonists are as well-armed as a cat. However, it is not yet certain when this ability arose, as the social biology of *F. s. libyca* has been little studied.

Domestication presumably favours those individuals capable of communicating effectively with their human owners. Furthermore, given the short length of time that the cat has been domesticated, and has simultaneously come to live at much higher densities than its territorial ancestors, it is likely that its communicative capabilities have not yet reached a state of evolutionary equilibrium. Thus any evolutionary approach to the signalling repertoire of the domestic cat will need to take into account both the variety of putative selection pressures that have shaped it, and the possibility that particular signals, both intra- and interspecific, are still evolving.

Communication is said to occur when one animal responds to a signal sent out by another. This is a more general definition than normally applies to communication between people, when it is usually assumed that information is both being exchanged and reasonably accurate. Unfortunately, this ‘conventional’ definition has often been carried over to communication between animals, implying that animals that are signalling to one another agree about the message being transmitted (Zahavi, 1993). In many instances there is no reason to believe that this is the case; signallers often attempt to

manipulate the behaviour of recipients to their own advantage, while recipients attempt to 'mind-read' these deceptions (Krebs & Dawkins, 1984). In this chapter we have speculated as to the evolutionary origins of some signals, such as the odour of tomcat urine, purring, and agonistic visual signals, and also which signals, or signalling abilities, appear to have been affected by domestication.

## Sensory constraints on communication

As with any species, communication between cats can only take place within the limitations of their sensory apparatus. Sensory abilities primarily evolve to allow the animal to obtain food most effectively and to navigate successfully around its environment, in order to survive day-to-day. Communication then evolves within the constraints imposed by those sensory capacities. Sensory specialisations of cats that have an impact on their ability to communicate in different ways are summarised below. A more detailed account of their sensory characteristics can be found in Bradshaw *et al*. (2012).

## Visual factors

With almost three times the number of rods (the most sensitive visual receptors) combined with the reflective layer (tapetum) behind the retina, the eye of the cat is much better equipped to see at very low light intensities than is the human eye (Bradshaw *et al*., 2012). This is an adaptation to crepuscular hunting in the cat, but has its costs in allowing less space on the retina for the less-sensitive colour-detecting cones. Using these, it now seems fairly certain that cats only see blue and green colours and their combinations, lacking the cones required to see the colour red. Presumably due to this, colour seems to play little importance in cats' visual interpretations of their environment, or in signalling.

Despite their reduced colour perception, behavioural research has shown that cats can distinguish differences in size, shape and texture of objects and are able to visualise partially hidden outlines, again presumably adaptations for detecting prey.

Focusing from near to distant objects is slower in the cat than in humans and they appear not to be able to focus at all on objects closer than around 25 cm away. They are also less able to detect objects moving slowly across their visual field, humans being able to detect movements 10 times slower. Rapid movement, however, to which their vision is highly adapted, is likely to elicit much more of a response from cats. They are able to track a fast-moving object (such as a mouse or other prey item) by rapid movements of the eyes called saccades during which the object is continually monitored while sensory information is transferred to and processed by the nervous system.

The reduction in certain elements of vision and advancement of others (by comparison with humans) is inevitably reflected in the use of visual signals between cats. Their reduced ability to discriminate colour means that in communication terms, unlike birds with their four-colour vision, visual displays based on colour contrast are likely to be

ineffective for cats. Instead, behavioural displays such as 'Tail Up' (described later in this chapter) that produce a distinct image may have evolved from a need for clear unambiguous signals easily distinguished by the recipient cat.

## Auditory factors

As with visual factors, most aspects of hearing in the cat appear to have evolved as a response to the need to detect prey. The range of sounds they can hear is one of the largest recorded in the mammals with an impressive ability to hear sounds at both the high- and the low-frequency ends. Detection of high-frequency sounds is presumably an adaptation to hunting of rodents which emit ultrasonic calls.

Humans are better than cats at distinguishing sounds of the same frequency but different intensities and also, when the frequency is below 5 kHz, at distinguishing between pairs of sounds of the same intensity but different frequency. Man's more advanced ability in this area may help explain the large number of subtle variations of 'miaow' types that cats have developed (and which are possibly still evolving) in their communication with humans, but which do not appear to play an obvious role in cat–cat communication.

The pinnae of cats are highly mobile and are used to amplify sound as they are turned towards its source. Being under subcortical control their movements are very rapid and, although again presumably having evolved to aid in prey detection, these have been capitalised on and developed as a form of visual communication. As illustrated later in this chapter (Figures 4.6 (i) and (ii)), pinnae movements are used to great effect as visual signals reflecting rapid changes in motivation.

## Olfactory factors

Cats communicate by a variety of olfactory signals, as described later in this chapter, and all of these signals require sniffing by the recipient of the signal. Based on the size of their olfactory epithelium and olfactory bulbs and the complexity of the olfactory receptors, it seems certain that smell forms an important part of the cats' sensory input.

Ability to smell and track prey is obviously an important function of such elaborate olfactory apparatus. Unlike the visual and auditory systems, however, the olfactory system also has a separate component known as the vomeronasal or Jacobson's organ, which appears in the cat to be specialised solely for detecting and processing social odours. The paired vomeronasal organs (VNO) are connected to both the oral and nasal passages via the nasopalatine canal and are thought to be used intermittently, as accessory olfactory organs. A cat encountering a new scent it wishes to inspect will initially sniff it. This may be followed by flehmen, in which the upper lip is raised and the mouth held partially open; this may persist for half a minute or more. During flehmen the cat may make physical contact with the source of the odour, and then moves its tongue to and fro behind its incisors, where the openings of the ducts that lead

to the VNO lie. Both airborne and fluid-borne molecules of the odorant are thereby carried into the VNO (Hart & Leedy, 1987). The requirement for actual contact with the material being investigated, and the fact that the stimulus may remain dissolved in saliva throughout, suggests that this process produces more of a 'taste' rather than a 'smell' sensation. As flehmen is only performed in response to odours from other cats, it presumably gathers (and possibly stores) social information.

## Communication between domestic cats

### Olfactory communication

The ancestral species of the domestic cat, *F. s. libyca*, is probably exclusively territorial (Smithers, 1983; Happold, 1987; Macdonald, 1996), as are most of the smaller species in the Felidae. Because widely spaced animals rarely encounter one another face to face, they tend to communicate by scent marks, which permit a delay of several hours or days between the deposition of the signal and its reception. For well-armed carnivores, the advantage is that potentially dangerous encounters with rivals can also be avoided by the use of olfactory signals, both those deposited on the substratum and those that are carried directly from the body surface by air currents. The potential disadvantage of relying on scent signals is lack of control, both of the direction the message is carried in, which is at the mercy of the wind, and of who receives it, as a scent mark cannot be switched off at will; both lead to potential exploitation of the information that the scent contains. Despite these potential problems, members of the Carnivora rely extensively upon scent for communication (Gorman & Trowbridge, 1989).

Many domestic cats live at a density several orders of magnitude higher than their wild counterparts, and it is therefore possible that their scent communication has been modified during the course of domestication. Cats that live in groups can potentially not only exchange information through scents, but also exchange the scents themselves to produce colony- or group-specific odours such as those seen in other species (e.g. badgers, see Buesching *et al.*, 2003). While several sources of odours have been documented, their functions in communication are generally still speculative.

## Urine

Cats can adopt two distinctly different postures for urination, indicating that at least one (possibly both) has some use in signalling. Kittens, juveniles and adult females usually squat to urinate and then often cover the urine with soil or litter. Although this can be interpreted as an attempt to hide the urine, and so presumably the information that its odour contains, such deposits are sniffed by both male and female cats if encountered. Moreover, the duration of sniffing tends to increase with the unfamiliarity of the depositor, suggesting that the sniffer is responding to and gathering information from the odour (Passanisi & Macdonald, 1990). This may only be a common occurrence

where cats are living at high densities; the attempted concealment may be effective in widely spaced territories.

Deliberate scent-marking with urine is performed by spraying, in which the cat backs up to a vertical surface and urinates backwards, usually while quivering its tail. While mature males are the most frequent sprayers, adult females also spray. Large individual differences in rates of spraying occur; for example, Feldman (1994a) recorded rates varying between 2.8 and 9.2 sprays per hour by male cats. The variation may relate to differences in age or territoriality, or reflect different strategic adaptations to avoid social conflict. For example, in closed or high-density colonies some suppression of spraying in females and younger males may occur, resulting in most spray marks being produced by a small number of more confident mature males (Natoli, 1985; Feldman, 1994a). Spraying by tomcats is enhanced by the proximity of oestrous females, who also increase their rate of spraying at this time. This results in an annual peak of spraying in the UK in February/March (Feldman, 1994a).

The odour of sprayed urine is pungent, prompting speculation that it carries other secretions, possibly from the preputial or anal glands (Wolski, 1982). The anal gland secretion, which is voided by very frightened cats, certainly has a distinctive odour, but this is not, to the human nose, similar to that of sprayed urine. The odour of sprayed urine increases after deposition (Joulain & Laurent, 1989), and this is probably largely due to the microbial and oxidative degradation of the two unusual amino acids which it contains, felinine (L-2-amino-7-hydroxy-5,5-dimethyl-4-thiaheptanoic acid, I) and isovalthene (2-amino-5-carboxy-6-methyl-4-thiaheptanoic acid) (Westall, 1953; Oomori & Mizuhara, 1962). The main degradation products, 3-mercapto-3-methyl-1-butanol (II) and 3-methyl-3-methylthio-1-butanol (III), and other disulphides and trisulphides, have strong 'tomcat' odours (Joulain & Laurent, 1989; Hendricks *et al*., 1995a).

The sulphur-containing amino-acid content of domestic cat urine has been found to vary according to gender, age, health and reproductive status (Miyazaki *et al*., 2008) Levels of the amino acid felinine are controlled by cauxin, a urinary protein which in turn is regulated by the level of testosterone in the blood. Entire males can excrete large amounts of felinine, up to 95 mg/day, whereas females produce less, up to about 20 mg/day, which correlates with the lesser pungency of female sprayed urine. Hendricks *et al*. (1995b) have suggested that this excretion may have a significant effect on the sulphur-containing amino-acid requirements of an entire male, as felinine is biosynthesised from cysteine and possibly taurine. It is therefore possible that the amount of felinine in the urine, and hence the strength of its odour, is an accurate reflection on the success of the male in obtaining high-quality food, and is therefore an 'honest' signal (Zahavi & Zahavi, 1997) advertising his fitness as a mate (to females) and competitor (to other males). This may help explain the use of spray marking during agonistic encounters between males with adjacent territories (Pryor *et al*., 2001a).

The function of urine spraying in demarcation of territories, if any, is unclear. Spray marks are rarely observed to act as a deterrent in their own right, but this is the case for most territorial scent marks (Gosling, 1982), even those which mark the edges of territories, which those of tomcats do not (Feldman, 1994a). Turner and Mertens

(1986) found urine marks of farm cat males and females to be fairly evenly distributed over their entire home range, not particularly on the borders. It has also been suggested that since the odour of scent marks changes with age, they could be used to assist cats to space themselves out while hunting, so that they could avoid areas which had been disturbed recently (Leyhausen, 1979). However, this is unlikely to be a stable strategy; cats that did not spray-urinate could put themselves at an advantage because other cats would waste time and effort hunting in places where prey was still wary due to the recent proximity of a predator.

All cats, but particularly adult males, investigate spray marks intently (Natoli, 1985; Matter, 1987; Passanisi & Macdonald, 1990), particularly if they are produced by oestrous females (Verberne & de Boer, 1976), which suggests that they do contain relevant information. Initial inspection is usually by sniffing, often followed by flehmen, which results in information being transferred to the VNO as described earlier in this chapter.

## Faeces

Many species within the Carnivora use faeces, often with glandular secretions added, to convey information (Gorman & Trowbridge, 1989). Domestic cats have been shown to spend longer sniffing the faeces of an unfamiliar cat when compared to its own or that of a familiar cat (Nakabayashi *et al*., 2012), suggesting that they too gain social information in this way. Near to the core of the home range, faeces are usually buried (Feldman, 1994a), but they may be left exposed elsewhere (Macdonald *et al*., 1987). Cats usually sniff the places where they have just buried faeces, but tend not to do so after leaving them exposed (Macdonald *et al*., 1987). This suggests that one of the functions of burying faeces is to minimise the likelihood that the olfactory information they contain will be detected by another cat, although hygiene may provide a more parsimonious explanation.

Some studies have found possible relationships between physical and social characteristics of cats and their faecal burying behaviour. For example, Ishida and Shimizu (1998) found that among male cats, heavier individuals did not leave their faeces exposed more often than lighter ones, but when they did bury them they tended to choose sites nearer their core area, compared to lighter cats. This was not, however, the case for females. This could be interpreted as defecation patterns in male cats being affected by the level of perceived threat to their core area, but in general, studies attempting to demonstrate that unburied faeces serve as territorial markers have produced equivocal results (Dards, 1979; Macdonald *et al*., 1987; Feldman, 1994a).

## Scratching

Although it undoubtedly has a role to play in the conditioning of the claws of the front feet, scratching must inevitably result in the deposition of scent from the glands on the paws (interdigital glands) (Ewer, 1973). The same scratching site is often

used over and over again, resulting in a clear visual marker which presumably draws attention to the olfactory information. Although no published studies appear to report the extent to which scratched sites are sniffed, Pageat and Gaultier (2003) observe that avoidance behaviour is enhanced when cats encounter sweat secreted by a fearful cat.

The scratching sites are distributed along regularly used routes, rather than at the periphery of the territory or home range (Feldman, 1994a). Tree characteristics also seem to affect the distribution of scratches with soft-barked trees being scratched more than hard-barked trees. Softer bark presumably produces a more effective visual mark when scratched compared to harder-barked trees (Feldman, 1994a).

Scratching may also serve as a visual display in the presence of conspecifics as feral cats have been observed to scratch more often when in the presence of other cats than when alone (Turner, 1988).

## Skin glands

In addition to the interdigital glands mentioned above, domestic cats also appear to communicate via secretions from several other skin glands (Prescott, cited in Fox, 1974). As Figure 4.1 shows, in the head region they have perioral glands at the corners

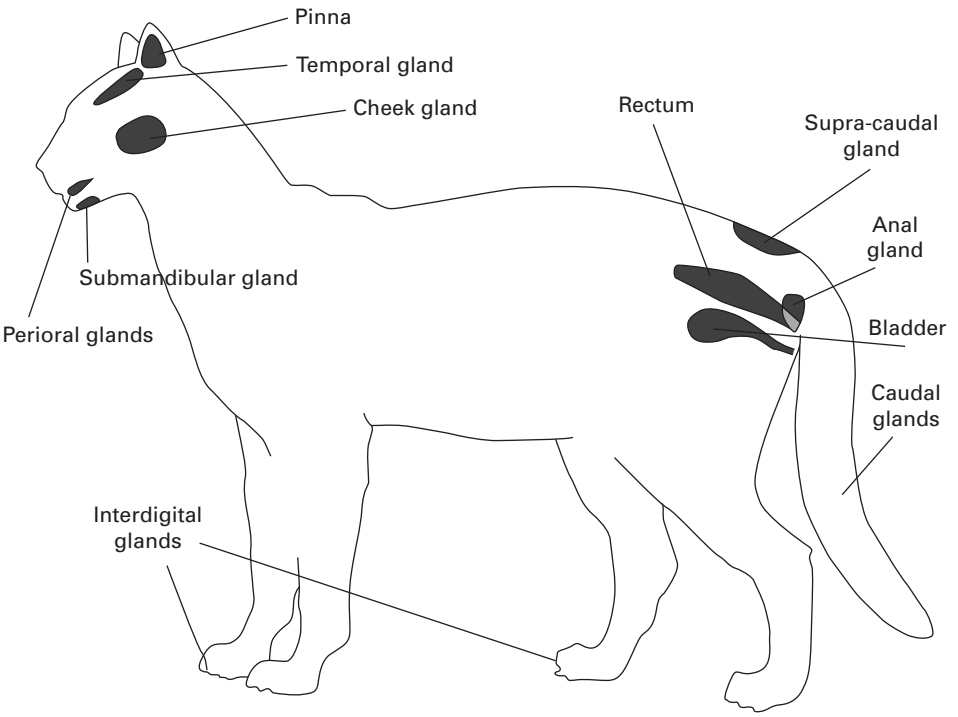



**Figure 4.1** The main scent-producing structures in the (male) domestic cat.

of the mouth, temporal glands on each side of the forehead, cheek glands on the side of the head, and the submandibular gland beneath the chin. The tail is endowed with sebaceous glands distributed diffusely along its length, known as caudal glands. Also a gland at the base of the tail enlarges as the cat matures – in entire males this can over-secrete, giving rise to the condition 'stud-tail' (Wolski, 1982). The pinnae (external ears) also produce a waxy secretion.

It is unclear whether each of these glands produces a unique secretion, each with a well-defined function. The secretions of the glands on the head are rubbed onto prominent objects by a behaviour pattern known as bunting (Houpt & Wolski, 1982). The precise form of this appears to depend upon the height of the object being rubbed, such that high objects are primarily marked with forehead and ears, objects at head height with a wipe of the head from the corner of the mouth to the ear, and lower objects with the underside of the chin and then the side of the throat (Verberne & de Boer, 1976). This plasticity suggests that similar odours are deposited from all parts of the head: either the glandular secretions have similar effects, or because they become thoroughly mixed on the coat through grooming.

Intact adult males tend to rub-mark more frequently than do anoestrous females or juveniles (Feldman, 1994a) and occasionally spray urine on top of their own rub marks (Dards, 1979; Panaman, 1981) or vice versa (Macdonald *et al*., 1987). Other rub marks, although performed on visually prominent objects, such as projecting twigs or corners of man-made structures, are not associated with any other visual or obvious olfactory cue and are thus not obvious to the human observer. Cats, on the other hand, appear to be able to locate them easily, suggesting that they are quite pungent to the feline nose, and frequently over-mark them with their own cephalic secretions. The rub marks of entire females contain information about the oestrous cycle, as indicated by the degree of interest shown by males (Verberne & de Boer, 1976)

Cat–cat rubbing (or allorubbing), in which two cats rub their heads together (Figure 4.2) and then often continue the rub along their flanks (Figure 4.3), is a visual and tactile display which must also result in the exchange of odours between the pelages of the participating cats. It is unclear whether this odour exchange has any social relevance, for example in the establishment of 'group odours' shared by cats that are friendly towards one another. When cats sniff each other, they tend to concentrate on the head region, rather than the flanks and tail where shared odours would presumably accumulate, suggesting that even if group odours do exist, individual odours contain more valuable information.

Rubbing is also directed by cats onto their owners, and it is possible that the human response of stroking is the nearest equivalent we have to a reciprocal rub. Cats appear to have a preference as to exactly where on their body they like to be stroked by their owner, their favourite place being the temporal gland, the cheek area between the eye and the ear, and their least favourite being in the caudal gland region around the tail (Soennichsen & Chamove, 2002). Such is their preference for particular areas to be petted they may indicate this through their body language – simply staying still, or closing their eyes or positioning their body so as to encourage rubbing of specific sites. Elaborate rituals may develop where the cat jumps on the owner's lap and/or rubs round

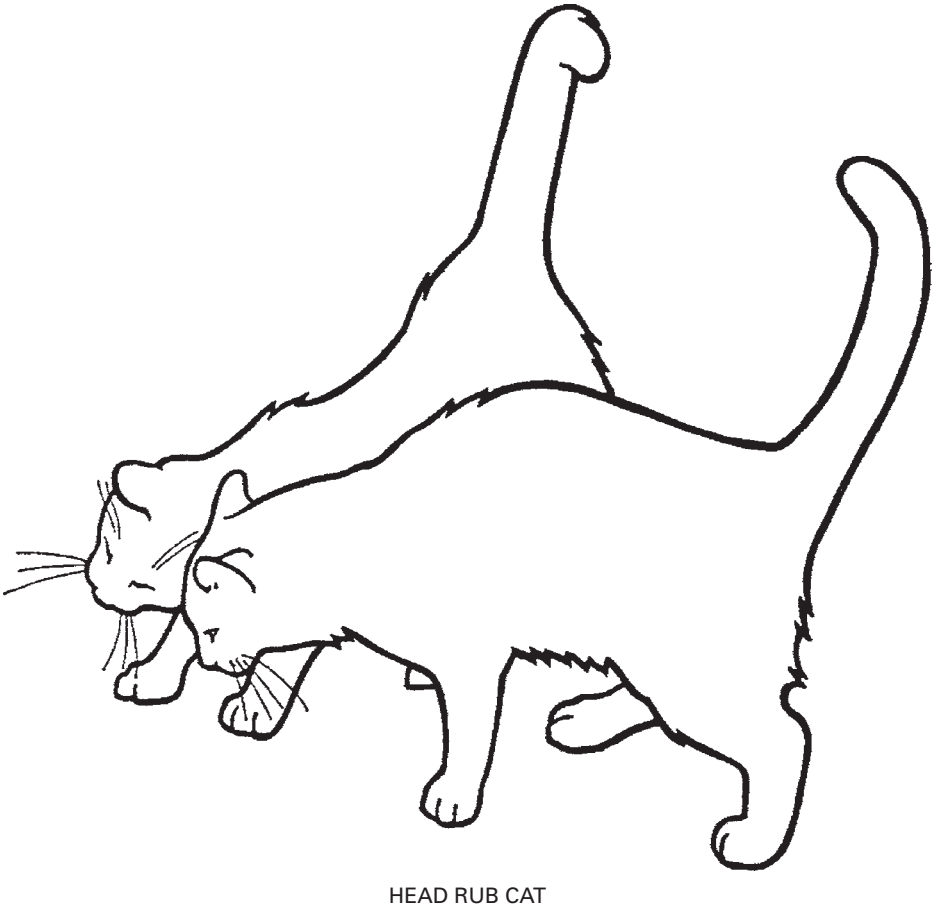



**Figure 4.2** Head-rubbing between two cats. From UK Cat Behaviour Working Group (1995).

their legs apparently in an attempt to invite petting from the owner (Bernstein, 2005). Some cats also rub-mark on objects repeatedly in the vicinity of humans, but this may possibly be a displaced version of cat–human rubbing (Moore & Stuttard, 1979).

The facial secretions of domestic cats have been characterised in some detail (see Pageat & Gaultier, 2003). Five different facial 'pheromones' have now been identified and their chemical components elucidated (Table 4.1).

While the functions of F1 and F5 have not yet been elucidated, the F2 pheromone is known to be deposited by tomcats when rubbing on objects during courtship of a female in oestrus. The F3 part of the facial pheromone is deposited during facial marking of objects, as a cat might do when patrolling its home range. F4 has been found to be involved in allorubbing (see below) behaviour between cats and it is thought (although not confirmed) to reduce aggressive behaviour between the cats involved. Both F3 and F4 have been artificially synthesised to produce commercial products for use in behavioural therapy.

**Table 4.1** Chemical components of the facial secretions in the cat (data from Pageat & Gaultier, 2003)

| Secretion | Components |
|---|---|
| F1 | Oleic acid, caproic acid, trimethylamine, 5-aminovaleric acid, *n*-butyric acid, α-methylbutyric acid |
| F2 | Oleic acid, palmitic acid, propionic acid, *p*-hydroxyphenylacetic acid |
| F3 | Oleic acid, azeliac acid, pimelic acid, palmitic acid |
| F4 | 5β-cholestan acid 3β-ol, oleic acid, pimelic acid, *n*-butyric acid |
| F5 | Palmitic acid, isobutyric acid, 5-aminovaleric acid, *n*-butyric acid, α-methylbutyric acid, trimethylamine, azelaic acid, *p*-hydroxyphenylacetic acid |

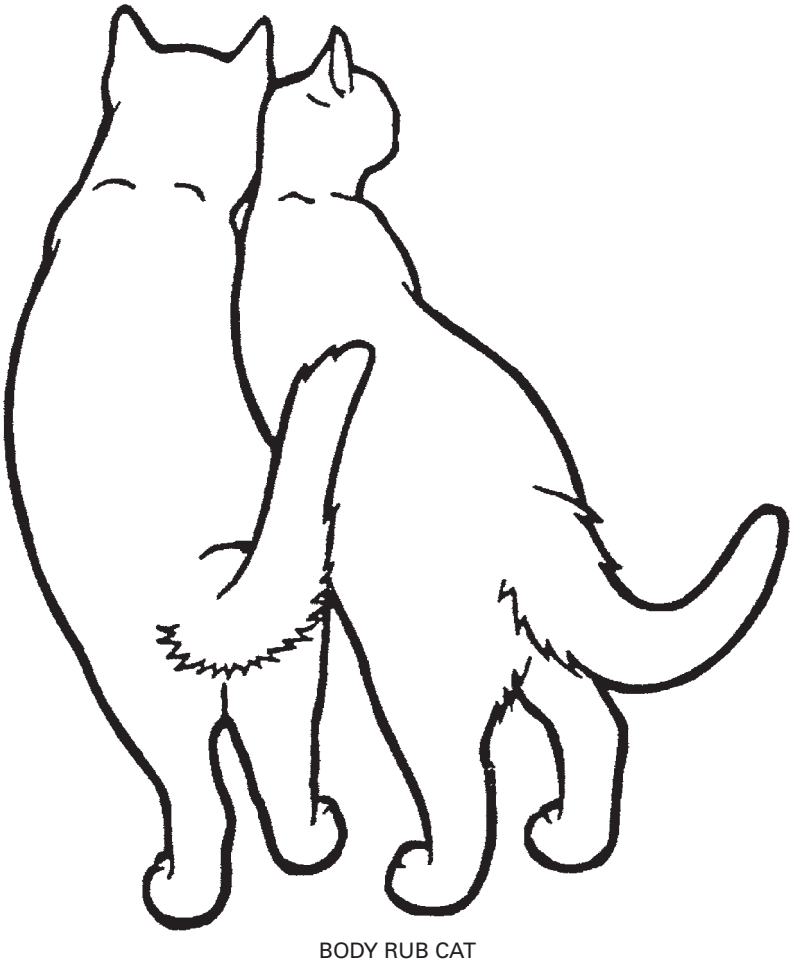



**Figure 4.3** Body or flank rubbing between two cats. From UK Cat Behaviour Working Group (1995).

## Auditory communication

Cat vocalisations are notoriously hard to categorise, partly due to the difficulty of distinguishing whether one sound is actually different from another or simply a variant of it, and partly due to individual differences in the production of sounds. Breed differences also add to the confusion, with many oriental breeds being generally more vocal than non-orientals (Marchei *et al*., 2009).

Compared to the familiar sound of a cat vocalising towards its owner, the amount of vocalisation heard between cats is surprisingly low. In fact the only contexts in which they are really heard outside the human–cat relationship are during agonistic, sexual and mother–kitten encounters.

Most of the aggressive and defensive sounds (Table 4.2) are strained-intensity calls (Moelk, 1944), as under these circumstances the cat is likely to be tensing its whole body in preparation for a fight. Tension in the throat is probably the reason why cats often drool during fights, or have to break off from vocalising to swallow repeatedly. The low pitch of the growl and the long duration of the yowl may convey the size and strength of the cat that is emitting them, and the abruptness and volume of the pain shriek may be designed to shock or startle the attacker into loosening its grip. Both females and males also produce sexual calls, specific to the breeding season (Table 4.2), which are also of high intensity (Shimizu, 2001), presumably advertising fitness to potential sexual partners and rivals of the same sex. Distinguishable yowls and mews which are not specific to the breeding season are also produced by both sexes.

The calls produced by kittens less than 3 weeks old are restricted to the defensive spit, purring, and a distress call which has aural characteristics similar to the adult miaow (see Figure 4.4). The latter is given when the kitten becomes isolated, or cold, or

**Table 4.2** Characteristics of the vocal signals used by adult domestic cats, compiled from Moelk (1944), Brown *et al.* (1978) and Kiley-Worthington (1984), and the circumstances under which each is most commonly used

| Name | Typical duration (s) | Fundamental pitch (Hz) | Pitch change | Circumstances |
|---|---|---|---|---|
| **Sounds produced with the mouth closed** | | | | |
| Purr | 2+ | 25–30 | – | Contact |
| Trill/chirrup | 0.4–0.7 | 250–800 | Rising | Greeting, kitten contact |
| **Sounds produced while the mouth is open and gradually closed** | | | | |
| Miaow | 0.5–1.5 | 700–800 | – | Greeting |
| Female call | 0.5–1.5 | ? | Variable | Sexual |
| Mowl (male call) | ? | ? | Variable | Sexual |
| Howl | 0.8–1.5 | 700 | – | Aggressive |
| **Sounds produced while the mouth is held open in one position** | | | | |
| Growl | 0.5–4 | 100–225 | – | Aggressive |
| Yowl | 3–10 | 200–600 | Rising | Aggressive |
| Snarl | 0.5–0.8 | 225–250 | – | Aggressive |
| Hiss | 0.6–1.0 | Atonal | – | Defensive |
| Spit | 0.02 | Atonal | – | Defensive |
| Pain shriek | 1–2.5 | 900 | Slight rise | Fear/pain |

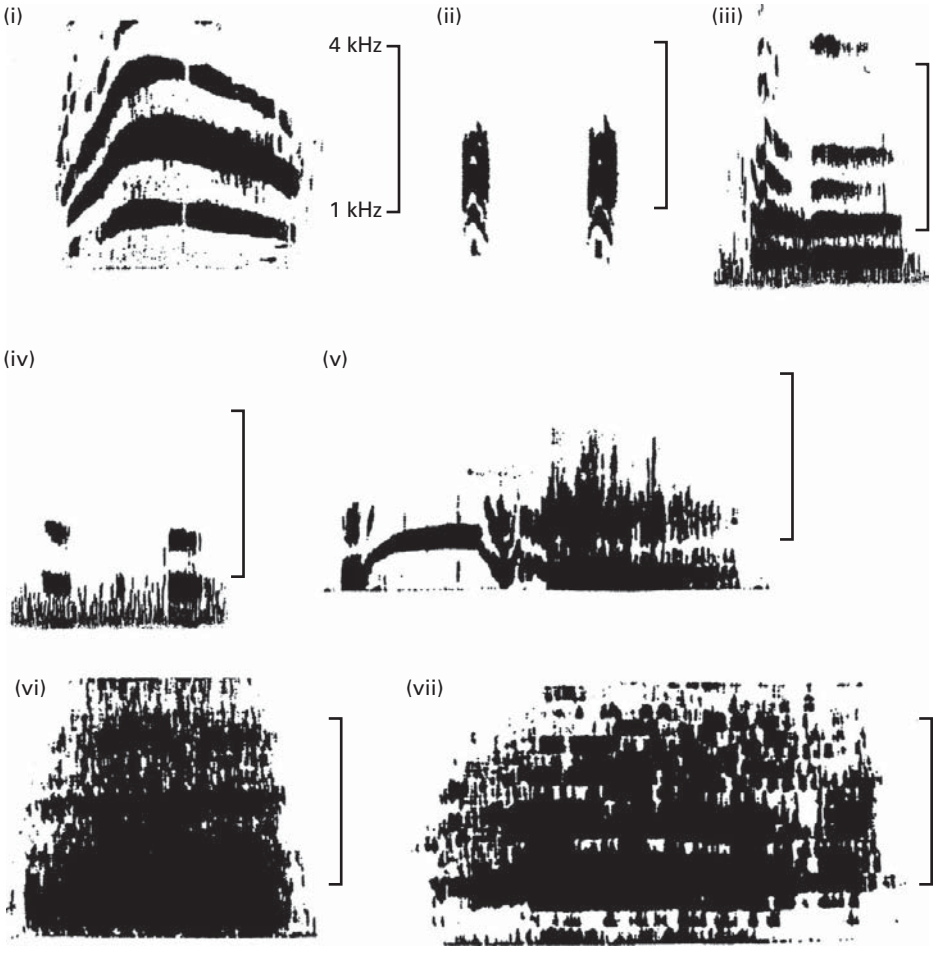



**Figure 4.4** Sonographs of typical kitten and cat vocalisations. **(i)** Kitten isolation call. **(ii)** Maternal chirrup. **(iii)** Miaow (typical). **(iv)** Miaow (atypical). **(v)** Howl. **(vi)** Hiss. **(vii)** Pain shriek. (iii, iv) provided by Jean-Luc Renck; others from Brown *et al*. (1978).

trapped, for example if its mother accidentally lies on top of it (Haskins, 1979). The call induced by cold is significantly higher-pitched than the other two, although this distinction disappears as the kitten becomes capable of thermoregulation at about 4 weeks of age. Restraint induces a call which is similar in pitch to that caused by isolation, but is significantly longer in duration, and the isolation call is generally the loudest (Haskins, 1979). It is therefore likely that mother cats can distinguish between these calls, and respond accordingly (Haskins, 1977).

Purring is a ubiquitous vocalisation among cats, but its function is not entirely understood and it was only 20 years ago that its method of production was finally elucidated. It is produced during both inhalation and exhalation, except for a brief pause at the transition between the phases of the respiration cycle, and therefore sounds as if it is a continuous vocalisation. The sound is generated by a sudden build-up and release of

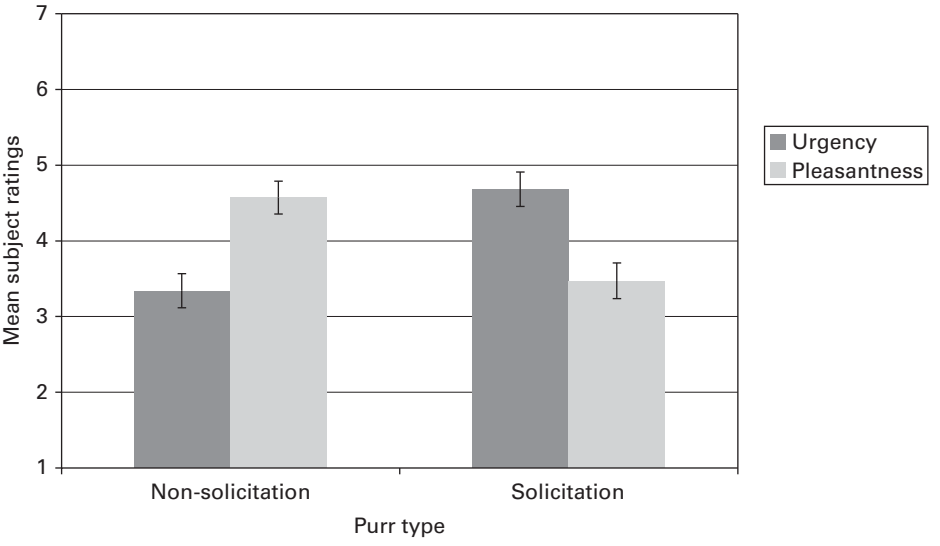



**Figure 4.5** Human judgements of the relative urgency and pleasantness of purrs recorded in solicitation (while cats were actively seeking food) and non-solicitation (cat in restful state) contexts. Solicitation purrs were found to be more urgent and less pleasant than those recorded in non-solicitation contexts. (From McComb *et al*., 2009, Supplemental Data.)

pressure as the glottis is closed and then opened, resulting in a sudden separation of the vocal folds, which generate the sound (Remmers & Gautier, 1972). The laryngeal muscles which move the glottis are driven by a free-running neural oscillator, generating a cycle of contraction and release every 30–40 ms (Frazer-Sissom *et al*., 1991).

Although it is traditional to interpret purring as indicating 'pleasure', it is produced in a wide variety of circumstances, most of which involve contact between the cat and a person or another cat. Kittens are able to purr almost from birth, and do so primarily when they are suckling, which may induce the mother to continue to nurse them (Haskins, 1977). Adult cats may purr when in contact with a familiar partner and during tactile stimulation with inanimate objects, such as when rolling or rubbing (Kiley-Worthington, 1984).

More detailed investigations into purring have found elements of miaow-like vocalisations contained within the purr when it is used in food-soliciting situations. Human observers are able to differentiate between 'normal' and 'food-soliciting' purrs and rate them quite differently (McComb *et al*., 2009; see Figure 4.5). The use of purring by cats in the food-soliciting situation suggests that purring appears to have been adapted by incorporating sounds that make it hard to ignore, thereby more successfully soliciting care from owners. This care-soliciting function may also explain the unexpected occurrence of purring sometimes observed when a cat is in severe pain. Purring may therefore function as a 'manipulative' contact- and care-soliciting signal possibly encouraged by the positive response of the owner.

Apart from purring, the vocalisation that is commonest in cat–human interactions is the miaow. This is very rarely heard during cat–cat interactions (Brown, 1993) and may

therefore be a learned response, based upon its effectiveness in getting human attention. It is certainly very easy to train in food-deprived cats; Farley *et al*. (1992) were able to induce a rate of two miaows per minute for a period of 2 h or more. Considerable variations in frequency, duration and form of the miaow occur, both within and between individuals (Figure 4.4, iii, iv) (Moelk, 1944) and they may contain additional noises such as growls, trills and clicks which vary the resulting sound produced (see Nicastro, 2004). This argues against these variations in the miaow having distinct (intra)species-specific meanings. The capacity to learn that this vocalisation is an effective means of gaining the attention of humans is therefore likely to be a product of domestication, even though the vocalisation itself is not. In this context, it has been shown that selection for tameness produces extensive changes in the vocal repertoire of the silver fox, especially in interspecific contexts (Gogoleva *et al*., 2011).

The use of miaowing mostly as a human-directed behaviour is supported by the discovery that house cats produce shorter, higher-pitched miaows when compared to feral cats (Yeon *et al*., 2011) and also when compared to the wild ancestor of the domestic cat (*F. s. libyca*) (Nicastro, 2004). This different miaow of the domestic cat is rated as far more pleasant sounding than that of *F. s. libyca*, even by listeners with no experience of cat vocalisations.

Perhaps surprisingly, humans find it difficult to accurately identify different calls when presented with miaows from unfamiliar cats. Nicastro and Owren (2003) presented humans with calls from 12 unfamiliar cats recorded in five different contexts, namely food-related, agonistic, affiliative, obstacle and distress. They found that while humans could differentiate between them, this was not achieved with a great deal of accuracy, although more success was achieved by people with previous experience of cats (either having lived with, interacted with or having a general affinity for them). Even then, their improved classification ability was only with the agonistic and affiliative calls. This may have been due in part to the absence of any associated visual cues, such as tail positions and bodily movements from the cat, which would normally be associated with vocalisation (Nicastro & Owren, 2003).

Finding only imprecise evidence for functional referentiality in the experiment above, Nicastro and Owren (2003) suggest that domestic cat miaows are basically designed to provoke rather than specify a reaction in humans. With continuous interaction cats and their individual owners may develop a system of different calls, which are recognisable and always specific to particular contexts. The term ‘ontogenetic ritualisation’ has been given to this process in other species (see Nicastro & Owren, 2003) and its possible existence deserves further investigation in cats.

## Visual communication

Wild-type (striped tabby) domestic cats are cryptically marked, and have no obvious structures that have been specially adapted for signalling. Despite its relatively immobile flat face, compared with the wolf, the cat has quite a varied repertoire of visual signals, mainly used in regulating aggressive behaviour. No evidence suggests that any

of the changes to the pelage introduced post-domestication (e.g. orange, white spotting, long hair) have had any substantial effect upon ability to signal, in contrast to the profound loss of visual signalling structures in some breeds of dog (Goodwin *et al*., 1997).

Many of the postures adopted in agonistic encounters can be interpreted as attempts by the cat to alter its apparent size, and thereby influence the outcome of the interaction. An aggressive cat will piloerect and stand at its full height, whereas a cat that wishes to withdraw from a contest will crouch on the ground, flatten its ears as shown in Figure 4.6(i) and withdraw its head into its shoulders, indicating that it is not ready to launch a biting attack. If threatened at length, the defensive cat may change its

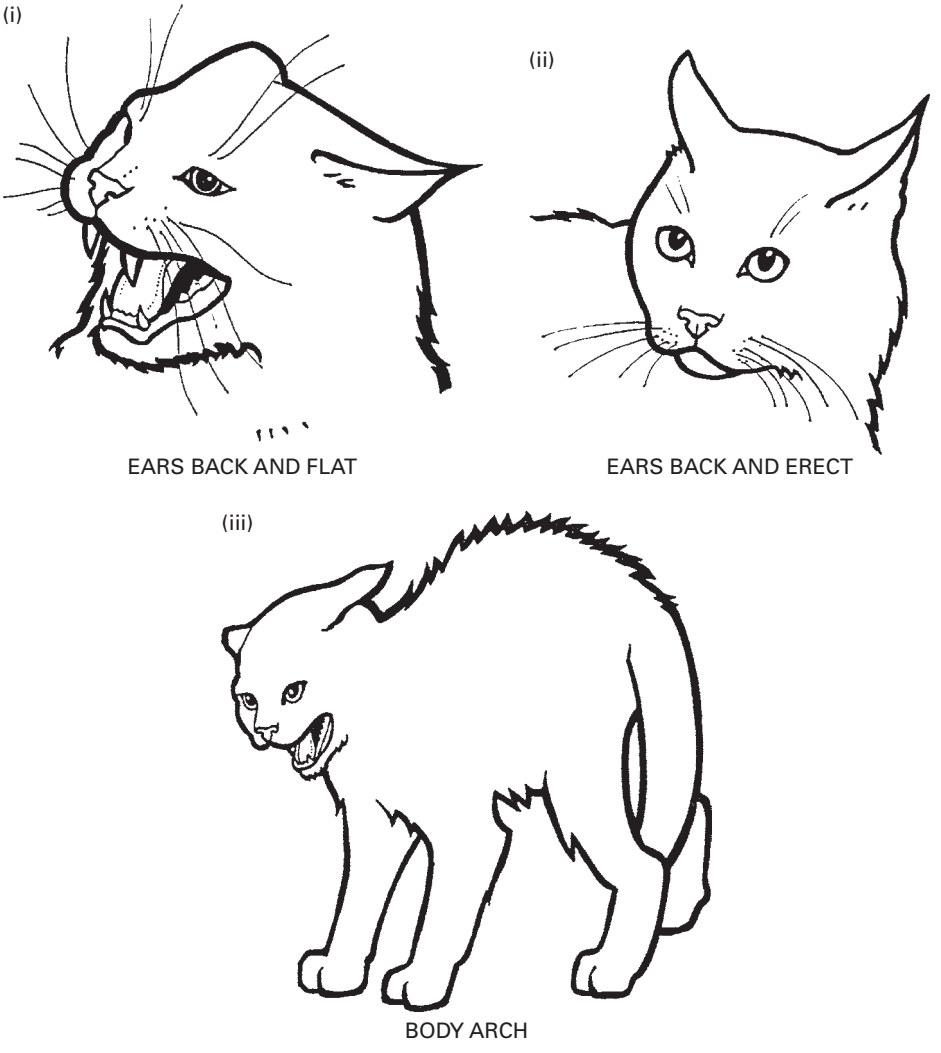



**Figure 4.6.** Ear positions associated with **(i)** defence and **(ii)** aggression. **(iii)** Arched back position suggesting conflicting emotions. From UK Cat Behaviour Working Group (1995).

behaviour to a more aggressive stance, possibly rotating its ears to a more threatening backwards position such as that shown in Figure 4.6(ii). The change from defensive to aggressive ear and body postures may be gradual, and often a cat will display conflicting emotions to attack and defend. Leyhausen suggested the arched back to be one such conflict behaviour (Figure 4.6(iii)). This is usually adopted side-on to the opponent, doubtless to maximise its visual impact. Although more extreme, it is similar in form to the 'Side-step' posture used by kittens in play; as this posture tends to disrupt bouts of social play (West, 1974), it is likely that one is the developmental antecedent of the other.

Presumably all of these postures are interpreted by the cat's opponent, and used in deciding how to proceed in the encounter, but little direct evidence indicates how each posture influences its outcome. Competitive encounters between animals of the same species tend to involve signals which are both unsubtle and aimed at manipulating the behaviour of the recipient, which attempts to combat this by 'mind-reading' (Krebs & Dawkins, 1984). The agonistic displays of cats are certainly easy to see, but the extent to which each posture is a form of 'bluffing' and how effective each is at deceiving its recipient remain to be investigated.

Rolling is a component of female sexual (pro-oestrous) behaviour, where it is usually accompanied by purring, stretching and rhythmic opening and closing of the claws, and is interspersed with bouts of object rubbing (Michael, 1961). Male-to-male rolling appears to be a form of submissive or appeasement behaviour, as it is never directed by mature males towards immature males, and is often followed by the mature male ignoring or tolerating the immature male's presence (Feldman, 1994b).

The cat's highly mobile tail, with its independently movable tip, appears admirably suitable for use as a signalling organ as well as assisting in balance. The tail is tucked away between the hind legs in the defensive posture, but this is unlikely to convey much information that is not already provided by the posture itself. Lashing of the tail from side to side is a component of aggressive behaviour (Kiley-Worthington, 1976), but its value as a signal is unknown.

The vertically held tail (Tail Up, TU) is associated with affiliative behaviour (Brown, 1993; Bernstein & Strack, 1996), and serves an important role in cat–cat interactions. In a colony of neutered feral cats, Cameron-Beaumont (1997) found that TU was particularly associated with rubbing on and sniffing of another colony member (TU occurred in more than 80% of these interactions). Almost all bouts of cat–cat rubbing were preceded by the initiating cat approaching with its tail up, and the probability of the rubbing occurring was further enhanced if the recipient cat also raised its tail. She confirmed the role of TU as a signal, and not simply a correlate, of affiliative behaviour, by presenting pet cats with silhouettes identical apart from the position of the 'tail'. The TU silhouette was significantly more likely to induce TU when it was first sighted by the responding cat, and was also approached faster than the silhouette with its tail down, which induced some tail-swishing or tail-tucked postures. The vertical tail therefore signals an intention to interact amicably; presumably it is necessary because of the potentially dire consequences of being approached by a cat whose intentions are unknown.

## Tactile communication

Although simple physical contact, as when two cats rest together, may have social significance, the two most obvious forms of tactile communication are cats rubbing their heads, flanks or tails on one another (allorubbing) and one cat licking another (allogrooming).

Even though Macdonald *et al*. (1987) proposed that 'cats in net receipt of rubbing would enjoy the benefits of dominance and, within their sex, greater inclusive fitness', little evidence has been forthcoming subsequently to confirm or refute this. In a breeding farm colony, they found that the flow of rubbing was asymmetrical in the majority of dyads, being skewed (a) from adult females to the male, (b) within adult females and (c) from kittens to adult females (Figure 4.7). Asymmetry in the flow of rubbing within dyads was also detected by Brown (1993) among neutered feral cats. She also found that interactions involving sitting together and allogrooming were unlikely to be preceded (or followed) by rubbing, which supports the suggestion of Macdonald *et al*. (1987) that rubbing tends to take place between cats of unequal size or status. Further research is needed to fully elucidate the social meaning of rubbing, including whether the transfer of scent that must inevitably take place has any significance.

While grooming of one member of a social group by another has significance in many species (Wilson, 1975), only one study has attempted to elucidate its role in the domestic cat (van den Bos, 1998). In an indoor colony consisting of 14 neutered males and 11 neutered females, the more aggressive individuals groomed the less aggressive more often than the other way around. In about one-third of the interactions, groomers were also aggressive

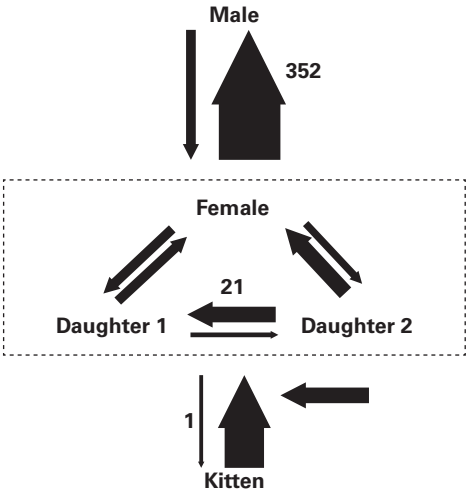



**Figure 4.7** Frequencies of cat–cat rubbing in a farm colony of five cats, comprising a female, her two adult daughters, an adult male and a male kitten. Widths of arrows are proportional to the square root of the number of rubbing interactions performed over an 8-month period (6 months for the kitten) by each age/sex class towards every other, and within the female sex class. Actual numbers of interactions are indicated for the largest, smallest and one intermediate arrow. All pairs of arrows indicate a significantly asymmetric performance of rubbing, except that between the Female and Daughter 1. Data from Macdonald *et al*. (1987).

towards the cats they were grooming, often immediately after the bout of grooming had finished. These results are consistent with the idea that allogrooming in the domestic cat is a form of redirected aggression or dominance behaviour. He found no evidence for any effect of kinship on the choice of partners for allogrooming (relatedness coefficients within the colony varied between 0 and $> 0.6$), which tends to argue against a role in maintaining bonds between kin. However, the possibility remains that allogrooming has other roles in free-ranging breeding colonies.

## Functional organisation of signals between domestic cats

Various techniques have been used to combine communicative patterns together into groups with overlapping functions, including subjective methods (Kerby, 1987), differences between pairwise relationships (van den Bos & de Vries, 1996) and probability of performance by an individual cat within a single interaction (Brown, 1993; Cameron-Beaumont, 1997). Direct comparisons between these studies are not straightforward, as different ethograms have been used, and different social compositions observed (Kerby: free-ranging breeding farm cats; van den Bos and de Vries: indoor colonies of breeding females; Brown, Cameron-Beaumont: neutered, mixed-sex indoor and free-ranging colonies). From data we collected from three neutered colonies, two free-ranging and one indoor, we detected five main groupings: contact including allogrooming, rubbing, aggressive, defensive and play (Figure 4.8; sexual and maternal behaviour were inevitably not included). The vertically raised tail (TU) was associated with both the grooming and rubbing groups, and also the aggressive group, and appears to be a key signal in determining the course of an interaction. In three colonies of entire females, groups of offensive, defensive and contact (including allogrooming) patterns were detected; allorubbing was grouped with sexual behaviour (rolling, lordosis) (van den Bos & de Vries, 1996).

These groupings are likely to be affected by the constitution of the group, in particular the age, sex and reproductive status of the individual cats. They may also be affected by genetics and early experience; the signalling patterns used by McCune (1995) in measuring cats' reactions to familiar and unfamiliar people show some differential effects of paternity (genetics) and early socialisation. Of the defensive vocalisations (directed towards a person), growl was inhibited by socialisation but unaffected by paternity, whereas hiss showed stronger paternal effects. The frequency of TU was highest in both friendly-fathered and socialised cats, but purring was not affected by paternity, and only enhanced by socialisation in the presence of a familiar person.

## Kitten–mother and kitten–kitten communication

Unlike the intermittent and sometimes long-distance communication that occurs between adult cats, the relationship between a kitten and its mother from birth to weaning is far more intense and involves much greater proximity. This requires them to communicate almost constantly, initially at least to ensure the safety and nutrition of

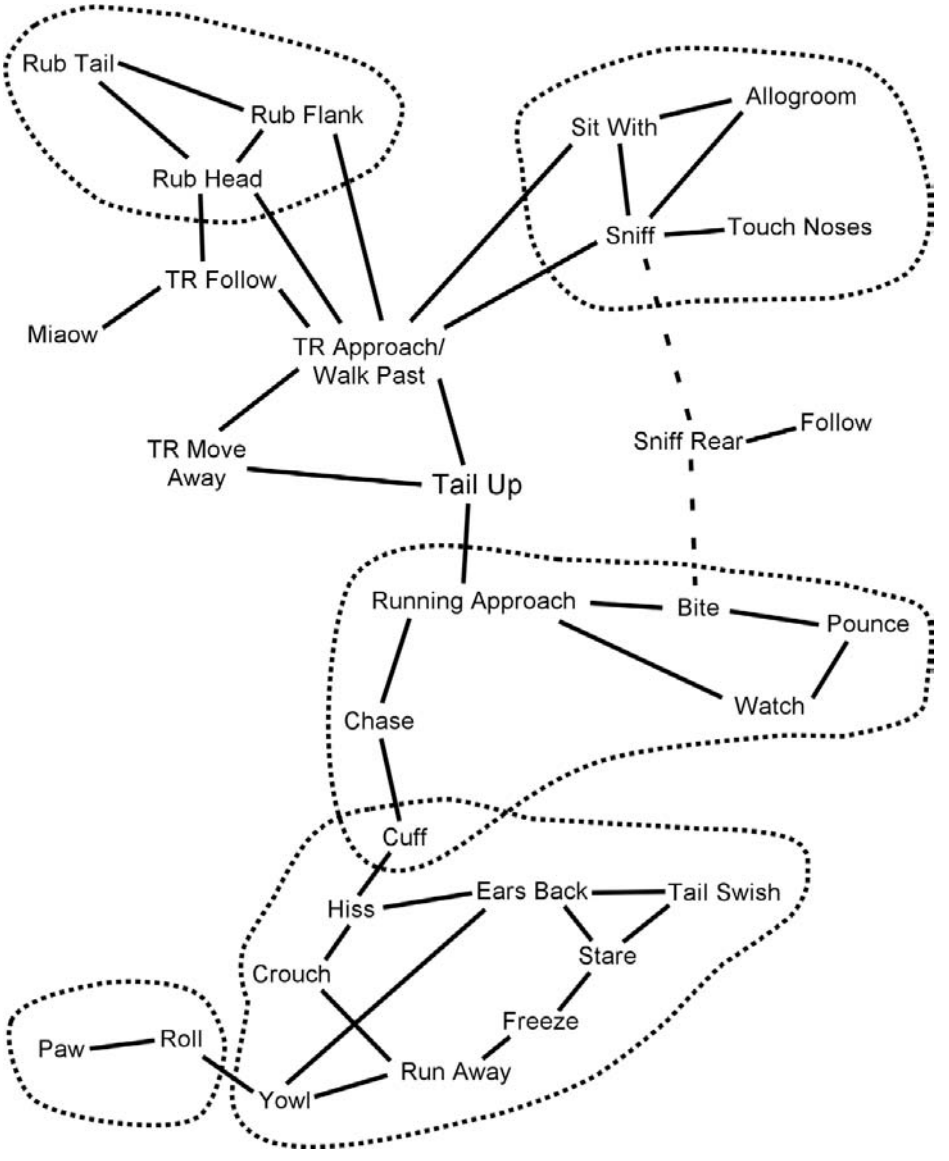



**Figure 4.8** A classification of social behaviour patterns performed by neutered cats (i.e. excluding sexual behaviour). Patterns which are very likely to be performed by the same cat during a single interaction with another cat in its own social group are joined by solid lines. The patterns fall into clusters, most of which have self-evident functions. Amicable interactions (top) often begin with the tail-up signal (centre) either when the cat is stationary (Tail Up) or moving (TR): these fall into two types, one consisting of allorubbing (top left) and the other mutual sniffing and grooming (top right). At the bottom right is a defensive cluster, and above it a cluster of aggressive patterns, linked together by Chase/Cuff. To its left are two patterns, Paw and Roll, normally associated with play behaviour, which may be attempts to deflect aggression by behaving in a kitten-like manner. Of the patterns not strongly linked to any of these groups, Miaow may be an attempt by one cat to alert another that it is following with the intention of initiating a bout of rubbing; Follow/Sniff Rear (only weakly linked to other patterns, shown by dotted lines) may be followed by amicable sitting together or by aggressive behaviour, presumably depending upon the reaction of the cat being sniffed. (Data collected by Sarah Brown and analysed by Charlotte Cameron-Beaumont, derived from 2044 interactive sequences between 42 neutered cats in three permanent groups. Solid lines represent positive $2 \times 2$ associations, $P < 0.001$ by chi-square.)

the kittens. Social contact with their mother during their first 4 weeks of life is also essential for the kittens to develop normally emotionally.

From the moment they are born a queen will communicate with her kittens, initially simply by lying on her side and encouraging them to suckle by nuzzling and licking them. Spending up to 70% of her time in the nest with them for the first 3 or 4 weeks, she lies with them to make them feed and grooms them, particularly around the perineal region to stimulate them to urinate and defecate.

Kittens rapidly develop a preference for a particular teat on their mother and appear to find their way to this via olfactory cues. Research has shown that while kittens will attach and suckle from other nursing queens, they are unable to find their preferred nipple as well as they would on their own mother (Raihani *et al*., 2009). This suggests that when born kittens initially use hormonally produced olfactory cues to find a lactating nipple but very soon respond to odour cues, probably deposited by their own saliva, that direct them specifically to their favourite nipple on their own mother.

From just a few days old, kittens will purr and knead the mother's ventrum when suckling. In such close contact, both the mother and any siblings will feel or hear the purring, which may indicate that the kitten is content and obtaining enough milk from its nipple. These behaviours may be carried forward into adulthood, often displayed by cats in pleasurable or amicable situations.

As the kittens become more mobile and stray out of the nest they communicate with their mother vocally via the calls described earlier in the chapter. She responds by finding the kitten and retrieving it by carrying by the scruff of the neck. The kittens gradually begin to start bouts of nursing themselves; the queen spends less and less time at the nest and eventually discourages the kittens from nursing. To achieve this she uses mainly postural signals to indicate her lack of enthusiasm, either by crouching on the ground with her paws all in contact with the ground, or by lying on the ground with her paws tucked under her. As well as discouraging them from nursing, the queen will start the process of weaning her kittens by encouraging them to hunt. This they learn by observation – she initially brings dead prey back to the nest, then will start to bring back live prey for them to practise their hunting skills on.

While feeding and learning from their mother, kittens in a litter of two or more will also be in constant proximity and learning to communicate with their siblings. Social play, involving much physical contact between kittens, contains many of the behaviour patterns seen later in life as an adult.

## Effects of domestication on intra- and interspecific communication

Based simply on the number of generations since it was domesticated, one would presume that the domestic cat's signalling repertoire should be relatively unchanged from that of its direct ancestor, the African wildcat *F. s. libyca*. With domestication, however, came an increased need to adapt not only to living alongside humans, but also to group-living situations, and therefore an increased requirement for both intra- and interspecific social communication.

Comparison of behavioural signals displayed by the domestic cat with those of undomesticated felids similar to its ancestors provides a method of examining what effect, if any, domestication may have had on particular signals. Differences between domestic cats and wild felids occur where domestication has altered the circumstances in which intraspecific behaviour is expressed (e.g. high local population densities) or where interspecific communication needs have increased (i.e. cat–human interactions).

One behaviour, and possibly the only one, that has received more detailed study in this respect is 'Tail-Up'. As part of the urine-spraying routine, with the tail raised vertically during spraying and then being immediately lowered, it seems to be exhibited in all felid species, both domestic and undomesticated. In this context the raising of the tail is a functional behaviour that enables the cat to spray efficiently, rather than an actual signal.

In domestic cats, Tail Up also appears as an affiliative signal, linked to other affiliative behaviours such as allorubbing and in such situations the tail is generally held upright for much longer periods of time compared to the urine-spraying context (Cameron-Beaumont, 1997). With the exception of the lion (*Panthera leo*), signals with the form of Tail Up have not been documented in undomesticated felids in association with social or object rubbing, situations where in the domestic cat the tail is almost always held vertically. This suggests that the use of Tail Up in this way may have evolved through the course of domestication, possibly as a response to increased sociality and the need for clearer, unambiguous visual signals. Similar selection pressures may possibly have led to its emergence as a signal in social situations in the lion (see also Chapter 16).

Domestic cats also display Tail Up as an affiliative signal during interactions with humans. However, in the cat–human context, perhaps the most immediately obvious (to humans) result of domestication on cat behaviour is the large variety of miaow-type vocalisations cats have developed in order to try and communicate with people. Described in more detail earlier in the chapter, these vocalisations, which are basically developments of the kitten mew sound, are rarely heard in cat–cat interactions (Brown, 1993). In a survey of zookeepers, Cameron-Beaumont (1997) found that adult undomesticated cats in captivity were very unlikely to miaow at humans, suggesting that adults of undomesticated species cannot spontaneously adapt kitten-type vocalisations for interaction with humans. This implies that via domestication the cat has developed, through some combination of culture and genetics, the ability to retain some kitten-type behaviours into adulthood when communicating with humans – a form of neoteny. Kneading and purring are further examples of juvenile behaviours retained into adulthood and directed towards humans by domestic cats.

## Concluding remarks

Although much has been discovered and is still being discovered about communication among domestic cats and between them and other species, particularly humans, it is possible that we will never have a perfectly complete picture of the subject. As human

observers we can only record signals, whether olfactory, auditory, visual or tactile, that are identifiable by us and which appear to elicit responses from other cats or from humans. It is possible that domestic cats actually produce some signals so subtle that to date they have remained unnoticed and unrecorded by us. It is equally possible that we credit some 'signals' with conveying more information than is actually the case. Take for example the apparent use of different vocalisations in different contexts by cats towards humans. While domestic cats undoubtedly try and often succeed in conveying different messages to their owners with specific calls, Nicastro and Owren (2003) showed that actually when the cat is unfamiliar to the human its miaow can only accurately convey the message 'I want *something*' as opposed to more specifically 'I want feeding' or 'I want to be petted'.

Sociality is, in evolutionary terms, fairly new in the domestic cat and has possibly developed as a consequence of cats' association with humans. This association and the opportunities and necessity for group-living for many cats continue to change in the modern world. Fortunately for domestic cats, they possess an enviable ability to adapt to almost any level of group-living with each other and to any level of dependency on man. As such, signals among group-living cats and between cats and their owners are under continued selection pressure to best fit an ever-changing ecological and social environment. Domestic cats of the future may develop new signals that enable them to communicate even more efficiently.

# III

# Social Life and Ecology

# 5 Social organisation and behavioural ecology of free-ranging domestic cats

Dennis C. Turner

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

This chapter reflects an amazing 'success story', the story of a predator species, the domestic cat, which has more or less conquered the world within a few thousand years – partly with the help of humans, but mostly because of its amazing flexibility. It is not a new story and therefore easy to summarise. The summary is based upon three chapters in the second edition of this book, namely Macdonald *et al*. (2000), Liberg *et al*. (2000), and Fitzgerald and Turner (2000), but of course updated with later findings. Nor is that success story without ecological consequences which continue to fire the debate between cat friends and cat foes – or at least cat lovers and conservationists. Both sides of this debate should view the evidence before making hasty judgements.

## Solitary life versus group-living: a question of resource availability

The domestic cat as a species and quite possibly as an individual shows amazing flexibility in its sociality toward conspecifics. Its ancestor, the North African wildcat, *F. s. libyca*, was (and is) indeed a solitary, territorial species, which presumably made use of the rodent populations concentrated in and around grain storage facilities of early farming settlements (see Chapter 7). As the likely story goes, this was beneficial to the farmers and they began provisioning the 'wild' cats with extra food, their home ranges became concentrated – and overlapping – around these human settlements and storage facilities, representing the first step toward domestication. The Resource Dispersion Hypothesis proposes that the dispersion of resources may be such that the smallest territory providing adequate security for the primary social unit (mother and offspring) may also support additional group members (Macdonald *et al*., 2000). In mammals, food and shelter are often the limiting resources for females, while females are often the most limiting resource for males. Field evidence supporting this hypothesis in domestic cats is presented in the next section, but the same authors also developed a theoretical model predicting when females of felid species should share food resources; only the lion *and* the domestic cat should do so under certain circumstances and be(come) social felids.

Clumped and abundant food resources have affected cat signalling behaviour over time (see Chapter 4), cat spatial patterns and population density, and with that, cat social organisation, natal dispersal and the mating system, socialisation of kittens toward conspecifics and humans, hunting behaviour and their effects on prey species populations.

## Home range size and overlap and cat density

Liberg *et al*. (2000) completed the most extensive analysis of cat spatial organisation and density over 10 years ago and little has been added to their findings since then. Home range size of cats with outdoor access shows considerable variation between the many study sites: for females it ranges from 0.27 ha in a city to 170 ha in the Australian

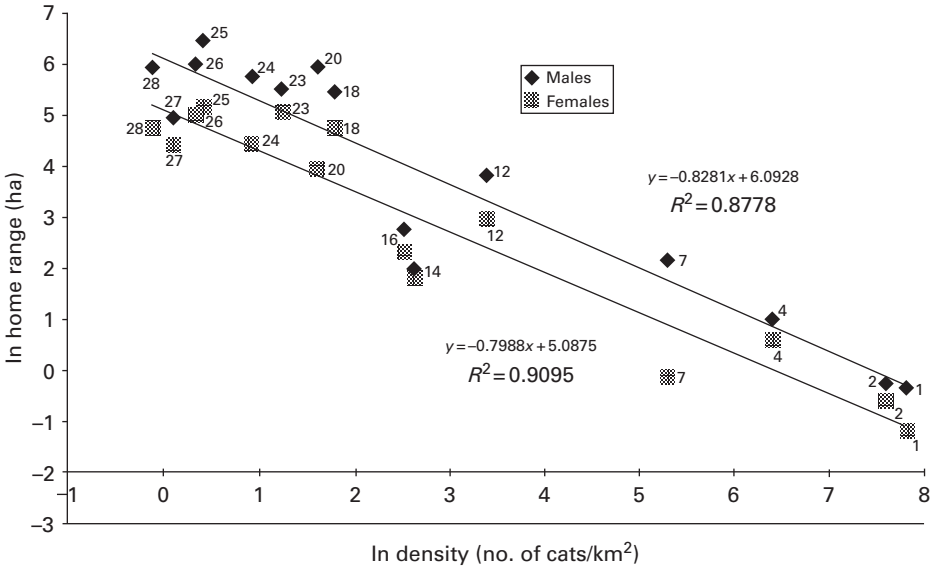



**Figure 5.1** Relationship between density and home range size in male and female cats. Numbers refer to study number in table 7.1 of Liberg *et al*. (2000). Scales are transformed to natural logarithms.

bush. Male ranges are on average about three times larger than those of females and range between 0.72 and 990 ha. Many factors affect range size of the individual animal, but the authors have successfully argued that female range size is determined by food abundance and distribution and that of males, primarily by female density and distribution (at most indirectly by food abundance and distribution). The males are competing for access to females in any given area.

Figure 5.1 from Liberg *et al*. (2000) illustrated the relationship the authors discovered between the home range size found at a field study site and the cat density reported at that site. The numbers inside the figure referred to 28 published studies with data on female and male home range sizes and cat density; the lines and equations are for regressions for the female (lower line) and male cat (upper line) data.

Although data on prey abundance and distribution are often missing in such field studies, the authors were able to categorise general characteristics of the food situation for most of those 28 studies. When the reported cat density was above 100 cats/km$^2$, the food was present in rich clumps, e.g. garbage bins, fish dumps or cat lover handouts. When the density was between 5 and 50 cats/km$^2$, food was present in smaller clumps, e.g. on farms or other households, bird colonies on islands, or abundant, dispersed prey. Where fewer than 5 cats/km$^2$ were reported, natural prey was scarce and dispersed (even though sometimes in patches) but no food for the cats was richly concentrated.

The degree of home range overlap or non-overlap (exclusiveness) indicates how animals in a population distribute resources among themselves. Most authors consider food to be the most critical resource for female cats. Group-living females utilise a food source that is predictable in time and clumped in rich, concentrated

patches (Liberg *et al*., 2000). A stable and rich clump of food can be defended by a group of individuals, even if not done so simultaneously. The authors argued that this is what group-living females do: within groups (or primary homes), female home ranges overlap considerably, especially at the primary feeding place (a barnyard, a refuse dump, the corner of a city park where cat lovers regularly place food), but even on the surrounding hunting grounds although these are rarely used simultaneously. The ranges of females from different primary homes or core living areas hardly overlap and Turner and Mertens (1986) have witnessed foreign females being chased away at the border. The ranges of adult males are not only larger, they show considerably more overlap, even during the breeding season when the males are out looking for receptive females (Liberg *et al*., 2000; see also Chapter 3).

## Social organisation of outdoor groups

Given that abundant, clumped food resources are associated with higher cat densities and groupings of animals, are these groups simply aggregations around a food source or do they exhibit true social structures? The latter is the case, again indicating the flexibility of the domestic cat. Macdonald *et al*. (2000) report on their various studies of farm cats in different-sized colonies: cats in such colonies have preferred social partners within the group, and in large colonies, the females tend to interact within their own lineages more than with other lineages. Lineages are the building blocks of cat society. In smaller colonies the females are usually related to each other (the same lineage) and it is not uncommon to observe communal nursing, indicating a very high degree of sociality, in this case, between related mothers. Adult males in a colony do not seem to be socially tied to a particular lineage, and are described as being either 'central' (near the resource centre frequently) or 'peripheral' (roaming rather widely). The consequences of being 'central' or 'peripheral' for the adult females of a colony are mentioned further below.

## Natal dispersal

When a young animal moves from the place it was raised to a new area where it will establish its own home range and begin breeding, this is called natal dispersal. This is fairly infrequent in female cats (probably due to adequate resources in the natal area), where female groups are built up and maintained because of philopatry in young females. Male dispersal, however, seems to be more frequent and has been described in both group-living populations and in solitary cats (Liberg *et al*., 2000). This is particularly frequent in the second or third year of life and where young males are not (at least partially) protected inside the pet-owning household from harassment by more dominant males outside. When young males disperse and move through unknown territory, they are more susceptible to environmental dangers, e.g. road accidents. Although they reach sexual maturity by the end of their first year, they are often not

integrated spatially and socially into a local cat society until their second or third year; only then do they become truly reproductively active, or so-called 'breeder-class' males (see Chapter 3).

## Consequences of group-living

In connection with the female lineages in group-living cats mentioned above, Macdonald *et al*. (2000) have discovered another interesting aspect: the bigger lineages in a colony tent do occupy the best 'central' area around the resource centre, while the smaller lineages tend to be on the periphery spatially, although they still have access to the central feeding area. This has consequences for the reproductive success of the females. Kerby and Macdonald (1988) reported earlier that in medium-sized and large cat colonies, central females produce more kittens per female per year than peripheral females, and they bring a higher proportion of their litters through the first year than the peripherals.

Living in groups can have adverse consequences for the health of the animals. Yamaguchi *et al*. (1996) and Macdonald *et al*. (1998) were among the first to look at health status and epidemiology in group-living cat society. They conclude that the strategies of pathogens affecting cats changed, as did the social system of the domestic form, adding cost to group-living animals. Perhaps the social system was more flexible than the cat's immune system in the rather short time since their domestication. Some of the pathogens affect the animals differently depending on their socio-spatial status – central or peripheral – and sex (Macdonald *et al*. 2000). Especially peripheral roaming males may pose a threat to wild felids in areas where they are sympatric depending on their epidemiological status.

## Hunting strategies

While ever more cats live in groups today, both on farms and in households, they still hunt for prey on their own, i.e. they do not hunt cooperatively, as lions do, which limits the size of prey items they can take. Cats from the same primary home may utilise the same hunting areas within their overlapping ranges, but rarely do so simultaneously (Turner & Mertens, 1986; Turner & Meister, 1988). Although it may seem as if cats spend hours waiting in front of a burrow to catch a prey item, they move about quite frequently and speedily in order to get to and from a hunting area within their ranges. Mother cats are especially under pressure to provision their offspring at home with prey items (see Chapter 2). Although all domestic cats are opportunistic hunters, observations indicate that males 'hunt' more often while simply moving about (Macdonald & Apps, 1978) and that females tend to move directly to a potential prey area and sit-and-wait, but not too long, before switching positions (Turner & Meister, 1988).

Various aspects of cat behaviour indicate that they have evolved primarily as predators of small rodents, which in nature live in burrows and are widely dispersed. As Paul

Leyhausen (1979; originally in German in 1956) noted decades ago, they are attracted to dark crevices and holes, as well as any moving (or moved) object that is not too large or too small, too slow or too fast. When they pounce, their rather efficient killing bite, which usually kills immediately, is also directed toward the slightly narrowed back of the neck behind the skull of the prey.

## When and where cats hunt

Although the ancestor of the domestic cat was nocturnal or at best crepuscular, house-cats today have apparently adapted to the diurnal human activity pattern (Fitzgerald & Turner, 2000). Most of their sleeping bouts occur during the night and activity phases during the day. In one study of hunting behaviour, most of the prey items were caught during the day, then during dusk or dawn, and the least (30%) during the night.

Cats evolved as opportunistic hunters and because their prey is small and normally widely dispersed, they had to be ready to stalk, pounce upon and handle a prey item whenever and wherever it appeared, even if not hungry (Fitzgerald & Turner, 2000). This explains at least in part why many cats still hunt and capture prey right after eating a dish of nutritionally sufficient cat food and why they sometimes play with their prey rather than consume it. Two of the author's Master students have conducted supplement feeding experiments on different Swiss farms (feeding the cat commercially available cat food at double the minimum daily requirement) without any measurable effect on their hunting behaviour or success. (Some farmers incorrectly assume that feeding their cats will reduce their hunting activity. Indeed, when they have a good mouse-catcher, farmers are more likely to keep it on their own farm by feeding it sufficiently!)

Cats are reported to return to the same field (e.g. mowed pasture or harvested grain field) or other places where they have recently been successful, but this needs more investigation. Gut examinations of cats shot in the forest indicate that the cats were usually not hunting there as they contain field-dwelling, and rarely forest-dwelling species, or worse yet from an owner's perspective – commercially prepared cat food (Turner & Meister, 1988; Fitzgerald & Turner, 2000).

## Hunting success rates

Cats are indeed very successful predators, requiring only between two and five 'pounces' to capture a prey item depending on the species involved – from mouse to rabbit (Fitzgerald & Turner, 2000). Another way of looking at this is to consider the amount of time spent per captured rodent, which of course varies seasonally – between just under 40 min and 3 h – and with hunting motivation: 1.6 h for mothers and 11.2 h for non-mothers (both sexes taken together). Leyhausen (1979) noted early on that the 'wait' before pouncing at a prey item was an integral part of the cat's hunting behaviour; presumably cats that did so were more successful and favoured, as a rodent would be far

enough from its burrow entrance so as not to just turn around and disappear. Whether this allows at least some birds to escape cat predation is unclear.

## Prey of domestic cats and effects on wildlife/prey species

When considering reports in the research literature on the prey diet of cats, it is important to realise that first, some statistics are given in percent frequency of occurences (% of cats with *x* prey types in their guts) while others list percent volume (or weight); second, where the studies were conducted (northern, southern hemisphere, latitude; on the continents or on small oceanic islands) influences the results; and third, if based upon what cats carry home to their offspring or owners, that is not necessarily representative of what they have eaten in the field (Turner & Meister, 1988; Fitzgerald & Turner, 2000). When considering the magnitude and effects of cat predation on their prey populations, it is further important to realise that what is observed locally is not necessarily representative on a wider scale, e.g. across different habitats or for other prey species; and that estimates of total predation, e.g. number of prey items taken by all cats over a one-year period, are meaningless from an ecological point of view unless put into relation to the entire population of that prey species and its annual production rate. Fitzgerald (1988), Turner and Meister (1988), Fitgerald and Turner (2000) and Turner (2012) have taken all of these points into account and come to the following conclusions.

As illustrated in Table 5.1, on the continents mammals occur in about 70% of the guts or scats of free-ranging cats, while birds occur in just under 21%. In the northern hemisphere, as opposed to Australia, reptiles are of little importance. A rather different picture emerges when islands are considered, and whether those islands have seabirds. With seabirds present on islands, birds are found on average in 60% of the guts or scats of cats on islands. When no seabirds are present, 84% of the guts or scats contain the remains of mammals. Again, island data indicate how flexible the domestic cat really is, but also that on a small ocean island, where prey species have evolved without any natural predators, cats brought in by people in the past should be removed or restricted to indoor living.

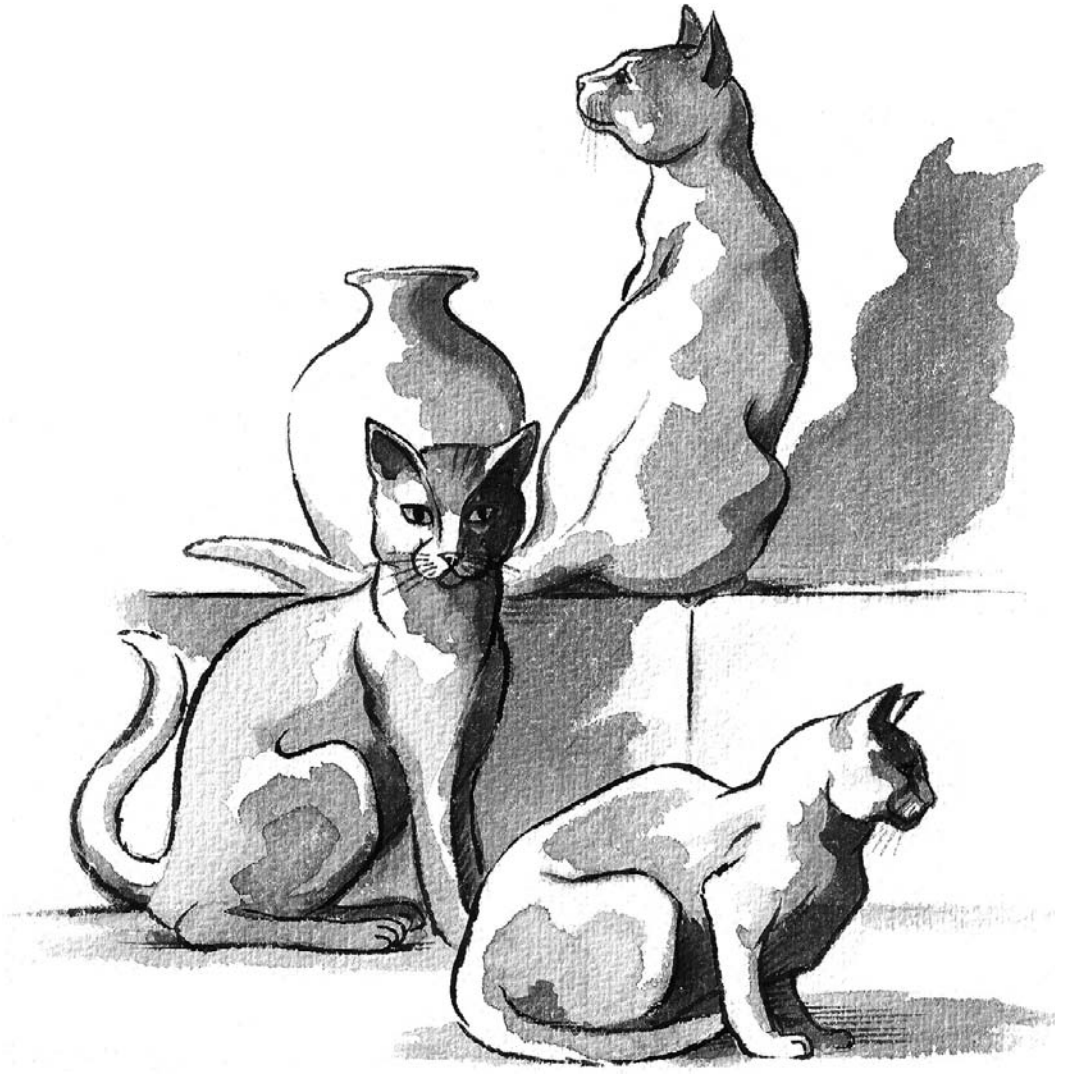
**Table 5.1** Average frequency of occurrence of mammals, birds and reptiles in the diet, based on gut or scat analyses in the northern hemisphere (Europe and North America combined) and Australia, and on islands, with and without seabirds recorded in the diet (number of studies in parentheses)

| | Mammals | Birds | Reptiles |
|---|---|---|---|
| Continents | | | |
| Northern hemisphere | 69.6(10) | 20.8(14) | 1.6(16) |
| Australia | 69.1(14) | 20.7(15) | 32.7(14) |
| Islands | | | |
| Without seabirds | 84.1(11) | 21.2(15) | 19.5(15) |
| With seabirds | 48.7(13) | 60.6(16) | 11.8(13) |

A widely cited study on bird predation (Churcher & Lawton, 1987) had precisely the methodological faults mentioned above and did not consider overall changes in the bird populations. Careful studies are still needed *before* 'condemning' all cats to an 'indoor' life, or even forbidding them as pets. One of the few fault-free studies was conducted by Weggler and Leu (2001) on Black Redstarts, a songbird thought to be particularly vulnerable to nest predators such as cats, in villages with a high density of feral cats. The purpose of their three-year study was to determine the mortality attributable to cats. Predation by cats caused 33% of egg fatalities, 20% of nestling fatalities, about 10% of fledgling fatalities and about 3% of adult fatalities. Cats indeed reduced the productivity of this population by 12% (from 1.20 to 1.06), but did not lead to a steady decline in the population. Nevertheless, two negative aspects of cat behaviour and ecology need to be mentioned: even if cats are not principally responsible for endangering their prey populations, little is known about how their hunting activities affect the welfare of individual prey animals (e.g. those wounded but not consumed). Second, domestic cats hybridise with other small wildcat species, several of which are endangered and need protection (Macdonald, 2012). When this is a serious problem, then outdoor access of the domestic cats should be restricted *locally* and in such a way that their welfare suffers least (Turner, 2012). The same is true for cats kept exclusively indoors for other reasons, e.g. fear of rabies from wildlife bites or traffic accidents. It is indeed possible to house cats well indoors, but based upon the higher frequency of behavioural problems shown by such cats, not everyone does this properly.

# 6 Social behaviour of domestic cats in the human home

Penny L. Bernstein[1] and Erika Friedmann



[1] The cat research community experienced the tragic loss of colleague Penny Bernstein in July 2012. But Penny had sketched out her chapter on the social life of indoor cats and discussed it several times with her good friend Erika Friedmann, who, with the permission of Penny's son, worked with her computer files to write this chapter 'together'. The editors are grateful for this contribution.

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

With so many people owning cats, understanding cat behaviour in the human home is important. Cats are the largest pet population in the USA. In 2011, of 374 million pets in the USA, 86.4 million were cats. In the same year, 78.2 million were dogs (ASPCA, 2012). In 2010 in the USA more than 22 billion dollars were spent on cat food (American Pet Products Association, 2011). Most of the research on domestic cat behaviour has been obtained from studies of cats in shelters, in laboratory situations or in free-roaming (feral) situations. Veterinarians and animal behaviourists have relied on information gained from studies of these populations for information about the normal behaviour of domestic cats. Most of the interactions people have with their cats is in the home. Domestic cats rarely accompany their owners outside of their homes. According to the recent American Pet Products Manufacturers Association's Pet Owners Survey, 3% of cat owners in the USA take their pets with them when they travel for at least two nights compared with 19% of dog owners (American Pet Products Association, 2011). In a recent repeated-measures study, cats were present with their owners 6% and dogs were present with their owners 19% of the time the owners were outside of the home (Friedmann *et al.*, 2010). However, very little is known about cats' behaviour in the home.

What is really known about cats in the home? Cat owners enjoy watching their cats. Part of the human fascination with cats stems from their unpredictability. Different cats have different ways of behaving. Cats may keep to themselves, or they can socialise with people or other cats. Cats' behaviour can change quickly from one moment to the next. All that is familiar, but a lot still needs to be studied.

Researchers have just begun to scratch the surface of analysing normal cat social behaviour in the home. Understanding normal cat behaviour can help us tell owners what to expect from their cats and the role owners play in cat–human and cat–cat interactions (Bernstein, 2005). Knowledge about normal cat behaviour will also help elucidate cat behaviour problems in the home, as illustrated in Chapter 14. This knowledge will be useful for devising strategies to decrease or eliminate problem behaviour (Overall, 1998).

A number of survey studies have obtained information about how owners perceive their cat's behaviour (Feuerstein & Terkel, 2008). They provide a context for understanding cat behaviour, but not a systematic effort to examine behaviour in detail. In fact, behavioural data contradict survey data in some cases (Feuerstein & Terkel, 2008). Only a few studies include actual observations of cat social behaviour *in the home*. The most seminal of those are discussed in temporal order below.

## What is known?

Miller and Lago (1990) studied the behaviour of 15 cats and 31 dogs owned by 46 elderly (60–91 years old) community-dwelling women living in a mostly rural area of the USA. The researchers interviewed the pet owners in their homes with their pets present and also observed the interactions of the pets with their owners during the

interviews. They classified observed behaviours into three categories: pet–owner interaction, pet behaviour toward owner, and pet behaviour toward interviewer. After leaving the home, the interviewer summarised the frequencies of different types of behaviours in each category for each pet. Cats exhibited less social behaviour during the interviews than dogs. Cats did not insert themselves into the interviews, dogs did. Cats did not mirror the behaviour of their owners, while dogs did. For example, when a dog was present, if the owner stood up the dog stood up too. Cats tended to be quiet, while dogs made noise. Owners gave dogs but not cats orders ('sit!'). Cats generally were described by the interviewer as 'calm, dignified, aloof or ignoring'. Cats were picked up by owners during interview more often than dogs and owners told more stories about their cats than about their dogs. The authors concluded that cats and dogs serve differently as companions.

Mertens (1991) observed human–cat interaction in the home and the complexity in these interactions. She observed 72 cats interacting with 162 people in the homes of 51 Swiss cat-owning families. Observation sessions lasted 210 min and took place over the course of one year. All cats observed were adult and had been in the household for at least 3 months. Two sessions, one in the morning and one in the afternoon, were conducted for each household. Mertens attempted to act as a normal visitor to the household to make the situation as comfortable as possible for the cats and their owners. She sat down or stood and talked with the cat owners and even ate with them if invited to do so. She did not interact with or respond to the cats. A pilot study was used to develop a list of 'social events' between cats and owners that occurred in the house. She created a checklist of behaviour patterns and observed and timed them. The behaviour patterns she identified included cats rubbing up against their owners' legs, a person picking up or putting down a cat, a cat approaching within 1 m or withdrawing from within 1 m of the owner, the owner speaking to the cat, the cat miaowing to the owner, and a wide range of other forms of behaviour. She examined the results looking at individual cats, individual owners and individual owner–cat pairs.

The list of behaviour patterns that were observed included the familiar interactions most owners list when talking about their cat's behaviour. Generally interactions were relatively few in number; most interactions lasted for less than 1 min. On average, people and cats were within 1 m of each other for less than 6 of the 210 min observed. People tended to approach the cat within 1 m more frequently than the cats approached the people. When the cat approached the owner, the cat and owner stayed within 1 m longer than when the owner approached the cat. The amount of interaction the cat had with the owners depended upon how much time the owner was home – the more the owner was home, the more interaction with the cat. Women were home more and had more interaction with their cats than men. Young people (11–15 years old) were least likely to be 1 m from the cat and had the least amount of interaction with the cats. The larger the number of cats in the home, the less interaction the cats had with people. A difference in behaviours of indoor- and outdoor-housed cats was not apparent, although outdoor-housed cats unsurprisingly spent less time inside the homes (Mertens, 1991). No one has conducted a similar study as a follow-up.

Bernstein and Strack (1996) studied how cats use space and patterns of interaction of 14 unrelated, non-reproductive domestic cats living in one household. Cats ranged in age from 6 months to 13 years. The behaviour of the cats who lived together in a single-storey American home with seven rooms, several closets and two baths was observed for a minimum of 4 h per day, 7 days per week, from late January to April 1981, for a total of 336 h. Observations were primarily in the hours just before and after morning or evening feeding. The cat owners were present during the study and interacted freely with the cats. The focus of the study was on the cats themselves and what they do in the home: what rooms they use, their favoured spots and which other cats they spend their time with. The interactions of the two human residents with the cats were not recorded systematically.

The most important finding was how patterns of behaviour changed over time and with the composition of the cat groups. Individual cats generally had places where they could predictably be found at various times of day. Not all cat–cat relationships are obvious. The death of a dominant cat affected spacing and behaviour of cats that rarely if ever were seen to interact with the dominant cat. Female cats were more likely to remain in fewer rooms, whereas male cats were more likely to roam between rooms. Kittens used more rooms than older cats and decreased the number of rooms they used as they aged within the observation period. Each cat had specific rooms it used on a regular basis – on average, each cat used 5 of the 10 available spaces. Favoured places were likely to be 'time-shared' rather than physically shared. That is, the places were used by different cats at different times of the day, not used by two cats simultaneously. Most time-sharing occurred among same-sex pairs: female/female or male/male. Within gender, specific individuals time-shared specific spots. Only one adult male/adult female time-shared. It began when the male was a kitten and the female took him in, even though the 'adoption' had taken place 8 years previously. There was little overt aggression and the cats seemed to have established relationships and knew their places. Certain individuals appeared to be dominant, they controlled who went where, who avoided whom, who conceded space to whom, and who took over places that had been vacated. No evidence of a hierarchy existed below the one or two dominant cats. The dynamics of space use and aggressive behaviour may be very different when animals are related or when a new cat is newly introduced into an existing community. The process of attaining the structure and balance demonstrated in this multi-cat household is a topic of applicability to cat owners and practitioners alike. It would be an interesting and worthwhile undertaking to follow up the study (Bernstein & Strack, 1996).

Bradshaw and Cook (1996) described pet cat behaviour including how they interact with their owners in one situation where interaction was likely to occur: immediately before and after feeding in the home. They conducted the first home study of cat feeding behaviour on 36 cats, one of which was an intact male, from 29 households in the UK. They studied eight sequences of cat feeding per cat consisting of the pre-feeding period when the female owner opened the can of food, through the cat eating the food, and 5 min after the cat ended the meal. Despite several cats living in some households, cats were fed individually. Each sequence began with the researcher handing the owner

a can of food for the owner to feed the cat in the owner's normal way. A total of 288 behavioural sequences were included in the analysis.

The major findings are consistent with what cat owners commonly describe. Before cats are fed by their owners, they are likely to interact with them, most frequently by miaowing, walking holding their tails up and rubbing against the owners' legs. They may also rub against stationery objects like furniture or walls. When the preparation phase is complete, the cat usually walks after the owner with its tail up until the food is placed in its usual position. After eating, most cats groomed themselves and had little interaction with their owners. The grooming sequence generally started with licking its lips and then moved to another part of the body. In approximately one-third of the cases the cat left the house before the full 5-min post-eating observation period was over. Cats had individual 'behavioural styles' (Lowe & Bradshaw, 2001) with considerable differences between individual cats in their behaviour. Owner and cat characteristics were not related to these styles. The authors conclude that the individual cat's style of behaviour may have origins in developmental and/or inherited factors (Bradshaw & Cook, 1996).

Barry and Crowell-Davis (1999) examined the behaviour of two-cat dyads in 60 US homes. The dyads were evenly split by cat sex: 20 pairs of females, 20 pairs of males and 20 mixed dyads (female/male). Each pair of neutered exclusively indoor-living adult (6 months to 8 years old) cats was observed for 10 h, 2 h per day for 5 days during periods when the owners were not in the house. All observations were between 7 a.m. and 9 p.m. The observer focused on each animal for alternate 15-min segments, recording its location, elevation and distance from the other cat every 60 s. Interactive social behaviour was recorded, irrespective of which cat was the focus during the segment. Continuous behaviour was considered a new bout if it lasted more than 30 s.

The most important finding of the study was that most cats got along well. Fewer aggressive and more affiliative behaviours were observed than expected based on studies of cats in other situations. Neither affiliative nor aggressive behaviour frequency differed according to cat sex. Cats did not demonstrate typical asocial behaviour of remaining far away from each other. Despite ample room for spacing of 5 m or more, cats spent more than one-third of their time within 3 m of each other. Male pairs spent more time within 1 m of each other than others. A wide variety of affiliative behaviour patterns were observed, mostly allorubbing, allogrooming and sniffing. The behaviours shown in these two-cat households were more typical of a social than of an asocial species. These findings challenged our assumptions about cat behaviour and made it clear that the behaviour of neutered domestic cats in the home is very different from what is seen in outdoor-living domestic cats and other species of cats (Barry & Crowell-Davis, 1999).

Turner (2000a) investigated differences in how people interact with purebred cats compared with non-pedigree cats. The study involved observation of the behaviour of the cat and the human–cat interaction in the cat owner's home as well as owner assessments of their cat's behavioural traits. These assessments involved a series of semantic differential scales for cat traits that were marked for the degree the cat possessed the trait and the degree the ideal cat would possess that trait. The European owners of 117 cats who were at least one year old included 61 people who owned

non-pedigreed cats, 21 owners of Siamese cats, and 35 owners of Persian cats. Two observers visited each cat-owning household on three consecutive days and recorded all interactions between the cat or cats and their adult owners.

Siamese and Persian cats spent more time interacting with their owners and more time in close proximity (less than 1 m) to their owners than non-pedigree cats. Differences were also observed in interactions with indoor and outdoor cats. Owners interacted with indoor cats more often and for longer when they were further apart and spoke more often to their cats. Women spent more time petting the cats, spent a greater proportion of the time interacting from a distance and spoke more frequently to the cat. The results of the surveys were consistent with the behavioural observations. Owners of purebred cats indicated that their cats were better-behaved, more interested in owners, more predictable, in other words closer to their expectations of the traits they wanted in a cat (Turner, 2000a). This finding has implications for owners who desire specific traits in their cats. As might be expected, the behaviour of purebreed cats is more consistent and more predictable than that of domestic shorthaired mixed-breed cats.

Turner and Reiger published a series of three papers examining the role of cats as emotional support for their owners (Rieger & Turner, 1999; Turner & Rieger, 2001; Turner *et al*., 2003). The first two studies included data from 47 women and 45 men who lived alone with one or two cats. The third paper with Gygax (Turner *et al*., 2003) included additional participants: 31 couples living without cats and 52 singly living people (43 women, 9 men) living without cats. The cats were at least 6 months old and had lived in their European households for a minimum of 6 months. The cat owners completed standardised mood questionnaires and cat attachment questionnaires and the behaviour of the cat owners was observed from 7 to 9 p.m. on one occasion. The cat non-owners (former cat-owners) completed only the surveys about mood.

Overall cats had little effect on their owners' moods. The presence of a cat was associated with lowered negative moods, e.g. depression or fear, but not with increased positive moods. Owners' moods had little effect on cat behaviour. It was noted that the more extroverted an owner felt, the more often their cat would approach them (Rieger & Turner, 1999; Turner & Rieger, 2001; Turner *et al*., 2003).

Wedl and colleagues (2011) videotaped and examined temporal patterns of human–cat interactions they observed in 40 European one-cat households. The dyads included adult owners with 7 male cat/male owner, 12 female cat/female owner, 18 male cat/female owner and 3 female cat/male owner combinations. Almost all cats ($n = 38$) were neutered and half of the cats had access to the outdoors. Two observers visited each dyad four times at approximately weekly intervals around the cat's feeding time. One observer interacted with the owner, who was asked to complete questionnaires and answer questions about his/her personality, cat ownership history and relationship with the cat. The other observer videotaped the owner, cat and interactions from 5 min before feeding the cat to 5 min after the cat stopped eating. Temporal patterns of behavioural interactions were identified via computer-assisted coding.

Female owners and their cats tended to interact more frequently and have more complex temporal interaction patterns than male owners and their cats. Cat gender did not matter. People's personality traits affected temporal patterning. People who scored

high on neuroticism had fewer and less-complex patterns of interaction with their cats. This study provided important keys to understanding human–cat interaction. Paying mutual attention and exchanging friendly tactile interaction are important components of these interspecific social interactions (Wedl *et al*., 2011).

Based on behavioural studies of domestic cats in their homes it is clear that despite the limitation of the relationship to the home setting, domestic cats and their owners have important social relationships. Observational studies have included only a limited number of situations and opportunities for behaviour. How this relationship is established and maintained and the support it provides requires further elucidation.

## Socialisation

Several studies conducted in the cat colony environment address the effects of early socialisation – handling by humans – on cat behaviour (see especially Karsh, 1983; Karsh & Turner, 1988). The animal colony research showing that inherited factors and socialisation early in life contributed to friendliness to people, McCune (1995) conducted a study combining the influence of both early socialisation (within the first 12 weeks of life) and inherited factors. This study was of 37 kittens from 12 different litters with 2 fathers, one friendly toward people and the other not friendly. When the cats were one year old, friendliness toward a familiar person was positively affected by both socialisation and a friendly father. Differences in boldness toward an unfamiliar object were related to paternity, not to socialisation. Socialised cats and cats with a friendly father were friendlier to unfamiliar people and less distressed when those people touched them.

A follow-up study in the home environment (Lowe & Bradshaw, 2001, 2002) confirmed and extended some of the findings using 29 household cats from 9 litters. The cats were held for 1 min by an unfamiliar person in their home environments immediately after meals fed by their owners when the cats were 2, 4, 12, 24 and 33 months old. Four elements of cat's behaviour – staying indoors, rubbing, investigative behaviour and boldness – were identified. They remained consistent as the cats aged. Littermates tended to have similar rubbing and boldness behaviours, indicating an inherited component to behaviour (Lowe & Bradshaw, 2001). By 2 months none of the cats were distressed by being held, indicating they all had received adequate socialisation. Amount of handling within the first 8 weeks was associated with boldness. These findings are consistent with both inherited factors and socialisation contributing to cats' behaviour. The consistency of individual cats' behaviour is striking (Lowe & Bradshaw, 2001, 2002). Nevertheless, some cats adore people whether handled or not and some remain aloof despite handling.

## Vocalisation behaviour

Cat vocalisations to humans is another obvious form of social behaviour in the home that could be interpreted, from the cat's perspective, as a communication with people. Understanding of the vocalisations could lead to better understanding of cat social

interaction with their owners. Few if any studies of vocalisations have examined cat vocalisation behaviour in the home setting. People are not good at evaluating the message of cat vocalisations without context (see Chapter 4). In the laboratory test setting, people were more successful at categorising positive and negative domestic cat miaow vocalisations when bouts of miaow vocalisations were presented rather than single miaow vocalisations. People who had more experience with cats did better at classifying cat vocalisations as positive or negative than those who were less familiar with cats (Nicastro & Owren, 2003). Again, in the artificial laboratory setting, people perceived the recorded miaows of domestic cats to be more pleasant than those of their closest relatives in the cat family, suggesting that cat vocalisations may have evolved to be more easily tolerated by people (Nicastro *et al*., 2004). A functional magnetic resonance imaging study demonstrated that central blood flow in humans responded differently to negative and positive cat vocalisations even though people could not accurately discriminate negative from positive animal vocalisation based on behavioural responses (Belin *et al*., 2008).

Vocalisations by domestic cats may have changed to promote interspecies communication with people. The human sensory system is able to distinguish at least some cat vocalisations in a controlled setting. Experience with cats improves sensitivity to vocalisations (Belin *et al*., 2008). These findings suggest that with effort people can learn to identify some miaows in their cats as communicating positive or negative mood. The communication roles of other types of vocalisation have not been examined. Normal cat vocalisation in the home remains to be explored. Chapter 4 includes research addressing vocalisation behaviour as cat–cat communication.

## Petting behaviour

Petting a cat is one of the most common interactions people have with their cats. Substantial bodies of research examined the contribution of petting cats to emotional support for people (Rieger and Turner, 1999; Turner & Rigger, 2001; Turner *et al*., 2003). Most studies that address petting as an aspect of cat social behaviour involve laboratory set-ups and are not natural. Two studies do address cat petting behaviour in the home. In a preliminary survey-based study, Bernstein (2000) found that owners of 90 cats could identify specific body areas that cats preferred for petting and specific areas in their homes where they preferred to be petted. The head area was preferred by 48% of the cats. The behaviour of the cats while they were being petted, for example closing their eyes, aligning their bodies to encourage rubbing of specific areas, or staying still, was used by their owners to understand their wishes. Petting behaviour resembled a reciprocal ritual, where cats were changing their behaviour, even leading their owners to specific places, to get their owners into the position that gave them maximum pleasure. A semi-structured behavioural observation within their own homes by owners of nine cats also suggested that cats prefer petting in certain body areas over others (Soennichsen & Chamove, 2002). The adult, neutered shorthaired cats were stroked by an adult member of their household for three 5-min sessions in four body areas, different areas on successive days. The owners recorded the cats' responses on a behaviour checklist that included

positive and negative behaviour elements. Cats had the most positive and fewest negative behavioural responses to petting between the eyes and ears and most negative and fewest positive responses to being petted around the tail. In many ways cats appear to train their owners to pet them in the ways they prefer. Petting provides an opportunity for mutual satisfaction for the cat and its owner.

## Cats and other species

Few studies have addressed interspecific behaviour of domestic cats in the home setting. Feuerstein and Terkel (2008) observed and video-recorded the behaviours of 45 pairs of cats and dogs living in the same household. Observations were partially structured and occurred shortly after the cat was fed between 4 and 7 p.m. Cats and dogs were observed in a closed room that was familiar to both animals without interaction with the owner. The free behaviour observations were followed by structured behavioural tests designed to evaluate aggression and play behaviour. The researchers also surveyed the owners of the pets about the history of the cats and dogs in the home and their behaviour with each other. Interactive behaviour between cats and dogs was classified as: dominance, fear/submission, aggression, play, or proximity. They also examined cat and dog behaviour in response to dog behaviour that has opposite meaning for cats and dogs such as tail wagging, stretching out the forefeet, lying on the back, and moving the head away. Finally, the way the cats interacted with the dogs was related to survey questions about the pets' ages and their ages when they began co-habitation.

Cats performed significantly more play, aggression and fear/submission behaviour than dogs; frequency of dominance and proximity-seeking behaviour did not differ significantly between dogs and cats. Observations of behaviour showed that female cats which had been neutered had more frightened and submissive behaviour than did those which had not, despite the owners' survey responses that indicated otherwise. Cats' and dogs' behaviour toward each other after seeing behaviour that has opposite meaning in the two species indicated that they understood the behaviour of the other species. Eighty percent of the opposite meaning behaviour by a dog was responded to by the cat in a dog-appropriate way and 75% of the opposite meaning behaviour by the cat was responded to in a cat-appropriate manner by the dog. The body language of the other species was more likely to be interpreted correctly when the introduction to the other species occurred at a younger age, especially less than 6 months old. Based on the survey and the behavioural observations the authors concluded that in most homes with cats and dogs living together they have an amicable relationship (Feuerstein & Terkel, 2008).

## General discussion

Many popular books have been published about cats and their behaviour and how to handle undesirable behaviour (Johnson-Bennett, 1994; Tabor, 1995; Dodman, 1997; Johnson-Bennett, 2000, 2004, 2007; Moore, 2007; Rainbolt, 2008; Ackerman, 2012;

Galazy, 2012). They were not based on formal study of cat behaviour in the home. Their sources of information were studies conducted in laboratory or shelter settings, case studies, or anecdotal information. Applied behaviourists spend considerable time and effort treating cat problem behaviour in the home, such as spraying, inappropriate elimination, fighting, aggression toward humans and clawing. Yet little is published about therapies for cats except case studies and popular books. Actual clinical trials with rigorous statistical analysis of therapies for changing cat behaviour in the home would be very helpful for evaluating the utilities of strategies for addressing particular undesirable cat behaviour.

A number of excellent studies have provided a window into normal cat behaviour in the home. Some findings will be of great importance for cat owners, for example the lack of aggressive behaviour by cats in multi-cat households indicates that in most cases cats are able to work out their social structure to establish an equilibrium where each cat has its place and role relative to the other cats (at least if well-socialised as kittens). Unfortunately, large gaps remain in information about normal cat behaviour in the home. Additional research is needed before reliable and valid information can be provided to pet owners, veterinarians and applied behaviourists. Formal observations in the home environment are required to evaluate petting behaviour, rubbing behaviour (is it marking or social or both?) and tail signals. More information is also needed about interactions with individual human family members, with other cats, and with other non-human animals. Finally, investigations are needed of the development and maintenance of interspecific communication with humans and with other animals in the home.

Rochlitz (2005 and Chapter 10) suggests that the standard for appropriate housing of cats in the home should be adapted from the 'Five Freedoms': freedom from thirst, hunger and malnutrition, freedom from discomfort, freedom from pain, injury and disease, freedom to express normal behaviour, and freedom from fear and distress. She proposes that to adapt these standards for laboratory and captive animals to domestic cats, the fourth freedom should be modified to 'Provision of opportunities to express most normal behaviour, including patterns directed towards conspecifics and toward humans'. Based on that standard, a lot must be known before the appropriateness of housing for household cats can be assessed. The big question is, what is normal cat behaviour? The question of normal behaviour in the home is pressing, especially when cats do not have access to the outdoors. In the USA, for example, approximately half of cats are not permitted outdoors.

Cats have lived with humans for possibly as long as 9500 years (Vigne *et al*., 2004). Evidence of cats living in close association with people goes back to well before the commonly known domestication of African wildcats by ancient Egyptians approximately 4000 years ago (Bernstein, 2005). If cats have been domesticated for so many years, perhaps their natural state is living with humans in homes rather than being out on their own. Or their more natural state could be in a more symbiotic relationship such as barn or farm cats. Feral behaviour is often used as a model for behaviour in the home, but perhaps it should be the other way around: behaviour in the home should be used as the model. Much about normal cat behaviour remains a mystery.

# IV

# Cats and People

# 7 Domestication and history of the cat

James A. Serpell

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Origins of the cat

Although the ancestors of the domestic cat (*Felis silvestris catus*) first appeared about 35 million years ago (MYA) during the late Eocene, the cat family or Felidae, to which all living cat species belong, emerged somewhat later during the Miocene about 10–11 MYA (Johnson & O'Brien, 1997; O'Brien *et al*., 2008). Morphological and molecular studies of phylogenetic relationships among living felids indicate that the 37 extant species can be divided up into 8 major phylogenetic groups or lineages: the *Panthera* lineage; the bay cat lineage; the leopard cat lineage; the caracal lineage; the ocelot, lynx and puma lineages; and, finally, the domestic cat or *Felis* lineage (Leyhausen, 1979; Collier & O'Brien, 1985; Salles, 1992; Johnson & O'Brien, 1997; O'Brien *et al*., 2008). The latter is believed to have diverged from the others around 6.2 MYA, and comprises four species of small cats that seem to have originated around the Mediterranean basin: the jungle cat (*Felis chaus*), the black-footed cat (*F. nigripes*), the sand cat (*F. margarita*) and the wildcat (*F. silvestris*) (O'Brien *et al*., 2008).

The last of these, *F. silvestris*, now inhabits a huge geographic range stretching from southern Africa through Europe to East Asia, and is currently divided into five, relatively distinct allopatric races or subspecies: *F. silvestris bieti* (the Chinese desert cat), *F.s. ornata* (the Central Asian wildcat), *F.s. silvestris* (the European wildcat), *F.s. cafra* (the southern African wildcat) and *F.s. libyca* (the North African/Near Eastern wildcat) (O'Brien *et al*., 2008). The difficulty of distinguishing morphologically between feral domestic cats and local wildcats, as well as occasional interbreeding, has generated a certain amount of disagreement among authorities regarding which of these subspecies gave rise to the domestic cat (*F.s. catus*). For example, based on morphometric and allozyme variability comparisons of ostensibly pure *silvestris*, *libyca* and *catus* populations from Sardinia, Sicily and the Italian mainland, Randi and Ragni (1991) concluded that *libyca* was the most likely ancestor of the domestic cat, and that hybridisation between feral domestic cats and either *libyca* or *silvestris* was 'improbable'. In contrast, a study of pelage and other morphological variation in a large sample of 'wild-living' cats from Scotland challenged the view that wildcats and domestic cats can be reliably distinguished from each other based on physical characteristics (Daniels *et al*., 1998). Anecdotally, Smithers (1968) also reported extensive natural hybridisation between urban feral cats and *F.s. cafra* in southern Africa. These observations suggest that gene flow between domestic, feral and wild populations may be sufficiently common in some areas to effectively blur the morphological and genetic distinctions between them.

Recent genetic studies have put most of these uncertainties to rest. Analyses of variation in mitochondrial and microsatellite DNA[1] have determined that all domestic cats, including purebred and free-roaming animals, are descended from the North African/Near Eastern subspecies, *libyca*, and that domestication probably occurred

[1] Mitochondrial or mtDNA is found in cell mitochondria and is inherited exclusively from the mother. Microsatellite DNA consists of short repetitive sequences of nuclear DNA and is derived from both parents.

somewhere in the Fertile Crescent (the Levant, southern Turkey and Iraq) of western Asia (Driscoll *et al*., 2007; O'Brien *et al*., 2008). Indeed, surviving subpopulations of *libyca* wildcats from remote desert areas of Israel, United Arab Emirates and Saudi Arabia were found to be almost indistinguishable genetically from domestic cats, further suggesting that the original progenitors of *F.s. catus* came from this same geographic region (Driscoll *et al*., 2007, 2009a).

There are additional reasons favouring *libyca* as the most likely ancestor of the domestic cat. All of the available archaeological evidence points to a North African or western Asian origin for *F.s. catus* (Zeuner, 1963; Baldwin, 1975; Todd, 1977; Ahmad *et al*., 1980; Clutton-Brock, 1981). Behavioural evidence also tends to exclude *silvestris* as the probable ancestor. European wildcats have a reputation for extreme timidity and ferocity when cornered, even when hand-reared as kittens. Experimental attempts to rear them and tame them from an early age have been largely unsuccessful owing to their exceptional shyness and intractability. First-generation hybrids between European wildcats and domestic cats also tend to resemble the wild parent in behaviour (Pitt, 1944; Cameron-Beaumont *et al*., 2002). Although *silvestris* is unlikely to be entirely untamable, it would appear to be a relatively unsuitable candidate for domestication.

Some of the other wildcat subspecies, in contrast, are reported to possess more docile temperaments, and often live and forage in the vicinity of human villages and settlements. On a trip to the southern Sudan during the 1860s, the botanist-explorer, Georg Schweinfurth, observed that the local Bongo people frequently caught these animals when they were kittens and had no difficulty 'reconciling them to life about their huts and enclosures, where they grow up and wage their natural warfare against the rats'. Schweinfurth was himself plagued by rats that periodically devoured his precious botanical specimens. In response, he procured several of these cats which 'after they had been kept tied up for several days, seemed to lose a considerable measure of their ferocity and to adapt themselves to an indoor existence so as to approach in many ways to the habits of the common cat'. By night he attached them to his belongings and by this means he was able to 'go to bed without further fear of any depredations from the rats' (Schweinfurth, 1878, p. 153). Roughly a century later, Reay Smithers (1968, p. 20) found that the wildcats of Rhodesia (Zimbabwe) made interesting, if somewhat demanding, pets. As with *silvestris*, the kittens tended to be intractable at first, but they eventually calmed down and became disarmingly affectionate:

> These cats never do anything by halves; for instance, when returning home after their day out they are inclined to become super-affectionate. When this happens, one might as well give up what one is doing, for they will walk all over the paper you are writing on, rubbing themselves against your face or hands; or they will jump up on your shoulder and insinuate themselves between your face and the book you are reading, roll on it, purring and stretching themselves, sometimes falling off in their enthusiasm and, in general, demanding your undivided attention.

Smithers also noted that these cats were more territorial than domestic cats, and that first-generation hybrids between them were more like the domestic parent in behaviour. The reasons for these striking differences in temperament between the different

subspecies of *F. silvestris* are unknown, although the European wildcat's reputation for 'wildness' would certainly point to a history of relatively intense persecution by humans.

Finally, there are etymological reasons for believing that the cat is of North African or western Asian origin. The English word 'cat', the French 'chat', the German 'Katze', the Spanish 'gato', the fourth-century Latin 'cattus' and the modern Arabic 'quttah' all seem to be derived from the Nubian word 'kadiz', meaning a cat. Similarly, the English diminutives 'puss' and 'pussy' and the Romanian word for cat 'pisicca' are thought to come from Pasht, another name for Bastet, the Egyptian cat goddess (Beadle, 1977). Even the tabby cat appears to be named after a special kind of watered silk fabric, once manufactured in a quarter of Baghdad known as Attabiy (*Chambers 20th Century Dictionary*).

## Domestication

Domestication is a gradual process rather than a sudden event, and it is therefore difficult to make precise claims concerning the exact time and place of cat domestication. Bökönyi (1969) has proposed dividing the domestication process into two distinct phases: (1) *animal keeping*, the practice of capturing, taming and keeping animals without any deliberate attempt to regulate their behaviour or breeding; and (2) *animal breeding*, eventually associated with the conscious, selective regulation and control of the animals' reproduction and behaviour. Phase 1, according to Bökönyi, is accompanied by only slight morphological divergence from the wild-type phenotype – usually no more than a slight decrease in body size – and these transitional forms of the species are often physically indistinguishable from the wild ancestor. Phase 2, in contrast, is usually associated with rapid and substantial divergence across a wide range of physical traits. Other important archaeological markers of full domestication include the occurrence of the species outside the geographical range of the ancestral species, artistic representations of the animal in an obviously domesticated state, and material objects associated with animal breeding and husbandry (Bökönyi, 1969).

Based on these kinds of criteria, it could be argued that the cat was only fully domesticated during the last 200 or so years, although it is probably more accurate to view *F. s. catus* as a subspecies that has drifted unpredictably in and out of various states of domestication, semi-domestication and feralness depending on the particular ecological and cultural conditions prevailing at different times and locations. Where and when Bökönyi's transitional *animal keeping* phase of domestication began for the cat is largely a matter of speculation. However, archaeological evidence from the Mediterranean island of Cyprus has provided important clues. Since its formation, the island of Cyprus has remained separated from mainland Asia Minor by a distance of some 60–80 km. As a result, it has no native cat species. Nevertheless, excavations at the sites of Khirokitia and Shillourokambos, some of the earliest human settlements on Cyprus dating from about 9500 years before the current era (BCE), have unearthed the unmistakable remains of cats, one of which was buried in association with a person.

The relatively large size of these animals suggests that they belonged to the subspecies *libyca*, and their presence on the island, living and dying in association with people, strongly implies that they were tamed and brought there in boats by the first human colonists. Assuming that Cyprus was not an isolated instance of cat taming, these discoveries indicate that the early Neolithic inhabitants of the Levant were already in the habit of capturing and taming wildcats, and taking them on ocean voyages, at least as early as 10,000 years BCE (Davis, 1987; Groves, 1989; Vigne *et al*., 2004). Significantly, this date also closely corresponds to the date when the domestic cat lineage is believed to have separated from its *libyca* origins based on genetic evidence (Driscoll *et al*., 2007).

Fragments of bone and teeth, identified as probably belonging to *F.s. libyca*, have also been excavated from Protoneolithic and Pre-Pottery Neolithic levels at Jericho, dating from between 7000 and 8000 years BCE. Although there are no obvious osteological indications that these animals were domesticated, and it is possible that they represent the remains of wildcats killed for food or pelts, it appears likely, in light of the Cyprus discoveries, that these animals were also tamed or semi-domesticated (Clutton-Brock, 1969, 1981). The earliest known cat remains from Mostagedda in Egypt, dating from sometime before 6000 years ago, were also found, together with the bones of a gazelle, in the grave of a man (Malek, 1993).

## Why cats were domesticated

The most widely accepted account of cat domestication posits that cats essentially domesticated themselves. According to the prevailing narrative, the advent of agriculture in the Middle East around 11,000 years ago, and the associated cultivation and storage of grains, such as barley and wheat, attracted the unwelcome attentions of small rodents, the natural prey of wildcats. Drawn by this local abundance of food, wildcats then invaded and colonised Neolithic towns and villages whose human inhabitants immediately saw the benefits of allowing these animals to live around their rodent-infested homes and granaries. This process, in turn, selected for the bolder, less-flighty individuals who eventually became the founders of permanent, urban domestic cat populations that relied increasingly on humans for food and shelter (Zeuner, 1963; Clutton-Brock, 1981; Leyhausen, 1988; Malek, 1993; Driscoll *et al*., 2009a; Faure & Kitchener, 2009). While this hypothetical scenario is superficially plausible, and certainly appealing to those who appreciate the cat's proverbially independent spirit, it tends to underestimate the active role that humans have played in the process of animal domestication through their habit of capturing and taming wild animals and keeping them as pets (Serpell, 1989).

Pet-keeping of this kind is extraordinarily widespread among living and recent hunting and horticultural societies, and there is no obvious reason to think that the inhabitants of the Neolithic Near East were any different. In the Amazon region, where hunting and gathering and subsistence horticulture is still practised by a handful of surviving Amerindian groups, hunters commonly capture young wild animals and

take them home where they are then adopted as pets, usually – although not invariably – by women. Such pets are fed and cared for with great enthusiasm. Typically, they are never killed or eaten, even though they may belong to edible species, and often they are mourned when they die of natural causes. A vast array of different birds and mammal species are kept in this way including members of the cat family, such as margay, ocelot, jaguarundi, and even jaguar (Serpell, 1989, 1996a). More to the point, these animals do not need to serve any functional or economic purpose in order to be valued by their owners. Rather, they are viewed, cared for, and indulged much like adopted children (Serpell & Paul, 2011). Based on these sorts of observations, it could be argued that the domestication of *F.s. libyca* occurred where and when it did because tamed wildcats were already an integral feature of village life as a result of people actively adopting, hand-rearing and socialising young wildcats to keep as pets (Galton, 1883; Sauer, 1952; Reed, 1954; Zeuner, 1963; Serpell, 1989; Erikson, 2000). Indeed, the practice of burying cats with their owners in early Neolithic Cyprus strongly implies that these primordial human–cat relationships were based on emotional considerations rather than mere utility (Vigne *et al*., 2004).

The Neolithic advent of agriculture, with its settled farming communities, storage of harvested grain and resulting proliferation of commensal rodents would certainly have enhanced the instrumental value of feline pets, as well as providing them with a more permanent ecological niche in which to flourish. However, it is unlikely that domestication would have proceeded at all in the absence of pre-existing social bonds between humans and cats.

## The cat in Egypt

On the basis of current evidence, it is likely that the cat first attained fully domesticated status (*sensu* Bökönyi, 1969) in ancient Egypt, although, again, the probable date of this event is, at best, an approximation (Faure & Kitchener, 2009). Although small Egyptian amulets representing cats may date from as early as 2300 BCE, the oldest pictorial representation of a cat in a domestic or household context dates from around 1950 BCE, and depicts a cat confronting a rat in a painting from the tomb of Baket III at Beni Hasan. In a small pyramidal tomb of similar age, Flinders Petrie excavated a chapel containing the bones of 17 cats together with a row of little pots that may once have contained offerings of milk (Beadle, 1977; Malek, 1993; Mery, 1967). From about 1450 BCE onwards, images of cats in domestic settings become increasingly common in Theban tombs, and it is likely that these animals were fully domesticated. The cats are usually illustrated sitting, often tethered, under the chairs of the tomb-owners' wives, where they are shown eating fish, gnawing bones or playing with other household pets. Although they comprise only a very small element of the paintings, the fact that they are there at all suggests that the presence of cats in Egyptian households was, by this time, taken for granted (Malek, 1993). Another popular motif in Theban tomb paintings – beautifully exemplified by the tomb of Nebamun, about 1450 BCE – depicts the cat 'helping' the tomb-owner and his family to hunt birds in the

marshes. Although some authorities have accepted this as evidence that aristocratic Thebans actually used house cats either to flush or retrieve game birds (Baldwin, 1975), the Egyptologist, Jaromir Malek (1993), cautions against taking these representations too literally. In his view, the marsh hunting scenes were largely imaginary and idyllic, and the artistic conventions of the period simply dictated that any representation of a family outing of this kind would have been considered incomplete without the additional participation of the family pet.

Because the ecological opportunities for cats in ancient Egypt were probably similar to those presented by other large agrarian civilisations in western Asia, it is necessary to offer some reason why cat domestication apparently proceeded further in Egypt than it did elsewhere in the ancient world. One plausible explanation may lie in the Egyptians' unusual affinity for animals in general. From the earliest dynasties onwards, animals appear to have played a particularly prominent role in Egyptian social and religious life. A diverse range of wild animals, including baboons, jackals, hares, mongooses, hippos, crocodiles, lions, frogs, herons, ibises and cats, came to be viewed as the earthly representatives of gods and goddesses, and many were the objects of organised religious cults (Smith, 1969). Cult practices often involved keeping and caring for substantial captive populations of these animals in and around temples dedicated to the worship of the appropriate deities. Species such as cats, which responded well to this sort of treatment, presumably bred in captivity, and so gave rise, over many generations of captive breeding, to a domestic strain more docile, sociable, and tolerant of living at high densities than its wild progenitor. The rodent-catching abilities of cats no doubt added to their value, but it seems likely that the Egyptians would have kept them as cult objects and as household pets regardless of any practical or economic advantages.

According to Malek (1993, p. 74), ancient Egyptian religion was 'a vast and unsystematic collection of diverse ideological beliefs which developed in different parts of the country in prehistoric times'. As a result, the belief systems of the Egyptians often appear little short of chaotic, with innumerable gods and goddesses – part human, part animal – merging, hybridising and diverging over time to produce a confusing array of bizarre and exotic deities. Most of these gods and their animal representatives originated in predynastic times as tribal emblems or *totems* which were then consolidated, under the Egyptian State, into a complex pantheon along the lines of those found in ancient Greece and Rome. As might be expected from their tribal and regional origins, the shifting status of these different deities often reflected the changing political fortunes of particular areas and groups within Egypt (see Mackenzie, 1913; Malek, 1993).

Until the end of the third millenium BCE, *F. s. libyca* appears to have been of little or no religious significance to the ancient Egyptians. From roughly 2000 to 1500 BCE, however, cats began to be represented on so-called 'magic knives': incised ivory blades that were intended to avert misfortune, including accidents, ill health, difficulties in childbirth, nightmares and the threat of poisonous snakes and scorpions. At roughly the same time, the male cat began to be represented as one of the forms or manifestations of the sun god, Ra, and it was in the guise of a tomcat that the sun god was believed to battle each night with the typhonic serpent of darkness, Apophis (Howey, 1930;

Malek, 1993). The Egyptians were doubtless familiar with the sight of cats killing snakes, and they evidently assumed that Ra would adopt the form of this animal when required to do likewise. The earliest representations of Ra in cat form depict animals that more closely resemble servals than cats, and it is probable that the switch to *F.s. libyca* coincided with this animal's increasing familiarity as a domestic pet. One of the cat forms of Ra known as 'Miuty' continued to be painted on the interior of coffins until the middle of the eighth century BCE, presumably as a protective or 'apotropaic' image.

During the New Kingdom (1540–1196 BCE) cats also began to be associated with the goddess, Hathor, and particularly one of her manifestations known as Nebethetepet, whose most salient characteristic was sexual energy. The natural sexual promiscuity of female cats was perhaps responsible for this link. The well-known association of domestic cats with the goddess Bastet did not become established until later, probably around the beginning of the first millennium BCE (Malek, 1993).

## The cult of Bastet

From the earliest period of Egyptian history, Bastet was the chief deity of the city of Bubastis (now Tell Basta) in the southeastern part of the Nile Delta. She was a goddess without a real name, as Bastet means simply 'She of the City of Bast'. The earliest portraits of Bastet, dating from about 2800 BCE, clearly depict her as a woman with the head of a lioness. On her forehead she bears the uraeus (serpent) symbol, and she carries a long sceptre in one hand and the *ankh* sign in the other. Her attributes appear to have included sexual energy, fertility, child-bearing and motherhood.

Despite her origins in Bubastis, Bastet soon came to be associated with other localities in Egypt, notably Memphis, Heliopolis and Heracleopolis. En route, and presumably through a process of local assimilation, she also became closely linked with a number of other important female deities, particularly Mut, Pakhet and Sekhmet (three goddesses who were also often represented as lioness-headed), as well as Hathor, Neith and Isis. Bastet and Sekhmet began to be paired as complementary opposites as early as 1850 BCE, and eventually came to be thought of as different aspects of the same goddess: Bastet representing the protective, nurturing aspects and Sekhmet the dangerous and threatening ones (Malek, 1993). Along with Hathor, Mut and Isis, Bastet was also sometimes referred to as the daughter or 'eye' of Ra.

It is not known precisely when domestic cats first came to be regarded as manifestations of Bastet, but it is likely that this occurred during the Twenty-second Dynasty (about 945–715 BCE), when the city of Bubastis rose to prominence during a long period of political instability in Lower Egypt. According to the Ptolemaic historian, Manetho, the Egyptian ruling family at this time was probably of Libyan extraction, and originated in Bubastis. As a result, the city became a major political centre and the scene of extensive building operations. Archaeological evidence suggests that the temple of Bastet was in a ruinous state at the beginning of this period, but it appears that several of the Bubastite pharoahs, particularly Osorkon I and Osorkon II, devoted considerable time and expense to its recontruction and expansion (Naville, 1892).

Contemporary information about the cult of Bastet, and her temple, is derived largely from the writings of the Greek historian, Herodotus, who visited Bubastis around 450 BCE during the heyday of the cult. Herodotus (1987, p. 191) equated Bastet with the Greek goddess, Artemis, and described her temple in the following glowing terms:

> There are greater temples, and temples on which more money has been spent, but none that is more of a pleasure to look upon . . . Save for the entrance, it is an island. For two channels from the Nile approach it, not mingling with one another, but each approaches it as far as the entrance, the one running round from one direction and the other from the opposite. Each is one hundred feet wide and shaded with trees. The propylaea [entrance] is sixty feet high and decorated with striking figures, nine feet high. The shrine stands in the middle of the city, and, inasmuch as the city has been raised high by the embankments and the shrine has not been stirred from the beginning, the shrine can be seen into from all sides. There runs round it a dry-wall, carved with figures, and within it a grove is planted round the great temple, with the hugest of trees, and in that temple there is an image. The temple is a square, a furlong each side. At the entrance there is a road made of laid stone, running for about three furlongs through the marketplace toward the east, and in breadth it is four hundred feet wide. On both sides of the road are trees towering to the sky.

Although Herodotus does not mention this specifically, it is likely that a sacred cattery or breeding colony of cats adjoined the temple. The job of 'cat keeper' was a hereditary position in Egypt, and strict rules evidently governed the care and feeding of these captive manifestations of the deity (Herodotus, 1987, p. 159).

The annual festival of Bastet, during April and May, was probably the largest in Egypt. As many as 700,000 people attended, having first performed a pilgrimage by water along the Nile. The ribald and licentious atmosphere described in Herodotus' (1987, p. 157) eye-witness description may help to explain the great popularity of the Bastet cult:

> Some of the women have rattles and rattle them, others play the flute through the entire trip, and the remainder of the women and men sing and clap their hands. As they travel on toward Bubastis and come near some other city, they edge the boat near the bank, and some of the women do as I have described. But others of them scream obscenities in derision of the women who live in that city, and others of them set to dancing, and others still, standing up, throw their clothes open to show their nakedness. This they do at every city along the riverbank. When they come to Bubastis, they celebrate the festival with great sacrifices, and more wine is drunk at that single festival than in all the rest of the year besides.

There is little reason to doubt the authenticity of Herodotus' account. Although superstitiously reticent about the theological details of Egyptian religion, he seems to have been a remarkably keen observer. Among other things, he was apparently the first to record the now well-known phenomenon of male infanticide in cats. 'When female cats give birth', he wrote, 'they will no longer frequent the toms, and the latter, for all their desire to mate with them, cannot do so. So they contrive the following trick. They steal and carry off the kittens from their mothers and kill them; but although they kill them, they do not eat them. The females deprived of their young and eager to have more, go then, and then only, to the toms; for cats are a breed with a great love of children' (Herodotus, 1987, p. 160).

The status of cats during this period of Egyptian history seems to have been roughly equivalent to that of cows in present-day India. Many people owned pet cats, and the death of one sent the entire family into mourning, shaving their eyebrows as a mark of respect.

Those who could afford it had their pets embalmed and buried in special cat cemeteries, vast underground repositories containing the mummified or cremated remains of hundreds of thousands of these animals. Cat cemeteries have been unearthed not only at Bubastis, but also at Beni Hasan and Saqqara, a clear indication of the spread of the cult of Bastet. Large numbers of small bronze statuettes of cats were also deposited in these sacred burial grounds. The act of dedicating one of these votive statuettes to the temple apparently assured the giver a permanent place at the side of the goddess (Malek, 1990; Naville, 1892). In 1888, one of these cemeteries was accidentally uncovered by a farmer, and the remains inside proved to be so numerous that an enterprising businessman decided to ship them to England for conversion into fertiliser. One consignment of 19 tons of mummified bones that arrived in Manchester was estimated to have contained the remains of 80,000 cats. The new soil additive, however, was mysteriously unpopular with English farmers, and the business venture proved to be a failure (Beadle, 1977).

Cats were a protected species in Egypt, and causing the death of one, even by accident, was a capital offence. Consequently, anyone encountering a dead cat fled immediately from the scene, lest others should think that they had a hand in its demise. Diodorus Siculus, writing in about 50 BCE, recorded a diplomatic incident involving a cat during a rather sensitive period in Romano-Egyptian relations. A Roman soldier made the mistake of killing one and 'neither the officials sent by the king to beg the man off, nor the fear of Rome which all the people felt' were sufficient to save him from being lynched by an angry mob. It is apparent from archaeological evidence, however, that the proscription against killing cats did not extend to those in charge of the temple catteries, at least during the Late and Ptolemaic Periods (*c*. 664–30 BCE). Radiographic analysis of cat mummies from this period has revealed that most of the animals were deliberately killed or 'sacrificed' by strangulation before they reached 2 years of age, presumably in order to supply the demand for dead cats to mummify as votive offerings (Armitage & Clutton-Brock, 1981).

## Out of Africa

The Egyptians generally restricted the spread of cats to other countries by making their export illegal. They even sent special agents out to neighbouring parts of the Mediterranean to buy and repatriate cats that had been illicitly smuggled abroad (Howey, 1930; Aberconway, 1949; Dale-Green, 1963; Mery, 1967; Beadle, 1977). Despite all these precautions, cats did eventually spread to other areas although, initially, progress was slow. The Indus valley Harappan civilisation (*c*. 2100–2500 BCE) has yielded surprisingly early evidence of the presence of urban cats. Bone remains have been excavated from the site of the city of Harappa and, more interestingly, the footprints of a cat being

chased by a dog are preserved in mud brick from the site of Chanu-daro (Ahmad *et al*., 1980). It is not known whether these cats were Egytian imports or the results of local domestication efforts. An ivory statuette of a cat, dating from about 1700 BCE, was found by archaeologists at the site of Lachish in Palestine. Egypt and Palestine enjoyed strong commercial links at this time, and it is likely that Egyptian entrepreneurs lived there and brought their cats with them. A fresco and a single terracotta head of a cat (about 1500–1100 BCE) are also known from late Minoan Crete, another area with which Egypt probably had strong maritime connections.

The cat does not appear to have reached mainland Greece until somewhat later. The earliest representation of the animal from Greece is on a marble block (about 480 BCE), now in the Athens Museum. It depicts two seated men, together with various onlookers, watching an encounter between a dog and a cat. The scene conveys an atmosphere of tense expectation, as if the observers were anticipating, and perhaps looking forward to, a fight (Zeuner, 1963). Cats were not apparently common at this time and were kept largely as curiosities, rather than for any practical purpose. When troubled with rodents, both the Greeks and the Romans used domestic polecats or ferrets in preference to cats. During the fifth century BCE, the Greeks introduced cats to southern Italy but, again, the animal does not seem to have been particularly popular, except as a rather unusual and exotic pet. An attractive Neapolitan mosaic, dating from the first century BCE, shows a cat catching a bird but, apart from this, there are few literary or artistic depictions of the species. The Romans failed to recognise the cat's vermin-destroying capabilities until around the fourth century AD, when Palladium recommended the use of cats, rather than the more traditional ferret, for curbing the activities of moles in artichoke beds (Zeuner, 1963; Beadle, 1977). Domestic cats were also slow to reach the Far East, probably arriving in China sometime after 200 BCE. Judging from contemporary illustrations, all of these early cats possessed the wild type, striped or spotted tabby coat colour, and many feral cats around the Mediterranean still retain this ancestral *libyca* appearance.

The Romans were probably responsible for introducing cats to northern Europe and other outposts of their Empire (Faure & Kitchener, 2009). Domestic cats were already present in Britain by the middle of the fourth century AD, and their remains have been found in various Roman villas and settlements in southern England. At Silchester, an important Roman site, archaeologists found a set of clay tiles bearing the impression of cat footprints. By the tenth century, the species appears to have been widespread, if not common, throughout most of Europe and Asia (Zeuner, 1963). Todd (1977) has pointed out that the cat owes much of its colonising abilities to the fact that it adjusts well to shipboard life. Judging from its present distribution, for example, the sex-linked orange colour mutant (i.e. ginger, ginger and white, calico and tortoiseshell) appears to have originated in Asia Minor, and to have then been transported, possibly in Viking long ships, to Brittany, northern Britain and parts of Scandinavia. Similarly, the tenth-century English blotched tabby mutant seems to have spread down a corridor through France along the valleys of the rivers Seine and Rhône. For centuries these rivers have formed part of an important inland barge-route between the Channel Ports and the Mediterranean.

The majority of modern cat breeds are of very recent origin and only a few, such as the Turkish Angora and Van cats, originated earlier than 1800. Twenty-two of the 38 recognised breeds were registered only within the last 100 years. The older 'foundation' breeds represent landraces – that is, naturally isolated geographic populations in which distinctive morphological traits became fixed due to founder effect and genetic drift – while the more recent breeds are mainly the products of deliberate hybridisation and selection from among these older forms (Lipinski *et al.*, 2008; Menotti-Raymond *et al.*, 2008).

## Changes in attitude

The gradual extinction of the pagan gods and goddesses, and the rise and spread of Christianity, produced a dramatic change in attitudes to cats throughout Europe. From being essentially benevolent symbols of female fertility, sexuality and motherhood, they became, instead, the virtual antithesis; malevolent demons, agents of the Devil, and the traitorous companions of witches and necromancers. It is not all clear what motivated this change in the perception of cats, although political forces doubtless played a part. In order to consolidate its power, the medieval Church sometimes found it necessary to employ extreme ruthlessness in suppressing unorthodox beliefs, and extirpating all trace of earlier pre-Christian religions. Perhaps because of its symbolic links with earlier fertility cults, the cat was simply caught up in this wave of religious persecution (Russell, 1972; Engels, 1999).

Between the twelfth and the fourteenth centuries, nearly all the major heretical sects – the Templars, the Waldensians, the Cathars – were accused of worshipping the Devil in the form of a large black cat. Many contemporary accounts described how their rituals involved the sacrifice of innocent children, cannibalism, grotesque sexual orgies, and obscene acts of ceremonial obeisance toward huge cats which were supposedly kissed on the anus (*sub cauda*). Many heretics, needless to say, admitted to engaging in such practices when subjected to physical torture. Alan of Lille in the twelfth century even attempted to derive the term 'Cathar' from the Old Latin word for cat, *cattus*. In reality, the Cathars derived their name from the Greek word *Katharoi*, meaning 'the pure ones' (Russell, 1972; Cohn, 1975).

Under Christianity, cats also came to be closely associated with witchcraft, although the nature of this association varied from place to place. In continental Europe, ecclesiastical and secular authorities during the fifteenth, sixteenth and seventeenth centuries had tended to depict witchcraft as another form of heresy; in other words, as an organised cult of Devil-worshippers that existed in opposition to the true faith. Like their heretical predecessors, witches were said to fly to their gatherings or 'sabbats', sometimes on the backs of demons disguised as giant cats. The Devil also displayed a strong preference for appearing to his disciples in the form of a monstrous cat (Russell, 1972; Cohn, 1975; Kieckhefer, 1976).

At the level of popular or 'folk' culture, it was more common, at least in northern Europe, for people to view both cats and hares as the preferred forms adopted by witches when engaging in acts of malefice. As early as 1211 AD, Gervase of Tilbury

attested from personal experience to the existence of women, 'prowling about at night in the form of cats' who, when wounded, 'bear on their bodies in the numerical place the wounds inflicted upon the cat, and if a limb has been lopped off the animal, they have lost a corresponding member' (Summers, 1934, p. 194). In 1424 a shape-shifting witch named Finicella was burned in Rome for allegedly attempting to kill a neighbour's child whom she visited in the form of a cat. The child's father managed to drive the cat away, wounding it at the same time with a knife. Later Finicella was found to have a similar wound on precisely the same part of her body (Russell, 1972). Stories of this type are extremely widespread in medieval and post-medieval witchcraft folklore, and they provide an interesting connection with another well-known diabolical role of the cat: that of the archetypal witch's 'familiar' (Campbell, 1902; Howey, 1930; Summers, 1934; Dale-Green, 1963; Mery, 1967; Beadle, 1977; Serpell, 2002).

Briefly defined, the familiar or 'imp' was a demonic companion whom the witch dispatched to carry out her evil designs in return for protection and nourishment. Although it crops up from time to time all over Europe, the concept of the familiar achieved its most elaborate and vivid expression during the English witch trials of the late sixteenth and seventeenth centuries (Serpell, 2002). A fairly typical example is provided by the 1582 trial of Ursula Kemp, during which her illegitimate son testified that his mother possessed:

> four several spirits, the one called Tyffin, the other Tyttey, the third Pygine, and the fourth Jacke: and being asked of what colours they were, saith that Tyttey is like a little grey cat, Tyffin is like a white lambe, Pygine is black like a toad, and Jacke is black like a cat. And hee saith, hee hath seen his mother at times to give them beere to drinke, and of a white Lofe or Cake to eat, and saith that in the night time the said spirites will come to his mother, and sucke blood of her upon her armes and other places of her body.

Various local women also came forward to testify that Kemp had used her familiars to make either them, or their children, ill (Ewen, 1933). Even in this relatively early trial, cats already predominate in the role of witch's familiar. They continued to do so throughout the entire period of witch persecution in England (see Figure 7.1), and have since become the ubiquitous ingredient of all modern Halloween iconography.

As demons incarnate, it might be assumed that these animal familiars possessed a degree of autonomy. Judging from various contemporary accounts, however, the line separating the 'cat familiar' from the 'cat-as-transformed-witch' was a thin one, at least in the popular imagination. In several cases, witches were reported to suffer parallel injuries when their familiars were wounded, and sometimes it is clear that prosecution witnesses believed that the familiar was simply the witch herself transmogrified. In the notorious case of the Walkerne witch, Jane Wenham, in 1712, several witnesses not only testified to being visited and 'tormented' by her cats, but also reported that one of these cats had the face of Jane Wenham. Jane Wenham was one of the last people to be formally condemned for witchcraft in England. Thanks to pressure from an increasingly skeptical London public, the verdict was eventually overturned and she was pardoned (Ewen, 1933; Summers, 1934; Serpell, 2002).

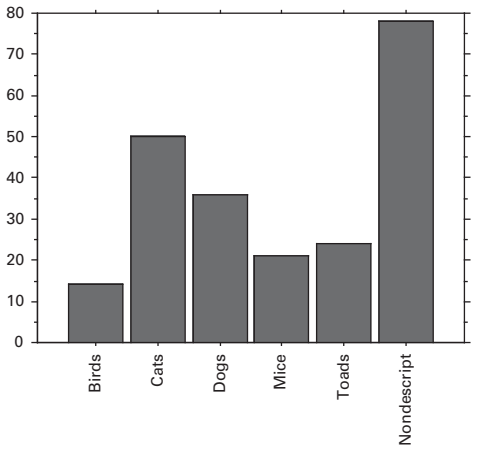



**Figure 7.1** Frequencies with which different animal species feature as 'familiars' or 'imps' in a total of 207 English witch trials between 1563 and 1705 (because of their particularly aberrant nature, the trials brought by Matthew Hopkins and John Stearne in 1645–6 are not included in this analysis). NB: If the 'nondescript' category is ignored, cats are the most frequently reported familiars.

Some of the hostility toward cats that emerged during this period may have had a medical basis. Witchcraft folklore abounds with stories of witches adopting the form of cats specifically in order to sneak into people's houses to smother them in their sleep (Briggs, 1996). In what is probably one of the earliest references to allergic asthma, Edward Topsell, writing in 1607, maintained that 'the breath and favour of Cats consume the radical humour and destroy the lungs, and therefore they which keep their Cats with them in their beds have the air corrupted, and fall into several Hecticks and consumptions'. Even as recently as the 1920s, local superstitions held that it was unsafe for a cat to sleep in a child's cot or bed because of the danger of suffocation (Opie & Tatem, 1989), and a recent survey in the USA found that respiratory allergies are one of the most common reasons given by people for relinquishing pet cats (but not dogs) to animal shelters and SPCAs (Scarlett *et al*., 1999).

Another source of ambivalence was the widespread belief that a cat's eye changes in shape and luminescence according to both the height of the sun in the sky, and the waxing and waning of the moon. The Egyptian author, Horapollon, writing in the fourth or fifth century AD, noted that the pupils of the cat's eye changed according to the course of the sun and the time of day. The Roman writer, Plutarch, also mentioned the phenomenon, as did the English naturalist, Edward Topsell, in his *Historie of Foure-Footed Beastes* (1607):

> The Egyptians have observed in the eyes of a Cat, the encrease of the Moonlight, for with the Moone, they shine more fully with the ful, and more dimly in the change and wain, and the male Cat doth also vary his eyes with the sunne; for when the sunne ariseth, the apple [pupil] of his eye is long; towards noone it is round, and at the evening it cannot be seene at all, but the whole eye sheweth alike.

The conspicuous eye shine produced by cats' eyes at night intrigued many early writers. The majority seems to have believed that cats were able to generate this light themselves

by storing light collected during the day (Aberconway, 1949). Many found the phenomenon disconcerting. Topsell, for example, states that the glittering eyes of cats, when encountered suddenly at night, 'can hardly be endured, for their flaming aspect'.

With such a wealth of negative associations, it is not altogether surprising that cats became the objects of widespread persecution throughout Europe during the Middle Ages and the early modern period. On feast days, as a symbolic means of driving out the Devil, cats, especially black ones, were captured and tortured, tossed onto bonfires, set alight and chased through the streets, impaled on spits and roasted alive, burned at the stake, plunged into boiling water, whipped to death, and hurled from the tops of tall buildings; and all, it seems, in an atmosphere of extreme festive merriment. Anyone encountering a stray cat, particularly at night, also felt obliged to try and kill or maim it in the belief that it was probably a witch in disguise (Howey, 1930; Dale-Green, 1963; Darnton, 1984; Engels, 1999). By associating cats with the Devil and misfortune, the medieval Church seems to have provided the superstitious masses of Europe with a sort of universal scapegoat; something to blame and punish for all of life's numerous perils and hardships.

A powerful element of misogyny also seems to have underpinned this animosity toward cats. Medieval and early modern Christianity was dominated by an overwhelmingly male priesthood with distinctly ambivalent attitudes toward women. This love–hate relationship with femininity was exemplified by the image of the asexual and immaculate Blessed Virgin on the one hand and Eve, the begetter of original sin, on the other. Deriving their authority from Aristotle, ecclesiastical scholars of the period not only promulgated the view that women were the weaker and more imperfect sex, but also portrayed them as lascivious temptresses with insatiable carnal appetites who used their sexual charms to beguile, bewitch and subvert men. These same characteristics also predisposed women to witchcraft, because, as one commentator put it, the Devil tends to resort, 'where he findeth easiest entrance, and best entertainment' (Clark, 1997, p. 113). Medieval clerics also accepted Aristotle's evaluation of the female cat as a peculiarly lecherous creature that solicits sexual attentions indiscriminately from any available male (Rowland, 1973). Thus, a strong metaphorical connection was established between cats and the more threatening aspects of female sexuality (Darnton, 1984).

No doubt the natural behaviour of cats helped to reinforce this association. Female cats, especially when in oestrus, solicit physical contact, and enjoy being stroked and caressed. But they are also notoriously coy and unpredictable; demanding affection at one moment, scratching or running away the next. Sexually, the female cat is highly promiscuous, unashamedly inviting the attentions of several males. She is also a back-biter, however, often turning and attacking her partner immediately after copulation. For the ancient Egyptians, these ordinary feline attributes, together with maternal devotion, were evidently admired and celebrated. For the sexually repressed clerics of medieval and early modern Europe, however, they seem to have inspired a mixture of horror and disgust.

Europe was not the only region to draw negative links between cats and women. Malevolent, spectral cats were a common element of oriental folklore, and in Japan, popular legends existed of monstrous vampire cats which assumed the forms of women in order to suck the blood and vitality from unsuspecting men. The Japanese also

applied the word 'cat' to Geishas on the grounds that both possessed the ability to bewitch men with their charms. According to superstition, the tail was the source of the cat's supernatural powers, and it was common practice in Japan to cut off kittens' tails to prevent them turning into demons later in life (Dale-Green, 1963). This belief may also help to explain the origin of the genetically unique, bob-tailed cats of Japan.

Finally, the cat's somewhat ambivalent relationship with human society provides another possible clue to its victimisation. Together with the dog, the cat is one of the few domestic species that does not need to be caged, fenced in, or tethered in order to maintain its association with people. Cats, however, tend to display a degree of independence that is uncharacteristic of dogs, and which inclines them to wander at will, and indulge in noisy sexual forays, particularly during the hours of darkness. In other words, cats lead a sort of double life – half domestic, half wild; part culture, part nature – and it was perhaps this failure to conform to human (and especially male) standards of proper conduct that led to their subsequent harassment.

According to Jung (1959), animals are often used to express, 'unconscious components of self'. Whether they are perceived in positive or negative terms as a result of this self-identification, however, depends presumably on the individual moral perspective of the person or culture involved. During the Middle Ages, church authorities went to considerable efforts to establish and maintain an absolute distinction between humans and other animals (Thomas, 1983; Salisbury, 1994; Serpell, 1996a). By exploiting the comforts of domestic existence while, at the same time, enjoying the pleasures of a wild night on the tiles, the cat perhaps invited official condemnation and persecution by challenging this conveniently dichotomous worldview. Attitudes to dogs during this period differed according to class. Like the cat, ordinary street dogs, mongrels and curs became symbols of mankind's baser qualities – gluttony, crudity, lust, etc. The pets and hunting companions of the nobility, on the other hand, represented loyalty, fidelity, obedience and other desirable human attributes (Thomas, 1983). The latter image of the dog is nowadays prevalent in western countries, but the image of the cat remains tarnished, to some extent, by its older unruly reputation.

Although behavioural characteristics of animals often provide the basis for intolerant or disparaging attitudes, it should be emphasised that such effects are culturally constructed. In the majority of Islamic countries, for instance, attitudes to dogs and cats are more or less reversed. The dog is regarded as unclean, and touching one results in defilement (Serpell, 1995). Cats, on the contrary, are tolerated and, to some extent, admired.

## Modern attitudes

From its sacred origins in ancient Egypt, the domestic cat has now spread to virtually every corner of the inhabited world. Indeed, across most of Europe and North America the species has now overtaken the dog as the most popular companion animal (Messent & Horsfield, 1985; Serpell, 1996a). This trend, however, is comparatively recent. In his best-selling *Histoire Naturelle*, published in the latter half of the eighteenth century, Georges Louis Leclerc, le comte de Buffon, described the cat as a perfidious

animal possessing 'an innate malice, a falseness of character, a perverse nature, which age augments and education can only mask'. Buffon also loudly reasserted medieval ideas concerning the female cat's insatiable craving for sex: 'she invites it, calls for it, announces her desires with piercing cries, or rather, the excess of her needs ... and when the male runs away from her, she pursues him, bites him, and forces him, as it were, to satisfy her' (cited in Kete, 1994, pp. 118–119). In nineteenth-century zoological literature, according to Ritvo (1985), cats were the most frequently and energetically vilified of all domestic animals. Whereas the dog was admired for its loyalty and obedience, the cat was despised and distrusted for its lack of deference and its failure to acknowledge human dominion. Cats were also negatively portrayed as 'the chosen allies of womankind'. In nineteenth-century Paris, and, one assumes, elsewhere in Europe, cats came to be associated with artisans and intellectuals, by virtue of their independence, and apparent lack of obedience to social mores and conventions (Kete, 1994). This represented a significant turning point in attitudes to cats, and presaged their widespread adoption into bourgeois society as fashionable middle-class pets.

Attitudes to cats remain, nonetheless, ambivalent to this day. In a large survey of contemporary American attitudes to animals, Kellert and Berry (1980) found that 17.4% of those questioned expressed some dislike of cats, as against only 2.6% who disliked dogs. Contemporary statistics on animal cruelty derived from humane societies and animal protection groups in the USA indicate that cats are still the most frequent victims of the more extreme forms of abuse, including burning, beating, torturing, mutilation, suffocation, drowning and being thrown from heights (Lockwood, 2005). The sporadic popularity of anti-cat literature seems also to reflect latent animosity toward felines. The small book of cartoons entitled *A Hundred and One Uses of a Dead Cat* (Bond, 1981) became a world bestseller, and sold over 600,000 copies in the first few months after publication. Various similar titles, such as the *I Hate Cats Book*, *The Second Official I Hate Cats Book* and *The Cat Hater's Handbook*, were also highly successful (Van de Castle, 1983). It is difficult to imagine *A Hundred and One Uses of a Dead Dog* or a *Dog Hater's Handbook* achieving the same levels of popularity, and the fact that such books have not appeared in print suggests that publishers do not regard them as viable commercial propositions.

Many people continue to regard the sudden appearance of a cat as a sign of bad luck, and others fear or dislike these animals, perceiving them as furtive and untrustworthy. The cat's longstanding association with women and female sexuality is still implied by the slang use of terms, such as 'cat house' or 'pussy', and although research in this area is sparse, it is also tentatively confirmed by the results of some attitudinal surveys. A study of 3862 children aged between 8 and 16, for example, found that 18% of girls questioned described the cat as the animals they would most like to be, while only 7% of boys gave the same response. Dogs, in contrast, were chosen with almost equal frequency – 34% and 32% – by both sexes (Freed, 1965). In all likelihood, this legacy of negative attitudes to cats will continue to dissipate, as increasing numbers of people learn to appreciate the benefits of living with this clean, affectionate and essentially companionable species.

## Concluding remarks

Molecular, archaeological and behavioural evidence suggests that the domestic cat was originally derived from the North African/Near Eastern wildcat, *Felis silvestris libyca* sometime around 10,000 years BCE, and probably attained full domestication in Ancient Egypt about 4000 years ago. Cats have been valued since antiquity for their rodent-catching abilities, and they have also acquired religious, symbolic and emotional value in many societies. Attitudes towards them as symbols, however, have ranged from reverence to abhorrence. In ancient Egypt, cats were worshipped and jealously protected as representatives of Bastet, a goddess of fertility and motherhood. In medieval and early modern Europe, on the contrary, cats became a metaphor for female sexual depravity and social unruliness, and were persecuted and despised for their alleged links with witchcraft and the Devil. In symbolic terms, cats still appear to excite a certain ambivalence of feeling in many Western countries, although within the last few decades they have successfully overtaken the dog as the world's most popular companion animal.

# 8 Cultural differences in human–cat relations

Dennis C. Turner, Eva Waiblinger and Barbara Fehlbaum

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

Given the worldwide distribution of cats, differences in attitudes and behaviour toward these animals in different cultures might be expected, especially given differences in levels of economic development and religious traditions in many countries. In 2006 the first author decided to examine those differences in a sample of countries across the globe which also exhibited differences in economic status and religious background. Despite a globalisation of interest in human–animal relations, few cross-cultural studies on attitudes toward cats and dogs were set against religious heritage and none considered simultaneously attitudes toward nature/conservation, wildlife, zoos, intensive farming and animal protection/welfare issues. Most of our results have been published or are in press (IEMT, 2009; Turner, 2010; Fehlbaum *et al*., 2010; Turner, 2013; Turner & Al Hussein, 2013; Turner et al., 2013). We can therefore summarise the results on human–cat relations while occasionally referring to dogs for comparative purposes. Before doing so, we shall give an update on other cross-cultural studies and provide the historical and social background for potential differences in attitudes and behaviour toward animals.

## Other cross-cultural studies

The few cross-cultural studies that existed before 2006 were relatively limited in scope (directly comparing attitudes in only one to three countries, sometimes only between 'western' societies, or of different ethnic groups within just one country) but indicative of the worthiness of this approach on a larger scale (see Herzog *et al*., 1991; Herzog, 1996; Bradshaw & Limond, 1997; Abromaitis, 1999; Herzog, 1999; Miura *et al*., 2000; Griffith & Wolch, 2001; Serpell & Hsu, 2001; Swabe *et al*., 2001; Miura *et al*., 2002). While a number of mono-cultural (mostly western) studies had applied appropriate and established methods of assessing attitudes towards nature, animals in general, and/or companion animals in particular, these methods had rarely been applied to compare attitudes between people in different cultures with some promising exceptions (Bradshaw & Limond, 1997; Miura *et al*., 2000, 2002; Griffith & Wolch, 2001; Serpell & Hsu, 2001). No cross-cultural *observational* studies of social interactions between owners and their pets had been published. Differences in attitudes toward companion animals would be expected to influence those interactions.

In the meantime, interest in cross-cultural studies on human–animal relations has grown (Passariello, 1999; Serpell, 2005; Podberscek, 2009; Wan *et al*., 2009; Burn *et al*., 2010; Gray & Young, 2011; Lakestani *et al*., 2011; Herzog, 2011; Hurn, 2012; Jegatheesan, 2012), some of which include cats, others discussing the influence of (and on) religion, and several of these will be referred to later in this chapter.

## Historical and religious background of potential differences in attitudes

Passariello (1999) has stated from the ethnographic record that each culture has various ways in which animals interact with people, both physically and metaphorically, and includes a variety of culturally specific attitudes toward other species. Among others,

she refers to the largely vegetarian cultures of parts of India, which both revere the cow and maximally utilise it as a resource. She also refers to the post-modern cultures of the USA and Great Britain with large pet populations, but also widespread production of food animals for the largely carnivorous human populations, the main topic of Herzog's (2011) book. Serpell (2005) has, in our opinion, successfully argued that 'moral anxieties about the exploitation of animals have been a primary driving force in the evolution of religious ideologies and practices throughout human history' (p. 20). The anthropocentric views forwarded by such monotheistic religions as Judaism, Christianity and Islam tend to view animals as 'secondary creations' designed primarily to serve the interests of humans. Serpell argues that this fairly extreme position is 'only an extension of precisely the same techniques of moral absolution employed by our hunting and gathering ancestors' (p. 21). That, however, man's domination has also brought responsibilities toward those other creatures in all three of those monotheistic religions will be demonstrated below.

## Information about cats in a selection of countries

Frauenfelder (2007) was able to find published information – often on the Internet – about the popularity of and attitudes toward cats in 6 of the 12 countries[1] included in the first author's field study, which will be discussed later. She also interviewed numerous officials and representatives of animal protection organisations in India, Great Britain, Brazil, China, Singapore and Japan. (Other countries were added later to Turner's field study, explaining why Frauenfelder did not include those at the time of her thesis.) As some readers will be interested in the historical and current aspects of cat-keeping in different countries, along with the influence of religion across different countries, we shall first summarise Frauenfelder's relevant findings.

### India

In India the dog is without a doubt the most popular pet species, as well as being the major feral or free-roaming pet species, while cats play a secondary role and are not particularly valued as companions. 'The domestic cat is the vehicle of goddess Shashthi, a goddess of fertility who is popular in West Bengal and Maharashtra. ... The cat is sacred to Shashthi. However, a cat crossing one's path is considered to be inauspicious, and a superstitious person would go back and restart his mission' (Krishna, 2010, pp. 72–73). Although cats are less common than dogs in India, they are encouraged to live in the compounds of homes and buildings as they hunt and kill rats and mice, making them quite acceptable. (See also Turner *et al*., 2013.)

[1] Japan, China, Singapore, India, UAE, Jordan, Israel, Switzerland, Germany, France, United Kingdom, Brazil.

### United Kingdom

England has a high density of cats and dogs relative to other countries, with cats recently replacing dogs as the most popular pet; the human : cat and human : dog ratios were 7 : 1 and 9 : 1, respectively, in 2007 (Frauenfelder, 2007). The country is well known for its cat fanciers (see Chapter 12) and is moving steadily toward a 'singles' lifestyle in urban environments as are many western societies, where the cat is considered by many to be an ideal pet.

Great Britain also has a long and active tradition of animal protection and welfare, with the RSPCA being founded already in 1824 (Frauenfelder, 2007). Surprisingly, the first author did not encounter a single cat during the day on the streets of London (or in Kensington Park) during his field study; presumably the owners of cats in the city keep them exclusively indoors for their own protection (Turner *et al*., 2013).

### Brazil

Between 11 and 13 million cats and 27 and 29 million dogs are estimated to live in Brazil, resulting in human : animal ratios of 17 : 1 and 7 : 1, respectively (Frauenfelder, 2007); the populations of both species are steadily increasing concomitant with increasing urbanisation, especially around Sao Paulo. According to Frauenfelder's research, one finds the whole range of relations with cats and dogs in Brazil: these animals assume important social functions, are considered family members, and are used in animal-assisted therapy programmes, but are also feared and mishandled by others.

### China

Frauenfelder (2007) found estimates of the cat population in China of 140 million, somewhat under that for dogs at 150 million. Since the end of food rationing in the 1980s, the pet population has jumped significantly. Further, she reports that it is incorrect to assume that the consumption of dog and cat meat resulted because of famine; they are simply considered a delicacy. Nevertheless, Shuxian *et al*. (2005) found in their study of attitudes among Chinese college students a high degree of empathy with animals and high interest in animal protection.

Frauenfelder (2007) concludes that the increasing popularity of pet dogs and cats in China is leading to increased lobbying in local media by animal protection organisations against the consumption of dog and cat meat. Also, known cases of animal cruelty raise huge outcries in the Chinese public, implying an awareness of animals' ability to feel pain and suffer. However, knowledge about the species-specific needs of the animals is still in its infancy.

### Singapore

This city-state has experienced a tremendous financial and developmental boom since the 1970s and the keeping of pets is becoming more popular. Still, the ratio of humans : dogs is extremely high with 113 : 1 (Frauenfelder, 2007), which is most probably related

to strict government housing regulations (including numbers of dogs per household and breeds that are allowed). No registration is required for cats, nor any estimate of the population size available; however, the stray cat population has been estimated at about 150,000 animals.

### Japan

Since the 1970s, interest in pets has grown steadily in Japan. The popularity of dogs, especially small breeds, has doubled since the 1980s and currently the human : dog and human : cat ratios are 10 : 1 and 11 : 1, respectively (Frauenfelder, 2007), with about 13 million dogs and 12 million cats inhabiting the country at that time. Unfortunately, anthropomorphism is quite widespread in urban areas and more education is needed about the species-specific needs of the animals (Turner, pers. obs.). As in China and most probably due to Buddhism, some resistance to euthanasia of animals exists both amongst veterinarians (Kogure & Yamazaki, 1990) and Japanese college students (Miura *et al*., 2000). The mutant coat colour orange present in ginger and tortoiseshell (calico) cats originated in Asia and is particularly frequent in India, SE Asia and Japan. Further, the Japanese 'Bobtail' breed has been known there for centuries, is often pictured in art works, and its favoured 'good-luck' colour (*mi-ke*) corresponds to the calico or tortoiseshell and white, also found in other bred cats.

### United Arab Emirates

No information could be found on the size of the owned or feral cat population in the UAE. However, it is interesting to note that the Emirati goverments are cooperating with the World Society for the Protection of Animals to establish humane control programmes for ferals, based on trap, neuter and release, and one of the largest domestic pet shows in the world, with over 35, 000 attendees on one day, takes place annually in Dubai (Dubai Pet Show, 2012).

### Jordan

No information could be found on the cat population (owned or feral) of Jordan. However, cats were often registered on the streets of Amman during the first author's field study, either resting in front of their homes or feeding from refuse bins. Almost all cats sighted were in good condition in the suburban/urban areas visited (Turner & Al Hussein, 2013; Turner *et al*., 2013).

### Israel

In 1996, Israel was reported to have only 140,000 owned cats (European Market Intelligence, 1998). The government's Veterinary Services has no estimate of the numbers of stray cats, but reports they number in the 'many thousands' (Chai-online, 2012).

### Switzerland

Switzerland can certainly be considered a cat-friendly nation with around 1.35 million cats (only about 400,000 dogs) distributed among 7.6 million persons. One reason for this is certainly the fact that 65–70% of the Swiss live in rented accommodations and the landlords more readily accept 'quiet' cats than dogs in such. The first author has also speculated elsewhere that the freedom-loving, independently thinking Swiss particularly appreciate the independent nature of the cat! Switzerland lends itself to comparative studies and the authors of this chapter have indeed published results comparing attitudes of German- and French-speaking Swiss adults (IEMT, 2009; Fehlbaum *et al*., 2010) and are preparing a comparison of each of those subpopulations with German and French adults, respectively.

### Germany

Market reseach shows that the domestic cat population in Germany has risen from 7 million in 2000 to 8.3 million in 2009 (Consumer Trends, 2012). This report also indicates that pet humanisation (anthropomorphic thinking) is driving product purchases in Germans. The owners are looking for products which, for example, support a healthy immune system, develop softer coats and promote healthier skin, or generally improve the pet's overall health.

### France

France, with 9.6 million pet cats in 2006, was one of the 10 countries of the world with the most cats (Maps of the World, 2012). Nevertheless, within Europe, France is 'the' dog nation, with 17 dogs to every 100 persons (Just Landed, 2012).

## Religious positions

What can be said about the effects of religion on the attitudes towards animals, especially cats?

### Judaism

The cat is not mentioned in the Bible (neither the Old nor New Testament) even though cats were present in Ancient Egypt. A few references to the cat can be found in the rabbinic literature: 'It was permitted to breed cats in Erez Israel together with other animals that rid the house of pests' (BK 801-b). In Babylonia the cat was highly regarded as a means of ridding the home of poisonous snakes, and it was even stated that entering after dark a house without cats was dangerous, for fear of being bitten by a snake (Pes. 112b). The cat was praised for its extreme cleanliness, and it was said: 'If the Torah had not been given, we could have learnt modestly from the cat' (Er 100b)

(*Encyclopaedia Judaica*, 2006). However, the Talmud also refers to the falsehood, gluttony and the dangerous bite of the cat, even though kept (only!) to rid the house of mice and weasels (*Jüdisches Lexikon*, 1928, Band 2, p. 600).

Even though the cat is not explicitly mentioned in the Bible, the five books of Moses, which include probably the oldest notion of animal protection, go hand-in-hand with a current paradoxical attitude, particularly among orthodox Jews, against the keeping of pets (Schmidt, 1966). Notwithstanding, animals have a soul and rights and a fairly well-developed animal ethic exists in Judaism (Tegtmeyer, 2005): 'You may not inflict pain or suffering on any living creature' is the well-known law 'Tsa ar ba alei chayim', which also forbids hunting.

## Christianity

As already mentioned, the cat does not appear anywhere in the Bible.[2] This is somewhat surprising given that many religious paintings of scenes from the Bible have cats in them. Depending on the period of the work, the cat is either peaceable or aggressive. Serpell (see Chapter 7; 1996a, 2002) has described the dramatic changes in appreciation and derogation of the domestic cat especially in connection with the rise of the Christian Church in Europe. During the Middle Ages, when women were hunted down as witches, their cats – especially black cats – were also tortured and put to death.

As one of the countries considered in the comparative study is largely Catholic (Brazil), Turner wrote to Pope Benedict XVI, known himself to be a cat lover, asking the Catholic Church's position toward animals in general. Monsignor Peter B. Wells answered in the name of the Pope on 26 March 2010, referring to paragraphs 2415–2418 of the *Catechism of the Catholic Church*, as follows:

**2415** The seventh commandment enjoins respect for the integrity of creation. Animals, like plants and inanimate beings, are by nature destined for the common good of past, present, and future humanity.[195] Use of the mineral, vegetable, and animal resources of the universe cannot be divorced from respect for moral imperatives. Man's dominion over inanimate and other living beings granted by the Creator is not absolute; it is limited by concern for the quality of life of his neighbor, including generations to come; it requires a religious respect for the integrity of creation.[196]

**2416** *Animals* are God's creatures. He surrounds them with his providential care. By their mere existence they bless him and give him glory.[197] Thus men owe them kindness. We should recall the gentleness with which saints like St. Francis of Assisi or St. Philip Neri treated animals.

**2417** God entrusted animals to the stewardship of those whom he created in his own image.[198] Hence it is legitimate to use animals for food and clothing. They may be domesticated to help man in his work and leisure. Medical and scientific experimentation on animals is a morally acceptable practice if it remains within reasonable limits and contributes to caring for or saving human lives.

**2418** It is contrary to human dignity to cause animals to suffer or die needlessly. It is likewise unworthy to spend money on them that should as a priority go to the relief of human misery. One can love animals; one should not direct to them the affection due only to persons.

[2] However, a cat is mentioned in the Buch Baruch (not included in all versions of the Bible) of the Prophet Jeremia in association with Mesopotamian Gods.

From these statements, it is clear that animals, plants and other resources are there to be used by humans (for food and clothing), but also for future generations (conservation), that humans are responsible for stewardship of those animals, and that they may not be caused suffering or killed 'needlessly'. The Church makes it quite clear that humans have dominion over animals, but also have responsibilities toward them.

## Islam

Many misconceptions circulate in the western world about Muslims' attitudes and behaviour toward animals and Islam's positions on conservation and animal welfare (Turner & Al Hussein, 2013). These need to be corrected.

The dog is referred to only once in the *Holy Qur'an* (18th Sura, 19), but this dog is considered to have access to paradise. The cat is not mentioned at all in the *Qur'an*, even though many popular articles refer to the valued position of cats 'in the *Qur'an*'. Probably these references are to the teachings and talks given by the Prophet Mohammed. Krishna (2010, p. 109) explains that the notion that dogs are 'impure' in Islam is false: 'Prophet Mohammed's injunction to wash one's hands seven times after contact with a dog's saliva had a very good reason. Rabies was rampant in medieval Arabia and in absence of running water and soap in the desert (the recommended first-aid for dog bites today), washing the hands several times was the best alternative.' According to Masri (1989; pp. 27–28): 'The Holy Prophet has even tried the "Punishment and Reward"' approach in the following *Ahadith*: 'The Prophet told his companions of a woman who would be sent to Hell for having locked up a cat; not feeding it, nor even releasing it so that it could feed herself.' (No. 53) 'The Prophet told his companions of a serf who was blessed by Allah for saving the life of a dog by giving it water to drink and quenching its thirst.' (No. 54) The Prophet was asked if acts of charity even to animals were rewarded by God. He replied: 'Yes, there is a reward for acts of charity to every beast alive.' (No. 55) Animal protection has always been important in Islam and Islamic law (the *Shari'ah*), in which humans have a superior position, but Masri (1989, p. 3) notes: 'Verses in the *Qur'an Majeed* lay down a very relevant principle that it depends on the conduct of man whether he maintains his privileged position as a human being or gets himself degenerated to a status lower than that of animals'.

Further (Masri, 1989, pp. 10 and 11): 'The Qur'an *Majeed* and *Hadith* also plead for the cause of animal rights by repeatedly citing their utility-value and worth. … According to the Qur'anic theology, all living creatures possess a non-physical force of spirit and mind which, in its advanced form, we call "psyche"'. As we shall see, these points are relevant to the field study results about Muslim attitudes toward cats and dogs.

## Buddhism

For both Buddhism and Hinduism (see below) with their belief in reincarnation, animals are found just slightly under the status of humans (Laukner, 2005). Theravada Buddhism has many rules concerning the killing and consumption of animals as a

source or meat and other commodities. Many Buddhist texts expound vegetarianism (Buddhism, 2009). For example, the Agulimaliya-Sutra states: 'Eating meat always means that one is eating the meat of living beings, whose core of being is identical with one's own person. Eating meat means to eat one's own flesh' (Buddhism, 2010). Or the Surangama-Sutra: 'The consumption of meat kills the seed of great mercy toward all living beings' (Buddhism, 2009). Kindness toward all living beings is stressed in the Metta Sutta: 'So with a boundless heart Should one cherish all living beings: Radiating kindness over the entire world Spreading upwards to the skies, And downwards to the depths; Outwards and unbounded, Freed from hatred and ill-will' (Metta Sutta, 2009). Nevertheless, animals in neither Buddhist nor Hindu countries were completely safe from exploitation as a food source, as working animals, or in blood sports (Laukner, 2005).

No references to cats or dogs were found in the Buddhist teachings. A personal interview with His Holiness the Dalai Lama XIV was turned down by his office for health reasons. Nevertheless, in the Dalai Lama's book *The Universe in a Single Atom* (2005), two passages are of interest: 'In Buddhism the highest spiritual ideal is to cultivate compassion for all sentient beings and to work for their welfare to the greatest possible extent' (p. 10). Regarding the Dalai Lama's personal experiences: 'In India later on, I did not have much luck with my cuckoo clock, whose poor cuckoo got attacked by my cat and never recovered' (p. 20). Obviously he had a 'soft spot' for cats.

In China and Japan, both with practising Buddhist populations, many legends are about cats, especially concerning their ability to 'see at night', which gave them the ability to protect people from bad spirits. However, less well-meaning spirit-cats were also feared (Laukner, 2005). Many eastern Asian temples are populated by cats, which are not revered, but are well cared for.

## Hinduism

Krishna (2010) states that the three ancient religions of India – Hinduism, Buddhism and Jainism – have never differentiated between the soul of a human and that of an animal, while the liberation of the soul depends on one's karmas (actions). All creatures are equally part of the cycle of life, death and rebirth. 'Animals, in the Indian tradition, are considered to have the same feelings and passions as human beings' (p. 3). The earliest religious text from India, the Rig Veda, contains old sections describing how, when and where animal sacrifices were to be performed (Serpell, 2005). However, after about 1000 BCE the Veda categorically rejects sacrifices and advocates the practice of *ahimsa* (non-injury) toward all animals.

Again according to Krishna (2010) the domestic cat (or *Billi*) is considered the vehicle of the fertility goddess Shashthi, particularly popular in West Bengal and Mahrashtra. While the cat is sacred to Shashthi, a cat crossing one's path is considered to be inauspicious. 'Unlike dogs, which are common companions in India, cats are not often kept as pets. They are, however, encouraged to live in the compounds of homes and buildings as they hunt and kill rats and mice. It is this role that makes the carnivore very acceptable' (p. 74).

Although no such reference is made for cats, the *Ramayana* prohibits the eating of dog meat and a Brahmin who beats a dog is punished (Krishna, 2010). Malinar (2009) mentions that the dog in Hinduism is an impure animal and after physical contact, ritual cleaning has to be conducted. However, if the dog is being used as a hunting aid, it is considered a pure (clean) animal.

### Shintoism

Shinto is an indigenous spirituality, or ethnic religion, of the people of Japan practised by about 4 million Japanese. Many more Japanese take part in Shinto rituals and festivals but practise Buddhism. The essence of Shinto is a devotion to invisible spiritual beings (*kami*), to shrines (including small shrines in the home) and to various rituals (Shinto, 2012a). The rituals enable humans to communicate with kami and help to establish a connection with the past. Because ritual is at the heart of Shintoism, as opposed to belief, it is simply an aspect of lifestyle of those practising it. However, it does teach important ethical principles, without resorting to 'commandments'. It is difficult to separate the ethic values of Shintoism, Buddhism and Confucianism because the former coexists with the latter two. Shinto ethics aim to promote harmony and purity in all spheres of life, but have no moral absolutes. 'Good' is the default condition of humans and the world. However, some things are still regarded as bad in Shintoism, e.g. things which disrupt the natural world.

Cats are often sighted at or even inside Shinto shrines (Turner, pers. obs.), which is somewhat surprising as among the kami, 'foxes, raccoons, rabbits and cats are the tricksters of Shinto and there are many stories of human encounters with these animals who cause problems for the unlucky enough to encounter them' (Shinto, 2012b). But also the opposite has been reported: 'As an example of the potential for divinity: there is a story of an emperor who, while traveling in a rainstorm encountered a cat on a porch that waved a greeting to him. Intrigued by this extraordinary phenomenon, the emperor dismounted and approached the porch. As soon as he reached the porch, a bolt of lightning crashed down on the spot his horse was standing and killed it instantly. From that point on, cats were, in Shinto, worshipped as beneficent and protective *kami;* if you walk into a Japanese restaurant, you are sure to find a porcelain statue of the waving cat, which protects the establishment from harm' (Shinto, 2012c). This is the famous *Maneki Neko*.

## The field study results

Are the above-mentioned facts and beliefs reflected in the attitudes of adults found in those selected countries with different religious traditions? Briefly, the study designed by the first author included two phases: first a 3-page questionnaire distributed in 12 countries in the local language containing demographic data on the adult filling it out and 27 statements, including 5 control statements to ensure understanding and concentration while completing it, to which the subject had to agree or disagree along

a 5-point Likert-scale; second, direct observations of random encounters between people and animals on the streets of cities and suburbs in three of those countries.[3] Well over 6000 questionnaires were returned and analysed by analyses of variance to test the influence of the factors: religious heritage; gender of the person; pet ownership; and sample type (convenience-'random' sample or 'animal friend' sample, e.g. from the waiting room of a veterinary practice). For methodological details see Turner *et al*. (2013). The 27 statements could be roughly grouped into those concerning nature/conservation and wild animals, pets, farming practices, meat consumption, and the feelings and cognitive abilities of animals in general. Summarising the results published in Turner *et al*. (2013), Turner (2013) and Turner and Al Hussein (2013), the numbers of statements where a main factor was significant were: religion 15 (out of 22 after subtracting the control statements); gender of the person, 10; sample type, 10; and pet ownership, 9. Concerning cats (and dogs for comparative purposes) and animals in general the following results are of interest: with respect to the statement 'Keeping animals as pets brings many benefits to the person', all four factors examined were significant. Although people from all religious backgrounds agreed with this, Jews agreed more strongly than people of all other religions, Christians as well, except relative to Jews (Turner *et al*., 2013). On the statement 'Cats are very likeable animals', both religion and sample type were significant factors. 'Animal friends' and Muslims were significantly more in agreement with this than either the random sample or persons from all other religions, although all persons agreed that cats are very likeable. Interestingly on the similar dog statement 'Dogs are very likeable animals', women (!), animal friends and pet owners agreed significantly more strongly than men, persons in the random sample and non-pet owners, although all basically agreed with the statement. Muslims and Hindus were less convinced of this statement, Jews most in agreement, but persons from all religions answered between 'agreement' and 'strong agreement' (Turner & Al Hussein, 2013). Further, women and Muslims were most strongly against the consumption of cat and dog meat though persons in all categories were against this. Interestingly, Podberscek (2009) found high support for the consumption of dog meat (but not cat consumption) in South Korea, linked to national identity, and that calls from the West to ban the practice were considered as an attack on the local culture. Herzog (2011) has discussed this issue in more detail also for China; nevertheless, adults from Beijing were sampled in the current study and opposed the consumption of dog and cat meat. Pet-keeping is on the increase in urban China and this may be already influencing attitudes on this.

Although generic and not specifically asked for cats and dogs, the reactions to the statements that 'Animals have the same feelings as people' and 'Animals can think like people' are relevant given the significant effects found of pet ownership and/or the 'animal friends' sample: animal friends, pet owners and women more strongly agreed with the 'feelings' statement than the random sample, non-pet owners and men, although all persons agreed. Jews and Christians, while agreeing, did so significantly

[3] London, UK; Chennai, India; Amman, Jordan.

less strongly than persons of all other religions. Regarding 'thinking like people', women and persons in the 'animal friends' sample agreed more strongly, Christians and Jews were neutral, and persons of all other religions were more in agreement.

## Conclusions

Indeed, differences were found in attitudes toward cats (dogs, and other animals and animal issues) in the countries studied and they were significantly influenced by religion, though the directions of attitudes were always the same. Whether social interactional *behaviour* between humans and cats in different cultures varies remains to be determined. The question whether a differential proportion of a population between countries even enters into closer relationships with cats (naturally corrected for abundance) remains unanswered. Furthermore, it might well be that once a person has included a domestic cat in his/her social network, the differences between cultures are too small for detection given individual differences in the personalities of both the persons and the cats (see Chapter 9).

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# 9 Human and cat personalities: building the bond from both sides

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## Introduction

### People and cats together

Domestic cats (*Felis silvestris catus*) are among the most common companion animals. This is particularly true in cultures with an Islamic background, where dogs are less acceptable as companion animals than in Western societies (Chapter 8). In Austria, for example, a human population of 8 million owns more than 2 million cats, in contrast to just about 700,000 dogs (Kotrschal *et al*., 2004). Consequently, the behaviour of cats and their interaction with people has attracted scientific interest (Leyhausen, 1960; Turner, 1991; Bradshaw, 1992; Turner & Bateson, 2000). Particularly in rural settings, the association between cats and people may still be loose; cats are mainly tolerated as pest controllers, but often people also sympathise with these cats and feed them. In urban areas most cats, nowadays, tend to be social companions of their owners. In parallel with the increase of one-person households, the keeping of companion cats seems on the rise. In order to ensure their safety, many of these urban cats are kept indoors. Such indoor cats tend to interact more with, and are more 'attached' to their owners than cats that have the option of going outdoors (Stammbach & Turner, 1999). People often engage in close and long-term relationships with their cats, and owners and cats may develop complex idiosyncratic and time-structured interactions (Wedl *et al*., 2011).

### Socialising with an asocial animal?

Interspecific socialising between people and cats raises at least two questions. First, how is it possible that a species which is intrinsically not very social can become mankind's most common and popular companion animal? And second, how can the wide range of dyadic interactions and relationships seen between people and their cats be explained?

People 'own' cats and generally care for them by providing housing and food. This invitation to coexist sets up some expectations about the relationship from both the human's and the cat's perspective. The expectations of the human may not be reciprocated by the cat in the desired way. Depending on genetic background, breed, individual history and owner effort, the meaning of owners to cats may range from a mere food dispenser to a close bonding partner (Chapter 6). The North African ancestors of domestic cats are relatively solitary. Seemingly, sociability has been increased through domestication, mainly by selection against shyness and anxiousness towards humans (Chapter 7). This may also have increased sociability between cats. Nowadays the feral cats of the world's big cities can be reasonably gregarious.

### Unique relationships?

The mammalian brain seems to be essentially 'social' and the degree of sociality is regulated by relatively minor adjustments in the oxytocin system (O'Connell & Hofmann, 2012). Hence, even if cats are relatively solitary as compared to wolves or dogs,

for example, they are not asocial. Whereas most dogs are inclined to bond strongly with their people, if properly socialised with humans early in life, this is more of an option for cats, making the strength of bonding and attachment styles with humans more variable in cats than they are in dogs; whereas for some cats, owners are mere food dispensers, other cats will happily greet their owners when they return home or even join them for walks. Most cat owners rightly believe that their relationship with their cat is unique. This is of course true for any long-term dyadic relationship, be it human–human or human–animal. Still, due to the great range of bonding and interaction styles between cats and people, these intraspecific companionships may be more variable and, therefore, individually unique than the relationships people maintain with any other companion animal species. In fact, bonds of cats with humans may exhibit features not seen or seen at different rates in interactions among cats (Mertens & Turner, 1988; Bradshaw, 1992; Rieger & Turner, 1999; Barber, 2005). This variation in bonding and interaction styles between people and cats is unlikely to be random, because what is generally called a 'relationship' is composed of three contingent complexes of mechanisms:

1. How *strongly* are the cat and owner bonded with each other? This relates to the urge of the cat or owner to be close to each other as mediated by the oxytocin system together with the mesolimbic reward system (Durr & Smith, 1997; O'Connell & Hofmann, 2012).
2. What kind of attachment quality does the dyad mutually have? This relates to mutual trust, whether and how much the person is a haven of safety for the cat in case of a stressful event (e.g. Julius *et al*., 2013) and, in general, the emotionality of the relationship. For example, are they calming each other down or do they sometimes cause stress for each other? As much as humans have an emotion–cognitive representation of the social partners they bond to, such an 'internal working model' of attachment figures, based on early social experience, will also be generated by companion animals in some form (Julius *et al*., 2013).
3. What are the partners actually doing together, what is their interaction style, the operationality of a particular dyad (Kotrschal *et al*., 2009), what kind of behavioural rituals have they developed which are potentially unique for a dyad?

Together, these three complexes will constitute the bio-psychological and behavioural syndrome of relational needs, attitudes, affects and interactions that we call a 'relationship'.

## Factors influencing dyadic interaction styles

Breed/genetic heritage, not the least paternal contribution (Turner *et al*., 1986; Reisner *et al*., 1994; McCune, 1995), development and early socialisation, housing conditions, owner attachment and other owner-related factors have been shown to affect cat behaviour and relational potential (Wilson *et al*., 1965; Moelk, 1979; Karsh, 1983; Meier & Turner, 1985; Serpell, 1986; Karsh & Turner, 1988; Adamec & Stark-Adamec, 1989; Cook & Bradshaw, 1995; McCune *et al*., 1995; Turner, 2000b). Aside from the genetic background, early socialisation with humans is a crucial factor affecting a cat's

attitude to approaching and relating to humans later in life (McCune, 1995). This is explained by the common social brain of mammals and the common rules of early socialising and developing proper social responses in the domains of behaviour and physiology (Kotrschal, 2009; Julius *et al*., 2013).

Generally, kittens socialised to people throughout their sensitive period of socialisation (2–7 weeks of age: Karsh & Turner, 1988) develop into well-adjusted cats that will approach people without anxiety and will engage in positive social interaction. As with other mammals and birds, such regular early handling of kittens may make cats generally less susceptible to a range of potential stressors they are likely to meet in life (comp. Hemetsberger *et al*., 2010). Socially relevant events early in ontogeny will affect phylogenetically more ancient mechanisms than events later in life and will produce more sustained effects than similar events later in life. During what used to be called the 'period of imprinting', from opening the eyes and ears during week three into weeks six to eight after birth, regular friendly contact with certain people probably affects the representations ('internal working model': Ainsworth *et al*., 1978; Bowlby, 1979) an individual kitten forms towards humans in general and its 'sociability' later in life, i.e. how interested and free of anxiety a cat will be when interacting with, and bonding to, a particular person (Julius *et al*., 2013).

Finally, based on genetic background and early development, any cat will develop particular interaction patterns and routines with certain persons, normally the owners. This is a systemic/dyadic process of mutual adjustment. In dogs we showed that behavioural expression from the side of the dog is significantly affected by owner gender and personality (Kotrschal *et al*., 2009). Also in cats, it was found that owner gender, age, prior cat ownership, attitudes (e.g. willingness to accept the cat's 'independence'), human attachment, housing conditions (indoors only or outdoors also) affect the structure, intensity and mutuality of interactions (Serpell, 1996b), as discussed in Turner (2000b). So, the social environment provided by the human partner may significantly and specifically affect behavioural expression on the side of the animal companion not only in dogs, but also in cats.

## Cat personalities

The formation of any cat–human dyadic relationship is not a unidirectional process. Cat individuality (Barber, 2005; Feaver *et al*., 1986; McCune *et al*., 1995) certainly interacts with the human social environment and may feed back to it (Turner, 2000b). Three basic cat personality dimensions have been proposed based on observer ratings: (1) bold, confident/easy-going, (2) shy/nervous and (3) active/aggressive (Feaver *et al*., 1986). However, the matter of cat personality remains complex, mainly because personalities do not develop independently of social context (Lewis, 1999; Magnusson, 1999; Mendl & Harcourt, 2000).

We recently found in owner–dog dyads that relationships and interactions were particularly affected by owner personality and owner gender (Kotrschal *et al*., 2009). Because these factors should be generally important in shaping long-term dyadic relationships, we expected to find similar patterns between owners and their cats.

The behaviour of dogs in relationship to their environment is also influenced by owner personality and attitudes (Serpell, 1983, 1986; Kotrschal *et al*., 2009), and has been found to be fairly consistent over time and situations (Svartberg *et al*., 2005), justifying the use of the term 'personality'. For cats, however, the results of comparable research remain ambiguous (Barber, 2005), particularly as the question of how a pet's personality affects the bond with the owner (or vice versa) has received only limited attention (but see Serpell, 1983, 1996; Dodman *et al*., 1996; Lowe & Bradshaw, 2001).

In fact, no formal connection has yet been made between cat and owner personalities or their mutual influence. As is the case in other animals, some components of a cat's personality will be heritable. However, much of it will be shaped early in life and in its long-term association with a certain environment and particular persons (McCune, 1995; Mendl & Harcourt, 2000). In alignment with biological personality theory, we predict that owner and cat personalities will show components of the behavioural syndromes characteristic of the 'proactive–reactive' or 'bold–shy' continuum (Wilson *et al*., 1994; Koolhaas *et al*., 1999; Gosling & John, 1999; Podberscek & Gosling, 2000; Sih *et al*., 2004a, 2004b). At least in theory, cats should be no exception. There should be cats which act 'boldly', confidently and even aggressively, towards strangers, which would also form routines readily but may not easily adapt to changing environments. Others will be rather 'shy' towards strangers and, in the sense that they attend to environmetal stimuli, are easily stressed, slow to explore, will not as readily form routines as 'bold' individuals, but will be more adaptable to changes in their environment.

## Why it is possible to socialise with non-human animals

The urge to engage in relationships with other animals seems to be part of typical human 'biophilia' (Wilson, 1984; Serpell, 1986; Podberscek *et al*., 2000; Turner & Bateson, 2000). Common ground for being able to do so is provided by conservatively maintained vertebrate brain structures and functions. For example, homologous brain centres for social behaviour and emotions, the so-called 'social brain network' (Goodson, 2005), and its main partner allowing for adaptive individual decision making in the (social) environment, the 'mesolimbic reward system', have remained virtually unchanged over 450 million years of vertebrate evolution (Panksepp, 1998; O'Connell & Hofmann, 2012; Julius *et al*., 2013). Such evolutionary conservatism not only applies to the brain as the command centre for social behaviour, but also to its executive partner, social physiology (i.e. hypothalamus–pituitary–adrenal (HPA) and sympathico-adrenergic stress axes: DeVries *et al*., 2003; McEwen & Wingfield, 2003; Kotrschal, 2005). Social vertebrates also share a need to properly socialise during early ontogeny in order to develop empathic understanding (de Waal, 2008a, 2008b) and across species, similar mechanisms underlie the expressions of individual behavioural phenotype (Gosling & John, 1999; Koolhaas *et al*., 1999; Gosling, 2001; Sih *et al*., 2004a, 2004b). Domesticated animals have been generally selected for tractability (Herre & Röhrs, 1973) and tameness (Belyaev, 1979), and thus can be more readily socialised to live

with humans than tamed (i.e. human-socialised) wildlife (Podberscek *et al*., 2000; Miklosi *et al*., 2004; Hare & Tomasello, 2005; Hare *et al*., 2005).

## Just peace and harmony?

Dyadic relationships between individuals may involve harmonious mutual emotional support and collaboration, particularly under conditions of balanced interests. For example, partners may attenuate each others' stress responses (DeVries *et al*., 2003; Scheiber *et al*., 2009; Julius *et al*., 2013); living with an animal companion may yield a range of benefits with respect to emotional and physiological well-being and health for the human partner (Wilson & Turner, 1998; Friedman *et al*., 2000; Beetz *et al*., 2012). However, in general, long-term valuable dyadic relationships (Kummer, 1978) will fit a model characterised by cycles of conflict and resolution (Aureli & de Waal, 2000). This is certainly true for within-species dyads, but probably will also apply to dyadic companionships between humans and other animals. Interests of partners will hardly ever be entirely stable or balanced over time. Consequently, individual positions within any dyad need to be negotiated dynamically. In essence, this should also apply to relationships between people and their companion animals.

Most dogs, particularly of the highly domesticated kinds (Parker *et al*., 2004), much more than their wolf ancestors (Kotrschal, 2012) will show a 'will to please', i.e. a willingness to cooperate just for the sake of social recognition. However, even dogs will sometimes ignore the will of their owners. In this case the owner is well advised to resort to appropriate training. If even in human–dog dyads matters are occasionally negotiated (e.g. the owner being interested in concentrating on work, while the dog whines to urge the owner to take it for a walk), this should be even more the case in human–cat dyads where such a will to please is less clear on the side of the cat partner.

For example, cats may negotiate friendly social attention via food. Some cats will eat whatever is given, others would only accept a certain kind/brand of food and still others engage in the opposite habit, accepting a certain kind/brand of food on only a very few occasions and then demanding change. Some cats are 'gluttons', i.e. they will eat fast, and large quantities of any food or of just their preferred variety; others are finicky eaters, being demanding of their owners and being behaviourally and acoustically communicative about it. So, some cats simply eat, while others make 'a fuss of it', i.e. negotiate occasionally, while still others will always interact and negotiate over food. This probably not just reflects 'individual differences' between cats, but may have developed in part in response to the owner's behaviour, attitudes and social needs. Owners willing to be persuaded may provoke negotiating cats and owners particularly needy of social attention from their cat may be particularly willing to give in, hoping to please the cat and thereby, in essence, trading food for social attention (Day *et al*., 2009).

With such an integrative theoretical background in mind we examined how owners and cats behave and interact during feeding. We chose this scenario because we predicted that this standard situation would reveal dyad-specific interactions and would be relatively robust despite the presence of visitors. Furthermore, we were interested in

identifying shared and unique components of dyadic behaviour and interactions and, finally, wanted to explore the idea that certain characteristics of the dyadic partners, such as gender and personality will affect the characteristics of these relationships. Past studies have found a significant contribution from owner gender (Mertens, 1991), but not sex of the cat (Mertens & Turner, 1988; Turner, 2000b). As the owner provides the socio-economic framework for the dyad, we predict that the nature of the owner–cat relationship will be particularly affected by both owner personality and gender because these factors will most distinctly affect the interactional goals of the human partners. For example, if owners with particular personality traits show a heightened urge to interact with their cats, they may match their cat's readiness to interact and may, thereby, strongly contribute to intense and qualitatively varied dyadic interactions. On the other hand, low human compliance with a cat's interactive overtures will probably produce a more distant dyadic relationship (Turner, 2000b).

## Methods

The results presented in this chapter are from a project on cat–owner relationships funded by Mars Inc. and WALTHAM®, conducted in 2005/2006 with 40 owner–cat dyads in Viennese households; only the interaction analysis using Theme® (Noldus; Magnusson, 1996) has been published previously (Wedl *et al*., 2011). Forty cats (25 males and 15 females, 0.75–13 years of age, most of them sterilised) and 39 persons (10 men and 29 women, 21–78 years old; one woman had two cats in separate apartments) participated in this study. Only an overview of the methods can be given here (for details and descriptions of the behavioural parameters coded, see Wedl *et al*., 2011). More than half of the cats (21) were able to go outdoors (gardens, rooftops), but all cats spent most if not all of their time indoors. We focused on one-cat households and visited each dyad four times at approximately weekly intervals at the cats' usual feeding times to observe the owner–cat interactions at that occasion. We predicted that this is one of the most interactive periods between cat and owner and would potentially be the most revealing with regard to potential negotiations (Bradshaw & Cook, 1996). Each observation session began 5 min before the cat was fed, then covered the feeding of the cat by the owner, which lasted approximately 10 min, and continued for 5 min after the cat had finished feeding. Visits were always made by two observers, one interacting with the owner and guiding the procedure, the other videotaping cat and owner behaviours and interactions throughout each session. In one of the visits, we also performed a novel object test by placing a plush owl on the floor and coding the response of the cat to this novel object when it first encountered it.

During the first visit we interviewed owners about their relationship with the cat. Interactions between cat and owner and cat behavioural personality tests were videotaped during all four visits. Human personality tests (NEO-FFI, see below) were completed by the owner during the second visit. Finally, subjective expert ratings of cat personality items were given by all three observers (every visit was done by just two persons from a pool of three, who took turns) after all visits to the dyads had been

**Table 9.1** Factor loadings of the two new owner personality factors obtained by a PCA (57.3% of total variance explained; Varimax rotation, Kaiser normalisation, KMO = 0.63) on the individual scores of the 39 owners in the 5 original NEO-FFI personality dimensions

| FFI-dimension | F1 new: Neuroticism | F2 new: Openness |
|---|---|---|
| Neuroticism | –0.79 | 0.15 |
| Extraversion | 0.69 | –0.01 |
| Agreeableness | 0.68 | 0.28 |
| Conscientiousness | 0.51 | –0.1 |
| Openness | –0.06 | 0.96 |

completed. From tape we coded durations and frequencies of all observable cat behaviours and interactions with owners (list of behaviours coded published in Wedl *et al*., 2011) using the Observer Video Pro 5.0 software package (Noldus, the Netherlands). Intra-observer reliability among three coders (Barbara Bauer, Dorothy Gracey and Elisabeth Spielauer), tested three times during the coding process – at the beginning, approximate midpoint and end – was in the range of 72–95%.

Owners were asked to take the The NEO-Five Factor Inventory for human personality (NEO-FFI; Costa & McCrae, 1992; German version: Borkenau & Ostendorf, 1989, 2008). This 60-item instrument measures normal adult personality in 5 dimensions: Neuroticism, Extraversion, Openness, Agreeableness and Conscientiousness (see Table 9.1). For descriptions see Borkenau and Ostendorf (2008). These five dimensions may not, however, be fully independent (Jang *et al*., 1996; DeYoung, 2006). Cross-correlations showed that in our data set, Openness was the only dimension independent of the others. This allowed the use of Principal Component Analysis (PCA) to condense the initial five dimensions into two, making it considerably easier to relate owner personality to owner–cat behaviour and dyadic interactions. The first of the two new PCA axes integrated Extraversion, Agreeableness and Conscientiousness on the one hand and Neuroticism on the other. The second factor mainly comprised Openness (see Table 9.1).

The three coders rated the cats' traits and behaviours, using a continuous scale modified after Feaver *et al*. (1986) along 11 items remaining: active–inactive, anxious–confident, excitable–imperturbable, curious–uninterested, gluttonous–picky, playful–not playful, rough–gentle, sociable–reserved, tense–relaxed, vigilant–inattentive, vocal–quiet. Each item was rated by the observers on a continuous scale. A PCA was used for generating cat personality profiles based on these observer ratings (see Table 9.2).

## Results

### Owner–cat behaviour and interactions

#### Variability between dyads

As most of the following results have not been published elsewhere before, we support the information given using footnotes which provide the relevant statistical details. During our four visits to the owners' homes, the cats were usually alert and active, in anticipation of

**Table 9.2** Factor loadings of a PCA with observer-rated cat personality items (modified, after Feaver *et al.*, 1986; KMO = 0.64, chi-square ~400.9, df = 91, Bartlett's $p < 0.0001$; 76.9% of cumulative variance explained) revealed 4 axes. Sufficiently high loadings printed in bold

| Behaviour | Active–playful | Anxious | Sociable | Feeding style |
|---|---|---|---|---|
| Active | **0.882** | 0.027 | 0.155 | –0.017 |
| Excitable | **0.846** | 0.353 | –0.002 | 0.102 |
| Playful | **0.803** | –0.061 | 0.337 | 0.039 |
| Rough | **0.721** | –0.203 | –0.179 | –0.106 |
| Curious | **0.711** | –0.144 | **0.585** | –0.069 |
| Anxious | 0.036 | **0.941** | –0.094 | 0.062 |
| Tense | –0.006 | **0.860** | –0.369 | 0.150 |
| Hide | 0.021 | **–0.837** | –0.142 | 0.070 |
| Vigilant | 0.534 | **0.536** | 0.389 | 0.005 |
| Vocal | –0.025 | 0.179 | **0.736** | –0.165 |
| Sociable | 0.158 | –0.206 | **0.677** | –0.062 |
| Attentive to visitors | 0.345 | –0.515 | **0.580** | 0.101 |
| Gluttonous | –0.037 | 0.008 | 0.111 | **–0.937** |
| Examine food | –0.059 | 0.068 | –0.072 | **0.924** |

being fed. Cats were present for most of the time (84% ± 12%) while being videotaped. They walked 9% of the observation time, stood still 29%, sat 29%, crouched 11% and were observed lying just 13% of the time, which indicates their activation around feeding. The most frequently observed behaviours were associated with attentiveness, and expression of emotion or arousal which involved mainly movements and postures involving the tail, ears and eyes. During our visits, owners directly interacted with their cats by feeding them (7%), talking to them (5%) and on average, encouraging them to eat for 30% of the time, which is per se a strong indication of the social context of the feeding situation. As expected, we found substantial variation in behaviour and interaction among dyads. Of the 218 behavioural variables coded, 89% were significantly different between the 40 owner–cat dyads.[1] During the feeding situation proper, 55% of the 218 variables differed significantly among the cat–owner dyads. Of the 39 variables which were most discriminating between dyads,[2] 36% were tail movements or tail postures, 15% locomotion or body postures and 13% owner-initiated interactions, indicating that the greatest differences were related to how emotionally expressive, agitated and interactive the dyads were.

These 'most discriminating variables' differed slightly by cat sex. Less so in tail movements and postures or locomotion, but mainly in owner behaviours such as calling the cat, which covered 8% of the time in male cats, but 18% in female cats. This is an indication that in general, owners may have put more emphasis in persuading female cats to eat, potentially reflecting a greater finickyness in female cats. In fact, male cats spent a significantly greater proportion of observation time eating steadily than females.

[1] Kruskal–Wallis, df = 39, $p < 0.05$.
[2] Meaning a chi-square value of Kruskal–Wallis greater than 99, = 18% of all variables.

This was one of 17 behaviours (8% of all behaviours coded) in which male and female cats differed significantly[3] when compared directly. All these significantly different behaviours were shown by male cats more often or for longer periods of time. These were mainly communicative and attentive behaviours towards the owner, such as tail and body rubbing, rolling, circling, eyes wide open, ears erect, trill purring, sitting, but also hiding. In summary, male cats behaved more expressively towards their owners than female cats, which may have prompted owners to spend more time in presenting the food to the male cats.[4]

Dyads with male or female owners differed in only 3 of the 218 variables analysed (1% of all behaviours), but it was the behaviour of the cat, not of the owner, reflecting owner gender. Cats of male owners were more often absent during videotaping than cats of female owners, while cats with female owners showed tail up half-curved for longer periods of time and circled more often in expectation of food than did cats of male owners. It is improbable that these differences are due to the sex of the cat because male and female cats were distributed rather similarly among male and female owners. More likely, these differences were prompted by female owners relating differently to their cats than male owners.

## Owner personality

The higher the owners were on the combined Neuroticism versus Extraversion, Agreeableness and Conscientiousness scale (low individual factor scores in F1, Table 9.1), the less their cats showed ears erect[5] and the more readily they accepted being picked up and held by the owners,[6] the more their cats squeaked, the more they face-rubbed and kissed their cats,[7] but the less they engaged in object play with them and the longer owners showed 'undefined' play and feeding behaviour. This indicates that particularly owners high on the Neuroticism dimension show varied and intense social interactions with their cats, including human-initiated face-rubbing and kissing, emphasised feeding, but were not so engaged in object play with their cats.

In contrast, social interactions between owners high in the Openness dimension (high individual factor scores in F2, Table 9.1) and their cats seemed less intense than those of owners high in Neuroticism. The higher the owners in Openness, the less vocal were their cats,[8] the less time their cats spent looking at their owners, the less often owners called, but the more often they spoke to their cats and encouraged their cats to eat, and

[3] Mann–Whitney U, $p < 0.05$.
[4] Mann–Whitney U: $Z = -2.7$, $n = 25/15$, $p = 0.007$.
[5] Duration: Spearman's: rs = 0.348, $n = 40$, $\alpha = 0.028$; frequency: rs = 0.439, $\alpha = 0.038$.
[6] Holding: both duration and frequency: rs = –0.33, $\alpha = 0.005$; squeaking: rs = –0.395, $\alpha = 0.012$.
[7] Hissing: rs = –0.323, $\alpha = 0.042$; object play: rs = 0.367, $\alpha = 0.020$; undefined owner and cat vocalisations: owners: duration: rs = –0.442, $\alpha = 0.004$; frequency: rs = 0.461, $\alpha = 0.003$; cats: frequency: rs = –0.409, $\alpha = 0.009$; undefined play: rs = –0.453, $\alpha = 0.003$; feeding behaviour owner: duration: rs = 0.476, $\alpha = 0.002$; frequency: rs = 0.459, $\alpha = 0.003$.
[8] Vocal cat: duration: rs = –0.329, $\alpha = 0.038$; frequency: rs = 0.339, $\alpha = 0.033$; cat look at owner: rs = –0.384, $\alpha = 0.014$; owner calling cat: rs = –0.415, $\alpha = 0.008$; owner speaking to cat: duration: rs = 0.336, $\alpha = 0.034$; frequency: rs = 0.415, $\alpha = 0.008$; feeding: rs = 0.44, $\alpha = 0.005$; encouraging cats to eat: duration:

the more time they spent touching the cat. However, the higher owners were in Openness, the more often they initiated object play with their cats. These behaviour patterns indicate that owners high in Openness are differently relationship driven than highly Neuroticistic owners, but are somewhat more operationally interactive and emphasise object play.

### Cat and owner personality

By PCA based on expert rating we identified four cat personality axes: (1) active–playful, (2) anxious–tense, (3) sociable and (4) feeding style (Table 9.2), which parallel results by Feaver *et al.* (1986), most clearly with regard to the first two axes. Male cats were more anxious–tense (F2) and also tended to be more 'gluttonous' in feeding style (F4) than female cats.[9] The higher owners scored in Openness, the less anxious and tense were their cats and the more often these cats ignored the object in the novel object test.[10] This may indicate that general owner emotionality significantly affects how cats relate to their environment. In parallel to what we found in dogs (Kotrschal *et al.*, 2009), owners high in Neuroticism turn to their cats mainly as emotional social supporters and hence, thereby, may offer a less secure base for the cat than the owners high in Openness, who consider their cats companions for play rather than social supporters. Hence, cats of open owners as compared to Neuroticistic owners may develop into somewhat more secure and less anxious individuals.

## Tuned towards each other? How owners and cats interact over time

Because many people regard their cats as social companions, we suggest that human–cat dyads may be similar in interaction structure to human dyads. Hence, we predicted that dyadic structure will be contingent on owner and cat personalities, sex, and age as well as duration of cohabitation of the partners. Behaviour was coded from tape and was analysed for temporal (t)-patterns using Theme® (Noldus; Magnusson, 1996). This information has been previously published (see Wedl *et al.*, 2011, for details).

### How humans affect the patterns of dyadic interactions . . .

The number of patterns per minute found by the Theme® algorithm tended to be higher in dyads with a female owner than in dyads with a male owner, indicating that female owners entertain a more structured interaction with their cats than male owners. The

rs = 0.350, α = 0.027; frequency: rs = –0.365, α = 0.021; touching cat: rs = 0.348, α = 0.028; owner-initiated object play: rs = 0.351, α = 0.026.

[9] Male cats more anxious–tense (F2) and gluttonous (F4) than female cats: Mann–Whitney U: F2: $Z = -3.003$, $n = 25/15$, $p = 0.003$; F4: $Z = -1.746$, $n = 25/15$, $p = 0.081$.

[10] Owners scoring high in Openness, cat less anxious and tense and ignoring object in novel object test: F2: rs = –0.363, α = 0.022 and rs = 0.340, α = 0.032; and ignoring: duration: rs = 0.324, α = 0.041; frequency: rs = 0.336, α = 0.034.

higher the owner's score in Neuroticism (NEO-FFI dimension 1), the lower was the number of patterns found. Hence, despite the fact that such owners spend a lot of effort in socialising with their cats (above), there is not much standard temporal structure to it. This is interesting, because the amount of internal behavioural structure and synchrony generally seems a fair predictor of dyadic operationality (Kotrschal *et al*., 2010), which is supported by the fact that the higher owners are in Neuroticism the more anxious are their cats.

The higher owners were in Extraversion (NEO-FFI axis 2), the higher was the number of 'non-overlapping patterns' per minute. This means that Extraverted owners have relatively varied interaction patterns with their cat, because using Theme® we found a greater diversity in Extraverted owners than in owners low on this dimension. Finally, the more Conscientious the owner (NEO-FFI axis 5) was, the higher was the complexity of the patterns found. This indicates that interaction patterns in these dyads consisted of more behavioural elements than in owners low in Conscientiousness and supports the interpretation that a conscientious personality structure furthers trust, dependability and the expression of regularity in temporal interactions by forming dyadic ritualisation.

### . . . and how the cat does

The older the cat, the lower was the dyadic event type complexity found using Theme®. This means that the strings of cat behaviour in interaction with their owners are shorter in older than younger cats, which probably reflects decreased activity levels and playfulness with age in cats. There were also results with regards to cat personality: The more 'active' the cat (PCA axis 1, Table 9.2), the lower was the diversity of temporal patterns in interaction with the owner, but the more complex and longer were the patterns found. This means that in 'active' cats richness of interaction with the owner is not expressed in the diversity of different patterns shown, but rather in the elaboration within these patterns. The more 'sociable' the cat (PCA axis 4) was, the lower was the number of patterns we found and also, the lower was diversity in patterning. This is certainly surprising, but may indicate that in owner–cat relationships which are characterised by a low degree of patterning or structure in the interaction, the cat may compensate by being socially more attentive than cats in a more patterned/structured relationship; this may correspond to owner Neuroticism (above).

## What this all means

Analysing the complete quantitative ethogram of owner–cat behaviours and interactions in the feeding context indicated that cat–owner dyads differ quite significantly in behavioural profiles of partners and in interactions. However, this variation is not entirely idiosyncratic or 'unique' to each dyad, but to a large extent follows general rules. Similar to relational patterns found in a recent study on owner–dog relationships (Kotrschal *et al*., 2009), much of the variation seen in interaction styles between cat–owner

dyads seems contingent with cat sex and owner personality. In contrast to Turner (2000b), we found a number of sex-related differences in cat behaviour in interaction with their human partner. This may have been due to exploring owner–cat interactions in the feeding situation, which may have resulted in a greater chance of capturing such behavioural differences; also, the ethogram we coded was more complete. Cats differed most markedly according to sex in behavioural expressiveness (i.e. amount of ear or tail actions linked with emotional states: Leyhausen, 1960; Bradshaw & Cook, 1996; Bradshaw & Cameron-Beaumont, 2000) and in locomotion. In all respects, male cats were found to be more expressive in their behaviour than female cats despite the fact that most cats were neutered and hence, sexually and hormonally not intact. Males were also more active with regards to communicating and interacting with their owners and were more gluttonous/less finicky feeders than females. The effect of owner gender on dyadic behaviour and interactions around the feeding situation was contrastingly much weaker.

Owner personality was significantly related to behavioural expression/personality traits in the cats. Owners high in Neuroticism (NEO-FFI, low individual factor scores F1; Table 9.1) tended to initiate and maintain varied and intense social contact with their cats, with their urge to interact seeming to match the cats' readiness to interact, resulting in mutually attached, interactive and behaviourally varied dyads, but in comparatively anxious cats. In contrast, owners high in Openness (NEO-FFI, high individual factor scores F2; Table 9.1) communicated with their cats less vocally and tactilely, also urged them less to feed than owners high in Neuroticism, but they interacted more on an operational basis, for example, by engaging their cats in object games. These differences substantiate the idea that particularly owners needy of close social contacts with their cats (i.e. those high in Neuroticism) will produce negotiating cats rather than accepting ones. Such owners spend more time feeding the cat and encouraging the cat to eat. It may be more rewarding for them to feed their cats and more worrying if the cat does not eat or is finicky. Hence, cats may read their owner's behaviour and use it as a lever to negotiate their interest or in making the owner even more socially dependent.

We found the expression of cat individual behavioural syndromes (generally referred to as 'personalities'; Wilson *et al*., 1994; Gosling & John, 1999; Koolhaas *et al*., 1999; Sih *et al*., 2004a, 2004b) to be contingent upon owner personality. Interestingly, owners high in Openness had relatively self-confident, bold cats (i.e. not anxious, not tense, not much impressed by novel objects; Mendl & Harcourt, 2000), possibly because these human partners are less of a social resource for their cats than owners high in Neuroticism or because the latter may provide a less 'secure base' and 'haven of safety' (in the sense of attachment theory; see Julius *et al*., 2013) for their cats than highly open owners. 'Open' owners may, in effect, prompt their cats to be relatively self-reliant when dealing with the daily challenges. Consequently, these cats may develop a bolder coping style (Koolhaas *et al*., 1999) than cats with a greater social dependence on their owners, or vice versa, a greater dependence of their owners on them. Still, the higher the owner in Neuroticism, the more trusting the cat appeared when being picked up by the owner. Hence, it seems that such owners (in contrast to more extravert–agreeable–conscientious owners, Table 9.1) particularly conform to our expectation that mutual social compliance would account for close and trusting relationships with their cat (Turner, 2000b).

It is possible that any particular owner would be both high in Neuroticism (F1, Table 9.1) and high in Openness (F2, Table 9.1) and, therefore, would have a very closely attached and at the same time confident–bold cat, whereas owners low in both Neuroticism and Openness may have less attached and somewhat anxious and tense cats. Such contingencies between owner personality and cat behaviour may be particularly pronounced in the case of the single-cat household, because with two or more cats, relationships and interactions will become more complex due to triadic or more polygonal, multi-layered relationships as more cats or people enter the scene. For example, typical 'audience effects' would cause the dyadic behaviour of an individual, person or cat, towards each other simply due to the presence of a third individual. Likely, such effects on dyadic behaviour also were produced by the presence of the observers, which is, essentially, an intrusion of strangers in the dyad's home. However, due to the standardised procedure and the four visits we are confident that we did the same in all dyads.

Because the owners generally provide the socio-economic environment for the cat and because our owners were already adults when they adopted their cats (Bateson, 2000), it would seem reasonable to assume that predominantly the owner influences the cat (Durr & Smith, 1997; Lowe & Bradshaw, 2001). However, it cannot be excluded that the cat also, through its behaviour or mere presence, influences the behaviour and emotional states of the owner. Our current analysis is primarily correlative and is thus incapable of proving causality or revealing the direction of interaction. For example, it is plausible that cats who are especially able to socially support their owners may affect the degree of measured Neuroticism in the latter, the more so as the socially closest and most interactive dyads may be those with a symmetric urge to interact (Turner, 2000b). However, the most parsimonious explanation for the patterns found seems to be that owner personality affects the owner's style and intensity of communication with the cat, which would be a major factor in the fine-tuning of expressed cat personality (Mendl & Harcourt, 2000). In fact, most of the cats included in this study were adopted as kittens and most seemed to have been well socialised with people in the crucial 2–7-week period after birth (Karsh & Turner, 1988). Our sample only included two clearly shy cats (McCune, 1995; McCune *et al*., 1995; Turner, 2000b). Still, these individuals were sufficiently approachable to warrant inclusion in our study.

To date, personality research in pet owners has focused on general questions. For example, whether pet owners are different from non-pet owners or whether dog owners are different from cat owners (summarised in Serpell, 1986). Surprisingly, hardly any research has addressed the obvious question of whether and how owner personality may be related to interactive behaviour. Even more surprising, such information seems to be rare even for human dyads, potentially because such research would be unacceptably intrusive or because there is still little focus in psychology research on behaviour. This suggests that human–animal dyads may even have some potential to serve as model systems for elaborating major principles applicable to human dyads. This seems particularly promising in light of the socio-cognitive convergence emerging in the homeothermic vertebrates, including humans (above). We propose that the kind of gender and personality interactions we found in human–cat dyads may

be regarded as common principles in within-species and between-species long-term dyadic relationships in vertebrates.

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# V

# Cat Breeding and Cat Welfare

# 10 Feline welfare issues

Irene Rochlitz

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## Introduction

Research activities on the welfare of domestic cats have increased greatly in recent years. Of particular note is the emergence, especially in the USA and to a lesser extent in the UK, of shelter medicine as a veterinary specialist discipline in its own right. Its emergence is immensely gratifying, and is already leading to major improvements and refinements in the ways that overpopulation, one of the most important global issues in cat welfare, is being tackled. Significant advances are being made in the ways shelters are managed and cats are cared for. In addition, we are beginning to understand better why cats end up in shelters, what to do about it and how to promote successful adoptions. As a result, the number of healthy cats and kittens euthanised in shelters has decreased in some countries, although it still remains much too high.

There have also been improvements in our understanding of the needs of cats and how they can be met, whether cats are housed in the home, the shelter or boarding cattery, the veterinary surgery or the research facility. Innovative ways of enriching the environment of cats in order to meet these needs and improve their welfare are being developed and applied in practice. By enriching the lives of cats under our care, we also enrich our own lives.

## Animal welfare and quality of life

When writing about animal welfare, it is helpful to define the terms used and to consider how welfare may be assessed. Animal welfare is the mental and physical state of an individual animal in relation to its environment (Broom & Fraser, 2007). Welfare state may vary along a continuum from good to poor, according to the success or difficulty experienced by the animal in coping within its particular physical and social environment.

To ensure good welfare in terms of good mental state, cats should be housed and cared for in ways that promote positive feelings such as pleasure and contentment, and that lead to rewarding interactions with conspecifics, and with humans where appropriate. Conditions should minimise negative feelings such as anxiety, fear, boredom and frustration. Good welfare also means that the animal is functioning well in the biological sense, i.e. be in a good physical state. It is healthy and protected from disease or illness by effective preventive health care, such as vaccination and parasite control and regular veterinary attention. In addition, its requirements for food, water, shelter, thermal conditions, air quality and space are met.

Animal well-being is a commonly used term and is best defined as a state of good mental and physical welfare (i.e. the animal is ‘fit and happy’; Webster, 2005), although it is sometimes used as a synonym for welfare. The term ‘quality of life’ is the overall welfare of an animal, based on a balance of experiences over an extended period of time. It may include a prognosis of likely future welfare. Finally, when considering welfare or quality of life, there is also the viewpoint that animals are more likely to enjoy good quality if they are able to live relatively natural lives and behave in ways that are consistent with their nature, or ‘telos’ (Rollin, 1993) (Figure 10.1). One can argue

**Figure 10.1** To ensure good welfare, cats should be housed and cared for in ways that promote positive feelings, ensure good biological functioning and respect the cat's 'telos', or essential 'catness'.

that certain behaviours constitute the essence and purpose, or 'catness', of a cat. Interfering with the ability to perform these behaviours, whether by selective breeding (e.g. causing difficulties in climbing and jumping due to shortened limbs, see Chapter 12) or by surgery (preventing claw-scratching as a marking behaviour by onychectomy, or declawing), unequivocally diminishes the cat's quality of life.

## Assessment of welfare and quality of life

Assessment of welfare in cats is commonly based on behavioural observations and tests, and physiological measures of stress. Studies of feral cat colonies, and comparisons between the cat's current environment and the environment in which its ancestral species evolved, are also useful to inform us on the needs of cats, and how one might go about meeting them in order to ensure good welfare. The UK Cat Behaviour Working Group (1995) has published an ethogram for behavioural studies of the domestic cat,

**Table 10.1** Some behavioural measures of good and poor welfare in domestic cats

| Behaviour | Good welfare | Poor welfare |
|---|---|---|
| Maintenance behaviours[a] | Normal levels | Reduced levels or absent |
| Activity, exploration and investigation of surroundings | Normal levels | Reduced levels or absent (rarely, high levels) |
| Social interactions with other cats in the household | Present; positive (affiliative) behaviours such as allorubbing, allogrooming, staying in proximity | Absent or negative: hostility, aggression, avoidance of each other |
| Interactions with humans in the household | Initiates positive interactions with humans; positive response to human initiation of interactions | Failure to initiate interactions with humans; absence or negative response to human initiation of interactions |
| Types of behaviours shown | Shows a wide range of normal behavioural repertoire; friendly behaviours (e.g. tail-up position, rubbing, vocalisation) | Persistent signs of timidity, anxiety, fear or aggression; hiding or attempting to hide for long periods; over-grooming; self-mutilation; excessive vocalisation; excessive vigilance; feigned sleep[b] |
| Play | Presence of play (on own, with objects, with other cats or with humans) | Absence of play |

[a]Maintenance behaviours: feeding, drinking, grooming, claw-scratching, resting, sleeping, urination, defecation.

[b]Feigned sleep: the cat appears to be asleep or resting (body is in sleep posture and eyes are closed or partly closed), but is awake and vigilant.

and Lincoln University, UK has a website where cat behaviour is described in detail in a multimedia format, with the aim of encouraging consensus of description among researchers in cat behaviour (Anon., 2011).

When assessing welfare, it is important to select behavioural and physiological variables that are relevant to the particular species being studied and to take into account its evolutionary history. The domestic cat has evolved from a carnivore with an essentially solitary lifestyle where, in many contexts, there is no need or function for large, overt, exaggerated or ritualised signals to develop. Cats do not have as wide a behavioural repertoire for visual communication as, for example, the highly social, group-living dog, so assessment of their welfare may initially seem more difficult. Cats are more likely to respond to poor conditions by becoming inactive and by inhibiting normal behaviours such as self-maintenance (feeding, grooming, resting, sleeping and elimination), exploration or play, than by actively showing abnormal behaviour (McCune, 1992; Rochlitz, 2005). Some behavioural measures of good and poor welfare in cats are presented in Table 10.1.

Based on the work by McCune (1992, 1994) and Kessler and Turner (1997), a composite behavioural scale has been devised for quantifying stress in confined cats. It integrates elements of posture, appearance, vocalisation and levels of activity and has seven levels, ranging from 1 (fully relaxed) to 7 (terror). This scale, called the

Cat Stress Score, has been widely used, particularly in studies of stress in cats entering catteries (Kessler & Turner, 1997) and rescue shelters (Kessler & Turner, 1999a, 1999b; McCobb *et al*., 2005), and of the effects of environmental enrichment (Kry & Casey, 2007).

In addition to behavioural observations and quantifying stress with the Cat Stress Score, a range of behavioural tests has been developed. The proximity of humans or conspecifics is a significant stressor for many cats, and there is considerable variation between individuals in how they react. The extent to which a particular cat is affected by such stressors can be assessed by standardised testing, usually involving the progressive introduction of a person or test cat towards the subject cat (Kessler & Turner, 1999a; Casey & Bradshaw, 2005; Marston & Bennett, 2009).

The range of physiological parameters that have been used to assess the welfare of an animal, largely by measuring the effects of stress, is wide (Broom & Johnson, 1993). As indicators of the activity of the hypothalamus–pituitary–adrenal cortex (HPA) axis, glucocorticoids are frequently measured and are usually sampled in blood or saliva. The cat is particularly sensitive to the effects of handling and blood sampling, which may cause increases in blood levels of cortisol and catecholamines and result in hyperglycaemia and transient glucosuria (Peterson *et al*., 1994). It can be difficult to collect a sufficient saliva sample for cortisol analysis from most cats. Another way of investigating the adrenocortical response to stress in cats is by measuring cortisol in urine (Carlstead *et al*., 1992, 1993). The advantage of measuring urinary cortisol is that the sample can be collected non-invasively. Most cats can be trained to use litter trays, and non-absorbent litter ensures that most of the voided urine is collected. The concentration of cortisol in the urine is related to the concentration of creatinine to account for changes in fluid balance, and the result is expressed as the cortisol to creatinine ratio. Adrenocortical activity can also be measured non-invasively in the cat by measuring cortisol metabolites excreted in the faeces (Graham & Brown, 1996; Schatz & Palme, 2001) and hair (Accorsi *et al*., 2008). Poor correlation between the Cat Stress Score and cortisol levels has been noted (Hawkins *et al*., 2004; McCobb *et al*., 2005), but this could be due to cats having different coping styles (Casey, 2007). Ways of measuring other physiological indicators of stress in cats, such as immune function and reactivity, are being developed. A review of welfare assessment in domestic cats can be found in Casey and Bradshaw (2005).

Methods of evaluating quality of life in cats within the context of veterinary medicine and surgery consist primarily of questionnaires, asking owners about the cat's behaviour and interactions with them. Studies have examined owners' perception of their cats' quality of life during chemotherapy (Tzannes *et al*., 2008) and during treatment for heart disease (Reynolds *et al*., 2010). A quality of life scale for humans, Karnofsky's score, has been modified for use in cats (Hartmann & Kuffer, 1998). Another questionnaire-based approach includes aspects of the cat–human relationship, such as the level of care received by the cat and owner characteristics (Adamelli *et al*., 2005).

## Animal welfare standards

In 1999 an Animal Welfare Act was introduced in New Zealand, which sets out general obligations relating to the care of animals (Animal Welfare Act, New Zealand, 1999). Then The Animal Welfare (Companion Cats) Code of Welfare, New Zealand (2007) was published, which describes in detail the minimum standards and recommendations relating to aspects of cat care. Similarly, the Animal Welfare Act (2006) was recently introduced in legislation in the UK. The Duty of Care section of the Act describes the needs of animals that must be met by their owner, or by any other person responsible for them, in order to ensure good welfare (Table 10.2). An accompanying Code of Practice for cats gives detailed advice and recommendations on how one might go about meeting these needs (Department for Environment, Food and Rural Affairs (DEFRA), 2011). It has been suggested that the duties of care outlined in the Animal Welfare Act, UK (2006) could serve as a framework for the regulation of shelters and sanctuaries (Companion Animal Welfare Council (CAWC), 2011).

**Table 10.2** The needs of an animal that must be met in order to ensure good welfare, under the Duty of Care section of the Animal Welfare Act, UK (2006)

| |
|---|
| 1. Its need for a suitable environment |
| 2. Its need for a suitable diet |
| 3. Its need to be able to exhibit normal behaviour patterns |
| 4. Any need it has to be housed with, or apart from, other animals |
| 5. Its need to be protected from pain, suffering, injury and disease |

## Shelters for cats

As mentioned in the Introduction, shelter medicine is a rapidly developing specialism in veterinary medicine. The Association of Shelter Veterinarians was established in the USA in 2001, and shelter residency programmes are available in a number of American universities (e.g. University of California at Davis Koret Shelter Medicine Program, 2011). Positions in shelter medicine also exist in the UK, and both countries run courses in shelter medicine for the veterinary profession. Collaboration between a veterinary department at a university and a shelter is beneficial for both parties (Smeak, 2008). Students gain expertise in animal handling, shelter medicine and sterilisation surgeries. This leads to greater awareness of shelter issues within the veterinary profession, while the shelter benefits from reduced costs of treatment and a high level of veterinary expertise.

### Regulation of shelters

The need to regulate animal shelters and sanctuaries has been recognised (Patronek & Sperry, 2001; Companion Animal Welfare Council, 2004), but in most countries there is no routine licensing, regulation or inspection of such premises. In the UK, the Association

of Dogs and Cats Homes (ADCH), which is run by volunteers, has a code of practice and full members are inspected (ADCH, 2011). Currently, only 18 states in the USA require animal shelters to be licensed or registered, and 6 require the establishment of an advisory board (Newbury *et al*., 2010). There is concern within shelter communities about the existence of some shelters providing very low standards of animal care.

Nevertheless, many organisations offer information and advice on management and how to achieve high standards. The Association of Shelter Veterinarians in the USA has published comprehensive guidelines on shelter management and standards of care (Newbury *et al*., 2010). There are also books on shelter medicine and the control of infectious diseases in shelters (Miller & Zawistowski, 2004; Miller & Hurley, 2009). The Koret Shelter Medicine Program at the University of California, Davis Center for Companion Animal Health provides a wealth of information on many aspects of shelter medicine.

## Euthanasia statistics

Euthanasia statistics for shelters are difficult to obtain because there is no legal requirement to keep records of the number of animals taken in, adopted (re-homed), euthanised, reclaimed or otherwise disposed of. The American Humane Association (2012) estimates that 3.7 million dogs and cats were euthanised in American shelters in 2008. Even though some of these animals would have had medical or behavioural problems severe enough to preclude adoption, most would have been healthy and adoptable. More cats (71%) were euthanised than dogs (56%) (American Humane Association, 2012).

One might expect an economic recession to have effects on feline relinquishment, adoption and euthanasia. Data from a shelter in Chicago, USA indicated that the recession (years 2008–10 compared with pre-recession years 2000–7) had not greatly affected relinquishment or euthanasia, and only slightly reduced adoption (Weng & Hart, 2012). In contrast, Morris *et al*. (2011) measured earlier trends, from 2000 to 2007, in shelter intake and outcome data for dogs and cats in Colorado, USA and found that the number of unwanted cats in shelters increased, while the number of unwanted dogs decreased. Lord *et al*. (2006) investigated even earlier trends, between 1996 and 2004, and also found that the number of cats taken in by agencies increased while the number of dogs decreased. The number of cats that were euthanised also increased, while the number of dogs euthanised decreased. Similarly, the Blue Cross and other shelters in the UK have reported an increase in the number of animals presented to their centres in 2009–12, especially kittens and cats (Khaleeli, 2011; Blue Cross, 2012; Wood Green The Animals Charity, 2012). Overall, these data indicate that cats are still more likely to be admitted to shelters and to be euthanised than dogs.

## Euthanasia of cats

Euthanasia of animals in shelters is an emotive subject. Shelters are concerned with animal welfare, and it is generally accepted that preventing or ending poor animal welfare must include the option of euthanasia for some animals. A euthanasia policy

with a transparent, consistent and defendable decision-making process helps to reduce disagreements and conflict within the shelter workforce; this process is also of interest to the public.

Particular challenges arise in the shelter environment where, in addition to the delivery of high-quality care to individuals, the health of the shelter population as a whole must be considered. Principles of herd health management may be called upon, especially when it comes to the control of infectious disease (Miller & Hurley, 2009). An animal may have a treatable but infectious disease that presents a risk to other animals in the shelter. If the disease spreads, it may be very difficult or costly to treat, and may be fatal in vulnerable animals. In this situation, euthanasia of the individual cat may be the most appropriate option. Shelters run on a tight budget and funds must be used judiciously. Can expensive treatment to save the life of one animal be justified when many more animals can be saved for the same amount or less?

Ethical objections arise when euthanasia is used as a population control method in the shelter, i.e. healthy animals are killed in order to make room for others. One healthy animal may be considered less adoptable than another, but there may be objection to denying it a life. Shelter managers, staff and veterinarians struggle with these dilemmas and have to make difficult choices.

A crucial component of euthanasia is humane handling of the cat or kitten immediately prior to its death. Staff in shelters must be properly trained on how to restrain animals gently, effectively and with compassion. If humane restraint is not possible then other methods, such as prior sedation or confinement in a trap cage, may be necessary.

## No-kill policy

In recent years there has been increasing public objection to the killing of large numbers of healthy animals in shelters, particularly in the USA. As a result, some shelters have adopted a 'no-kill' policy; many shelters in the UK aim to adopt this policy too. The term 'no-kill' usually means that euthanasia is considered appropriate only when an animal is either suffering or dangerous to people, and has a poor prognosis for rehabilitation and recovery. Suffering might be due to severe injury, chronic or severe disease, advanced old age or serious behaviour problems. It is generally recognised that achieving the goal of managing shelter populations with a no-kill policy is challenging, and must be accompanied by a range of additional shelter activities. These include active rehoming of cats, sterilisation and other veterinary services, a fostering network, a feral cat programme, behavioural advice and rehabilitation services, involvement of volunteers, public education and marketing. Shelters with a limited or selective admission policy only admit cats that fit certain criteria (i.e. they may not admit older cats, or those requiring long-term veterinary treatment), while shelters with open admission policies admit all cats. The former type of shelter will find it easier to follow a no-kill approach than a shelter with an open admission policy.

In 2004, a group of animal rescue and welfare organisations in the USA called for the development of a uniform method for collecting and reporting shelter data, in order to promote transparency, encourage cooperation amongst shelter organisations,

and reduce the number of animals euthanised. This initiative is described in the Asilomar Accords (2011). The Accords have been quite widely adopted by the animal rescue community in the USA but less so in other countries (see their website for a list of participants).

The Accords propose three main categories of animal: (1) 'healthy', (2) 'treatable' and (3) 'unhealthy and untreatable'. 'Treatable' animals are those that can be rehabilitated or managed (so this would include feral cats). Animals categorised as 'unhealthy and untreatable' are those that cannot achieve a satisfactory quality of life, based on the level of care typically provided to pets by reasonable and caring pet owners or guardians in that community. The inclusion of the latter qualification is useful, as it ensures that expectations of the level of care available to the animal are not unrealistic, and by implication that treatment costs are also kept within reasonable limits. The Asilomar categories can be used as the basis for a no-kill policy, with euthanasia as the most humane option for animals in the third category, those that cannot enjoy a satisfactory quality of life.

## Admission of cats to shelters

Many studies have shown that cats suffer from stress when moved into a novel environment such as a shelter. The period of time over which signs of acute stress decline and adaptation occurs varies between individual cats and individual situations, but has been described as lasting from a few days (Smith *et al*., 1994), to several weeks (Kessler & Turner, 1997; Rochlitz *et al*., 1998). It is affected by many factors, including the conditions the cat is housed in, the care it receives, its temperament, how socialised it is to humans or other cats, and previous experiences (Kessler & Turner, 1997, 1999a, 1999b; Kry & Casey, 2007). Many cats seem to require at least 2 weeks to adapt to their new environment.

Dybdall *et al*. (2007) found that cats relinquished to a shelter by their owner showed greater behavioural measures of stress (using the Cat Stress Score) in the first 3 days than cats entering the shelter as strays. Of the cats deemed suitable for adoption, cats relinquished by their owners were at greater risk of becoming ill sooner than strays. It may be that cats relinquished by their owner experience additional stress due to separation from their owner and home environment, or that the cat is being surrendered because of reasons that are already causing additional stress.

## Relinquishment of cats to shelters

A number of studies have looked at the reasons why large numbers of domestic cats are relinquished to rescue shelters every year. It is difficult to compare studies because of the diversity of peoples, regions and pet-keeping habits, socio-economic factors, policies of individual shelters, and because reasons for relinquishment are categorised in different ways between studies. Owners frequently make unsuccessful attempts at resolving the problems with their pets before giving them to an animal shelter, regarding

the shelter as a last resort rather than as a resource for dealing with pet ownership problems (DiGiacomo *et al*., 1998).

A study by Patronek *et al*. (1996) showed that risk factors for relinquishment are often ones that can be modified with proper intervention and education. Factors that increased the risk of relinquishment included the cat remaining sexually intact,[1] cats being allowed outdoors, cats being of mixed breed rather than purebred, the owner being uneducated about cats, and the owner having specific expectations about the cat's role in the household. Miller *et al*. (1996) obtained similar results in a smaller study, including the finding that young cats were more likely to be relinquished and that an owner's lack of understanding or knowledge of normal feline behaviour often led to unrealistic expectations. This study found that restrictive housing rental policies also played important roles in relinquishment.

The National Council on Pet Population Study and Policy (NCPPSP, 2010) examined the reasons for relinquishment of 1409 cats and litters at 12 animal shelters in the United States (Salman *et al*., 1998; Scarlett *et al*., 1999). The most common classes of explanations for relinquishment were issues related to human health and personal issues (35%), issues related to human housing (26%), cat behavioural problems (not including aggression towards animals or people) (21%), the household animal population (15%), owner preparation for and expectation of pet ownership (15%) and request for euthanasia for reasons unrelated to old age and illness (12%) (Salman *et al*., 1998). The most common human health and personal issues were identified as allergies in the family, owner's personal problems, the introduction of a new baby and no time for the pet (Scarlett *et al*., 1999). A high proportion (63.5%) of cats did not have access to the outdoors, which may account in part for 24% of all relinquished cats reported as soiling in the house and 24% as causing damage to the house (Salman *et al*., 1998). Further in-depth analysis of the NCPPSP findings, and of other American studies of factors associated with relinquishment, can be found in Kass (2005).

Casey *et al*. (2009) obtained records of 6089 cats relinquished to 11 centres belonging to the largest cat charity in the UK, Cats Protection. The most common reasons given for cats to be relinquished to the centres were that they were found abandoned or straying (31%), owner circumstances (19%), unwanted kittens (14%), cats were transferred from other facilities (9%), behavioural reasons (7%) followed by allergy/asthma sufferer in the household (5%). This study also examined why cats were returned to the shelter after adoption, i.e. the adoption failed. Of these cats, 38% were returned for behavioural reasons, 23% because of owner circumstances and 18% because of allergy or asthma in the household. Neidhart and Boyd (2002), in a study of cats returned to shelters, found that 20% were returned for behavioural reasons, 10% for allergies and asthma and 7% for illness.

While the number of pet cats in Australia is decreasing, there has not been a corresponding reduction in admissions to welfare shelters. Marston and Bennett (2009) tracked 15,206 cat admissions to one large Melbourne shelter over a 12-month

[1] Intact means entire, i.e. not sterilised.

period. The majority (82%) of admissions were strays, and sterilisation levels were low (4%), even among owner-relinquished cats (13%). Many stray cats and kittens were socialised to humans, suggesting that they had a caretaker or owner, although the reclaim rate was low. The majority of cats admitted to the shelter were euthanised.

Clearly, stray or abandoned cats and unwanted kittens remain a significant problem for rescue facilities. In addition, the American and British studies indicate that changes in owner circumstances, human illnesses such as allergy or asthma and undesirable feline behaviours are also important reasons for relinquishment. Owners' circumstances are very varied, but common issues are those to do with health and personal issues, and housing. Better education of owners and the medical community on zoonoses and the likely involvement of cats in allergic disorders, and campaigns aimed at landlords to allow tenants to keep cats, may help to reduce the number of cats relinquished for these reasons. It is also evident that better education of owners about normal cat behaviour will lead to more realistic expectations of pet ownership and a stronger cat–human bond. Behavioural problems are also an important cause of cats being returned to centres after homing. Admittedly, identifying behaviour problems while the cat is in the shelter can be difficult due to the constraints of the shelter, and limited time for observation of, and interaction with, the cat. Behaviour problems may not become evident until the cat is in a home setting. A number of approaches can be used to reduce the number of cats relinquished or returned due to behaviour problems. They include improving the shelter environment so that the cat can express more of its behavioural repertoire so that problem behaviours can be identified, increasing the time the cat interacts with humans, reviewing the criteria used to match cats with owners, and providing appropriate behavioural advice both before and after homing (see Chapter 14).

## Adoption of cats from shelters

### Fee-based versus free adoptions

It is commonly assumed that requesting prospective owners to pay an adoption fee will ensure that they will be more committed to their animal; also, adoption fees bring in funds to the shelter. However, a recent study found that there was no significant difference between the value adopters placed on their cats whether they paid for them or got them for free (Weiss & Gramann, 2009). Adopters did not think that shelters that waived fees cared less about their cats; in fact, there was some indication that they believed the shelters valued their cats more because they were willing to forgo adoption fees in order to find them good homes. It seems that fee-waived adoptions can actually reduce costs by decreasing the length of stay for adult cats, and by getting more cats adopted. There is always the option to charge for kittens, for whom there is often a high demand.

A number of studies have explored ways of attracting the interest of viewers and of increasing the likelihood of a cat being adopted. Gourkow and Fraser (2006) found that the addition of toys to cats' cages increased adoptions. Fantuzzi *et al*. (2010) reported that cats housed at eye level (in the upper rather than lower tier of cages), and those

whose cages contained toys, were viewed more by adopters even though the toys did not affect the cats' behaviour. Adopters viewed active cats for longer periods of time, and these cats were more likely to be adopted during the study than less active cats. Upper-tier cats tended to be more active than lower-tier cats, possibly because they were being viewed more often and for longer than lower-tier cats. Also, cats prefer elevated areas which they can use as vantage points to scan their surroundings and monitor the approach of people (Rochlitz, 2005), so cats in the upper tier may have been less stressed and therefore more active than lower-tier cats. Improving the visibility of cages and placing a toy within the cage may help to increase adopter interest, which will be particularly useful for cats that are harder to find homes for.

This study did not find that the coat colour, sex and age of cats influenced viewing by adopters. In contrast, Lepper *et al*. (2002) found that factors affecting the likelihood of a cat being adopted included its age (cats under one year were preferred), sex (males rather than females), sterilisation status (sterilised rather than intact), fur colour (white, colourpoint or grey rather than brown or black), breed (Persian rather than domestic shorthair), and reason for relinquishment (stray rather than other reasons) to the shelter.

### Matching cat with prospective owner

The American Society for the Prevention of Cruelty to Animals (ASPCA) has developed a 'Meet Your Match® Feline-ality™' programme which matches cats, categorised by distinct behavioural characteristics such as enjoyment of being petted and held, playfulness, sociability, inquisitiveness and activity levels, with adopters whose expectations, personality and lifestyle are also evaluated (ASPCA, 2011). While owners are not obliged to choose a particular cat, this matching aims to ensure that the adoption is a success. Siegford *et al*. (2004) describes a behavioural test using a Feline Temperament Profile, which essentially evaluates the cat's sociability to people, that can also be used to match cats with prospective owners. In certain situations where a large number and types of cats are offered for adoption, narrowing down the number of cats available to a particular owner may actually help the owner to make a choice.

## Feral cats and shelters

The terminology used to discuss feral cats can be confusing (see Chapter 15). Generally, 'free-roaming' is a term used for any cat living outdoors for at least part of the time. This would include feral and semi-feral cats, lost or abandoned pet cats and owned cats allowed outside. Feral cats are those who have not received appropriate social interaction with people during the socialisation period, and hence remain wary of them throughout adulthood (Slater, 2005). Cats may alter their behaviour towards humans through their lifetime or in different environments. However, feral cats typically remain too frightened of humans to be placed into a home as a companion animal. Semi-feral or loosely owned cats have had some degree of socialisation with people, and may approach a caregiver for food or even solicit some social interaction depending on the cat and the circumstances. These cats are usually cared for by caregivers in a community but do not have a specific owner (Figure 10.2). Abandoned and lost or stray pets,

**Figure 10.2** A cat 'shanty town', consisting of a row of improvised shelters for a colony of free-roaming cats on the outskirts of a town in the UK. These cats were cared for by two caretakers and managed by a trap–neuter–return programme.

generally, were once well socialised and lived in close association with people but in certain circumstances, such as being in an unfamiliar or frightening environment, they may display extremely fearful behaviour when approached. Usually, however, under certain conditions these cats can overcome their fear of people and once again become pets (Slater *et al*., 2010).

A major dilemma that shelter staff have to wrestle with frequently is whether the cat presented to the shelter is feral or not. The cat may be found wandering as a stray, so there is no information on its history. It presents as a very frightened animal, resistant to human contact. Is it genuinely feral, or is it a previously owned, socialised cat that has been abandoned or lost and upon entry to the shelter is terrified? Because a feral cat is managed differently from a socialised cat, it is vital that they are differentiated reliably. In most circumstances, feral cats are best managed with a trap–neuter–return programme (TNR; see Chapter 15), while semi-feral, loosely owned cats, as well as those that are abandoned or lost, may be adoptable. Slater *et al*. (2010) carried out a survey of the methods that were used in shelter and rescue programmes to differentiate feral from non-feral cats. The survey found that a wide variety of methods were used. However, only 15% of 555 respondents, who were mainly non-profit shelters (32%), organisers of TNR programmes (18%) and animal control organisations (15%), had written guidelines. Holding periods of 1–3 days were common, and cats deemed to be feral were often euthanised. About half the shelters transferred ferals to TNR programmes at least occasionally. This survey highlights the need for validated assessment

methods, which preferably can be applied soon after intake, to reliably differentiate feral from non-feral cats. If decisions are made on the basis of unreliable assessments or are made hastily and too early, socialised cats, including lost owned cats, may be categorised as feral and killed mistakenly.

## Sterilisation of cats

Litters of kittens are over-represented in the population of cats presented to shelters. The most obvious way to address this is by preventing the birth of unwanted litters, but despite major efforts by the veterinary profession, animal charities and other organisations in recent years, this is proving difficult to achieve. Surveys of cat owners in Australia (Toribio *et al*., 2009), the USA (Chu *et al*., 2009) and the UK (Murray *et al*., 2009) found that there were high levels of sterilisation[2] of owned cats (over 80%), but 13–20% of females had mainly unplanned litters before sterilisation. In a survey of cat ownership in central Italy 43% of cats were sterilised, about 1 in 3 cats had had a litter, and all litters were considered accidental rather than planned (Slater *et al*., 2008). Clearly, achieving high levels of sterilisation is not sufficient if females are allowed to breed beforehand.

One way to address this is by sterilising cats before they are able to reproduce, i.e. early-age sterilisation (also known as pre-pubertal sterilisation, pre-pubertal neutering or early-age neutering). Many shelters and companion animal welfare organisations endorse early-age sterilisation (Joyce & Yates, 2011; The Cat Group, 2011; Thomas *et al*., 2011). The American Association of Feline Practitioners (AAFP, 2010) regards early sterilisation, i.e. sterilisation occurring between 6 and 14 weeks of age, as a safe and effective means of population control. In the UK, The Cat Group (2011) advises that sterilisation of owned pets at 4 months (16 weeks) should be regarded as the normal convention, and that earlier sterilisation (at 8–12 weeks of age) should be regarded as appropriate for rescue and feral kittens. However, despite this, and despite no evidence from either short- or long-term studies of significant problems following early sterilisation (Howe *et al*., 2000; Spain *et al*., 2004), only 28% of veterinarians in private practice in the UK agree with sterilising kittens between 12 and 16 weeks of age (Murray *et al*., 2008). Because most sterilisation is carried out by veterinarians in private practice, early-age sterilisation is unlikely to have a major effect on the number of litters born as long as it is only offered by rescue shelters. Shelters should aim to promote early-age sterilisation among the veterinary profession, by holding educational workshops to demonstrate anaesthetic and surgical techniques and to highlight the problem of overpopulation. It is vital that protocols minimise, and ideally eliminate, any pain, fear and other negative effects at a time, the end of the sensitive period (see Chapter 2), when kittens may be particularly vulnerable.

[2] Sterilisation means the removal of gonads of either sex. The term neutering is sometimes used synonymously, although it may also refer to the orchidectomy procedure in the male (castration is another commonly used term). Spay describes the ovario-hysterectomy procedure in the female.

Long-term fertility control of both cats and dogs using chemical sterilants or contraceptives is an active area of research, but such products are not yet commercially available. However, the activities of the Found Animals Foundation and of the Alliance for Contraception in Cats and Dogs (ACC&D), which offer substantial funds, resources and support for research in this area, give hope that such products will be available in the near future (ACC&D, 2012; Michelson Prize & Grants, 2012).

## Identification of cats

A shelter statistic that is particularly striking initially is the very low reclaim rate for cats (Morris *et al*., 2011); only between 2% and 5% of cats in shelters are reunited with their owners (Lord *et al*., 2007a; Marston & Bennett, 2009; NCPPSP, 2010; HSUS, 2012). On consideration, this is perhaps not surprising as a large proportion of cats entering shelters do not have any identification, either in the form of a collar and tag, or microchip. Lord *et al*. (2007b) found that only 19% of lost cats had any kind of identification, a much lower figure than the proportion of dogs (48%; Lord *et al*., 2007a).

Slater *et al*. (2012) noted that despite 80% of pet owners believing it is very or extremely important for pets to wear identification tags (ID), only 20% of their pets wore an ID at all times. The most common reason for not placing a tag was that their pet was 'indoor only' (35%), with another 10% reporting their pet did not wear ID because wearing a collar was uncomfortable for them. While a high percentage of pets did not have identification, there seemed to be a positive attitude among pet owners toward ID. Weiss *et al*. (2011) tested whether providing owners with free collars with ID at the time of a veterinary or sterilisation clinic visit, or at adoption from a shelter, increases the chance that the animal will continue to wear identification. Post-intervention (4–8 weeks later), there was a significant increase in ID use for both dogs and cats. For already owned pets the use of ID went from 16% to 84%, and 94% of the adopted animals were still wearing their ID. Importantly, of 18 animals that had become lost after receiving their ID, 17 were returned to their owners. Admittedly there was a 44% response rate to the post-intervention survey from owners recruited at the veterinary and sterilisation clinics, and a 41% response rate from adopters from the shelters. If non-responders to the survey were those no longer using the ID provided, then the overall percentage of pets still wearing ID would be lower. Nevertheless, there may be a case for shelters, veterinary and sterilisation clinics and other agencies involved in cat welfare and rescue to supply cat owners with free collars and ID.

By means of a telephone survey of owners of lost cats, Lord *et al*. (2007b) examined the process by which owners search for their cats. Most cats (66%) that were recovered returned home on their own or were found in the neighbourhood (7%); other cats were recovered through posting of neighbourhood signs (11%) or calling or visiting an animal agency (7%). Only 19% of cats had some form of identification at the time they were lost (ID, rabies tag, or microchip). Altogether, just over half (53%) of 138 lost cats

**Figure 10.3** All cats, those with outdoor access as well as those confined indoors, should wear some form of identification, either in the form of a collar with tag or a microchip, and preferably both.

were recovered; median time to recovery was 5 days. It is fortunate that some cats are able to find their own way home, but if more cats wore ID more would be reunited with their owner (Figure 10.3). Owners must be informed about the advantages of having some form of ID on their cat, even for indoor-only cats as they may escape to the outdoors and get lost (Lord *et al*., 2007b, 2010).

Some owners believe their cat could be injured by, or will not tolerate, wearing a collar. This is not borne out by another study by Lord *et al*. (2010), where collars and microchips were evaluated. Over 70% (391 of 538) of cats successfully wore their collars for the entire 6-month study period. Type of collar influenced how often collars needed to be reapplied. Plastic buckle collars seemed to stay on better than the two other collar types (a breakaway buckle collar or an elastic stretch collar), although the difference was not significant. Overall, owners' expectations were exceeded with 56% stating their cats tolerated the collars better than they expected. Eighteen cats caught a forelimb in their collar or caught their collar on an object or in their mouth. The authors emphasise that, with any collar type, it is important to teach owners the importance of checking the collar periodically to see whether it needs adjustment. Of the 478 microchips that were scanned at the conclusion of the study, 477 were functional. The authors conclude that, because for some cats collars may come off frequently and become lost, microchips are an important form of backup ID. Even with microchips, however, there can be problems. Only 63.5% of owners of microchipped stray cats entering an animal shelter were traced. Issues related to registration undermined the potential of microchipping as a method for permanent pet identification.

# Housing

## Introduction

It is obvious that the way a cat is housed and looked after will have a profound influence on its welfare. The range of housing conditions in which cats may be kept include boarding, breeding and quarantine catteries, rescue shelters and sanctuaries, research facilities, veterinary practices and the home. It may initially seem important that housing should be particularly good when cats spend their entire life confined there, such as pet cats kept indoors or cats in research facilities. However, whether the cat will be housed in a specific environment for 2 days (for example, in a veterinary hospital), for 2 weeks (in a boarding cattery), 2 months (in a shelter) or 2 years (in a laboratory) is of little relevance to the animal. Its welfare is determined by the conditions it lives in day-by-day, so the aim should be to achieve high standards of housing and care in all the conditions in which cats are kept.

An important objective of good housing is to improve welfare by giving the animal a degree of control over its environment (Broom & Johnson, 1993). Providing extremes are avoided, a cat that has a variety of behavioural choices and is able to exert some control over its physical and social environment will develop more flexible and effective strategies for coping with stimuli. Control is linked with predictability; cats do not like unpredictability such as irregular contact with unfamiliar cats or humans, or an unfamiliar and unpredictable routine (Carlstead *et al*., 1993).

### Housing in research facilities

Whenever animals are to be used in biomedical research, consideration should be given to the implementation of the 'Three Rs': replacement, reduction and refinement (Russell & Birch, 1959). While the ultimate aim should be to replace all live animal use in experiments with non-sentient material, it is likely that cats will continue to be used in such research in the near future, albeit in decreasing numbers, and refinement remains very important. Refinement applies both to experimental procedures and to the way cats are housed and looked after. While much attention, justifiably, is paid to the regulation of experimental procedures with the emphasis on the control of pain, housing conditions also have a major impact on the cats' welfare so they too should be well regulated to the highest standards. Keeping cats in an enriched, stimulating environment that encourages a wide range of normal behaviours will, by enhancing their welfare, make them better subjects for scientific investigation (Poole, 1997), have a positive effect on the public perception of the treatment of animals in laboratories (Benn, 1995) and, when these cats are no longer required for research and are re-homed, they will be more likely to adapt successfully to their new home environment (DiGangi & Levy, 2006).

The European Convention for the Protection of Vertebrate Animals used for Experimental and Other Scientific Purposes (ETS 123), Appendix A Council of Europe (2006), states that one cat should have an enclosure[3] with a minimum floor area of

[3] The term enclosure refers to a cage or pen in a cattery, shelter or laboratory, as well as to the home environment.

1.5 $m^2$ and a shelf of at least 0.5 $m^2$. Another 0.75 $m^2$ of floor space and 0.25 $m^2$ of shelf space are required for every additional cat, and the cage should be 2 m high (walk-in). These dimensions are considerably larger than the minimum dimensions stated for the housing of cats in research facilities in the USA. A 4 kg cat can be housed in an enclosure with 0.37 $m^2$ of floor space and a height of 0.60 m (National Research Council (NRC), 2011). In the author's opinion, the NRC minimum dimensions are too small, and research facilities should aim to exceed them in order to create enclosures that are well designed to meet the needs of cats.

## Housing in shelters

The population of cats entering shelters is often extremely heterogeneous (Evans, 2001), differing, for example, in origin (feral, stray, owned), socialisation status, age, vaccination status and health. The control of infectious disease in shelters, especially of viral origin, is very important in cats so care should be taken to ensure that management and environmental enrichment procedures do not increase disease risk (Miller & Hurley, 2009).

Upon admission to shelters, cats are usually housed singly or in pairs while group housing is less common despite space being often at a premium. Enclosures may vary from small, stainless steel cages where there is barely enough space for a litter tray, feeding and drinking bowls and a rest area, to generously sized walk-in enclosures with indoor and outdoor sections (Figure 10.4). It is increasingly recognised that these small cages are not suitable for more than very short-term housing (a day or two). In order to improve conditions, advice is available on how to transform two adjacent cages into one double compartment cage unit using a PVC portal, and how to build a raised perch within the unit (Koret Shelter Medicine Program, 2012). Kessler and Turner (1999b), based on their observations of group-housed cats in shelters and catteries, suggest that there should be at least 1.7 $m^2$ of floor area per cat, but as this figure is for cats that are familiar with others in the group, it is likely to be higher for cats in shelters, whether singly or group-housed.

There has been much discussion and some research on whether single or group housing is best for cats in shelters (Smith *et al*., 1994; Ottway & Hawkins, 2003). In the author's opinion, cats entering shelters should be housed in discrete units and kept in their original groups (four or more cats from the same household can be split into smaller groups of two to three cats), rather than introduced into groups of cats with which they are not familiar. This period of discrete housing will also allow caretakers to find out more about the individual cat's health, behaviour and personality, and to identify, treat and control disease. If adoption is not imminent after a period of several weeks, it may be worth considering moving the cat into communal housing providing that the group is not too large, there is plenty of space that is suitably enriched, and that there is some stability in group composition (Dantas-Divers *et al*., 2011). Cats previously socialised toward people and conspecifics will adapt better to group housing than non-socialised cats (Kessler & Turner, 1999a). There will be some cats that are unable to adapt to communal housing; they should be identified and housed separately.

**Figure 10.4** This enclosure in a cat shelter has generous dimensions. It consists of a heated inner section and an outer section accessed via a catflap, and is walk-in (2 m high).

### Long-term housing

Some cats may be housed in shelters for long periods of time (months or even years), especially if the shelter has a 'no-kill' policy. Due to the social disruption, lack of control, and both acute and chronic fear-inducing conditions that may exist in the shelter environment, concerns about the welfare of these long-stay animals have been raised (Patronek & Sperry, 2001). A study by Gouveia *et al.* (2011), who noted that cats group-housed for 7 years or more in a shelter were less active, ate less and had more agonistic interactions than cats group-housed for 6 years or less, supports these concerns.

There is no consensus on when a short-term stay becomes a long-term one; some estimate it to be after as short a period as 2 weeks (Newbury *et al.*, 2010), although one month seems reasonable. Length of stay is likely to affect each individual cat differently. Any cat showing consistent signs of poor welfare, or showing deterioration over time, should be targeted for additional attention and intervention, such as increased opportunities for social contact and mental stimulation or relocation to a foster home or sanctuary.

## Environmental enrichment

Environmental enrichment describes modifications made to an animal's environment with the aim of improving its welfare. Allowing caregivers to enrich the environment of cats

under their care can also enrich their own lives (Young, 2003). A comprehensive review of environmental enrichment can be found in Chapter 13 and in a number of publications (Overall & Dyer, 2005; Rochlitz, 2005; Ellis, 2009; Herron & Buffington, 2010).

When a cat first enters a new environment such as a shelter, boarding cattery or research facility, the priority is to facilitate quick and uneventful adaptation of the cat to its novel surroundings. This can be achieved by providing the following: hiding places, raised surfaces such as shelves and perches, no or minimal exposure to unfamiliar cats, olfactory continuity, a predictable routine, low noise levels and gentle human contact from a limited number of handlers. Olfactory continuity occurs if the immediate olfactory environment is kept constant and familiar. This is important in ensuring that the cat feels secure and unthreatened within its enclosure, and facilitates adaptation (Casey, 2007). In the shelter or similar environment, olfactory continuity can be achieved by providing at least two items of bedding in the cat's cage and only replacing one item every day with a clean one. In addition, daily spot-cleaning rather than cleaning the whole cage will ensure that some of the cat's marks remain; pheromonotherapy using Feliway™ may also be beneficial (see Chapter 14). Once the cat shows signs of adaptation (an increase in maintenance behaviours, reduced time spent hiding, normal activity and responsiveness, lower stress score) then other forms of enrichment, such as toys or increased human contact, may be appropriate.

The British Columbia Society for the Prevention of Cruelty to Animals has developed a Hide, Perch & Go Box™. It consists of a cardboard box for hiding in, and a tray-like structure with a raised 'lip' or edge on its top where the cat can perch and still be partially concealed. Kry and Casey (2007) found that this box facilitated adaptation of cats in a shelter, who used the box both for hiding in and for perching on top of. The use of this box did not decrease the likelihood of these cats being adopted (despite the fact that they spent some of their time hiding and not visible to the public). The Hide, Perch & Go Box™ can be transformed into a temporary carrier to transport the cat to its home when it is adopted. Once in the new home, the carrier can be reassembled. Because it will be familiar to the cat and still carry the cat's scent, it will facilitate adaptation to the new setting.

When considering strategies for improving welfare by means of environmental enrichment, Ellis (2009) distinguishes between two main types of behavioural responses in cats: active and passive. In response to confinement, behaviours shown by active responders include making attempts to escape, pacing, vocalising, and aggression towards people or other animals, while passive responders show inhibition of maintenance behaviours, immobility, attempts to hide, absence of vocalisation and lack of interest in interacting with the environment. Active responders may benefit more from stimulatory forms of enrichment (e.g. toys) while passive responders may benefit more from enrichment that increases security (e.g. hiding). Ellis (2009) also makes the distinction between enrichment that is appropriate for cats that are feeling frustrated, and enrichment for those that are feeling anxious or fearful. Cats that show behaviours indicating frustration need more stimulation (social, sensory), feeding

enrichment and play, while anxious or fearful cats need more hiding places and bolt holes, more opportunities to use the vertical space, social interaction with humans if they are well socialised, and may benefit from pheromonotherapy (see Chapter 14). Further work on environmental enrichment strategies, and specific responses of cats to them, is required. Ideally, enrichment strategies should be tailored to the needs of the individual cat; this is probably more feasible in the home setting.

## Chronic pain

Long-term, or chronic, pain in cats is an important welfare issue but is often overlooked (Robertson & Lascelles, 2010). Changes in behaviour and lifestyle are the most important signs of chronic pain in cats, but signs are often subtle and covert and can easily be missed by the inexperienced or uninformed observer. It is not unusual for signs of pain to be ascribed to ageing, and mistakenly to be dismissed as inevitable and/or unlikely to respond to treatment.

While the prevalence of degenerative joint disease (DJD) appears to be high in cats of all ages, diagnosing DJD and assessing DJD-associated pain can be a challenge (Lascelles & Robertson, 2010). Bennett and Morton (2009) were able to identify behavioural and lifestyle changes in cats that were associated with chronic pain caused by musculoskeletal disease, by assessing their response to analgesic treatment. The cats' owners completed questionnaires before and 28 days after the start of treatment, and were able to detect improvements in their cats' level of mobility (e.g. jumping, gracefulness, use of litter tray and toileting behaviour), activity (sleeping habits, playing, hunting), grooming habits (including claw-scratching) and general temperament (interaction with owner or other animals, general attitude). Their assessment was in general agreement with that of the treating veterinarian (who independently provided a global score before and after treatment), and the greatest improvement was noted in the cats' activity levels (there was no placebo group in this study).

In addition to DJD, other clinical conditions that are likely to result in long-term pain and discomfort in cats include interstitial cystitis (see Chapter 13), various cancers, many dermatological diseases, dental and oral diseases, slow-healing wounds, burns, certain neuropathies, and post-surgical conditions (Robertson & Lascelles, 2010). It has been suggested that onychectomy (declawing) causes long-term post-surgical pain in some cats (Robertson & Lascelles, 2010). Research on whether feline amputees experience phantom limb pain is currently ongoing (Forster *et al*., 2010).

How severely a cat is affected by chronic pain may not be evident until after a trial treatment with an effective analgesic. Cats with behaviour problems such as aggression may have an underlying painful medical condition. It is vital that the source of pain is identified, and that pain management forms part of the cat's treatment (see Chapter 14). The American Animal Hospital Association together with the American Association of Feline Practitioners have produced guidelines on pain management in cats (Hellyer *et al*., 2007).

## Ageing and age-related diseases

Davies (2011) carried out a survey to investigate internet users' perception of the seriousness of some of the signs often associated with common age-related disorders in pet animals, such as weight loss, reduced appetite, increased thirst and leg stiffness. There appeared to be a general lack of awareness about the importance of signs that are common in old animals with age-related diseases. The participants in this survey were computer-literate, animal-orientated, internet users seeking animal health advice. It is likely that an even lower percentage of the general population would have understood the seriousness of these signs. This lack of awareness may lead to cats being presented for veterinary treatment relatively late in the course of their disease, and not benefiting from treatment, such as analgesia, that could improve their quality of life.

With improvements in nutrition and veterinary medicine, pet cats are living longer. Accompanying this growing geriatric population are increasing numbers of cats showing signs of altered behaviour and apparent senility (Gunn-Moore *et al.*, 2007). These signs may be due to cognitive dysfunction syndrome, a neurodegenerative disorder which is increasingly being recognised in older cats and should not be dismissed as being a normal consequence of ageing (Landsberg *et al.*, 2010). Behavioural signs include aimless wandering, vocalisation (particularly at night), night-time waking, disorientation, restlessness, irritability, aggression and house soiling. A number of approaches have been used to treat this syndrome, and include dietary manipulation or supplementation, psychotropic drugs, pheromonotherapy, and enrichment of the cat's environment (see Chapter 14).

## Concluding remarks

Great progress has been made in the ways that welfare issues affecting cats are addressed. Nevertheless, major challenges still remain, particularly those to do with overpopulation and with feral cats. At least four strategies aimed at tackling the major cat welfare issues can be identified.

The first strategy is the education of cat owners and of the wider pet-owning and non-pet-owning communities on the responsibilities of pet ownership, the needs of cats and how they can be met, what constitutes normal cat behaviour, and how to address behaviour problems. Shelters, as well as other animal welfare organisations, have a vital role in educating existing and potential owners, in promoting adoption and in supporting owners who are considering relinquishment. The veterinary and allied professions (such as animal behaviourists) also have a role to play in educating owners. Veterinarians are well placed to focus on particular conditions that raise welfare concerns such as chronic pain, ageing and age-related diseases, and cognitive dysfunction.

The second strategy is to prevent the birth of even more cats. Despite the widespread availability of low-cost sterilisation, too many litters of kittens are born and most of them are unplanned and unwanted. Future research should aim to unravel the complex reasons for owner resistance to pet sterilisation, and what incentives are most

effective in overcoming this resistance. Ideally, all kittens from shelters should be sterilised before adoption, and there is also a place for early-age sterilisation in private practice. Fortunately, it is likely that other effective options for fertility control, such as chemical sterilisants and contraceptives, will soon be available and reduce the need for surgical sterilisation.

The third strategy is aimed at stray cats, which commonly represent a high proportion of cats entering shelters. Stray in this context means that the cat is socialised and has had an owner in the past but because of a lack of effective identification, the owner cannot be traced. Ensuring that all owned cats have some form of identification, whether by collar and tag or by microchip and preferably by both, is likely to have a major effect on cat welfare and on shelter activities. Stray cats with identification can be rapidly reunited with their owners, leaving the shelter to focus its resources on sections of the cat population that need their help most. Lack of identification is often a problem in veterinary practice too, when an injured cat is presented for treatment. It is clearly owned but without locating an owner veterinary treatment, especially if it is complicated or expensive, may not be undertaken or may be delayed.

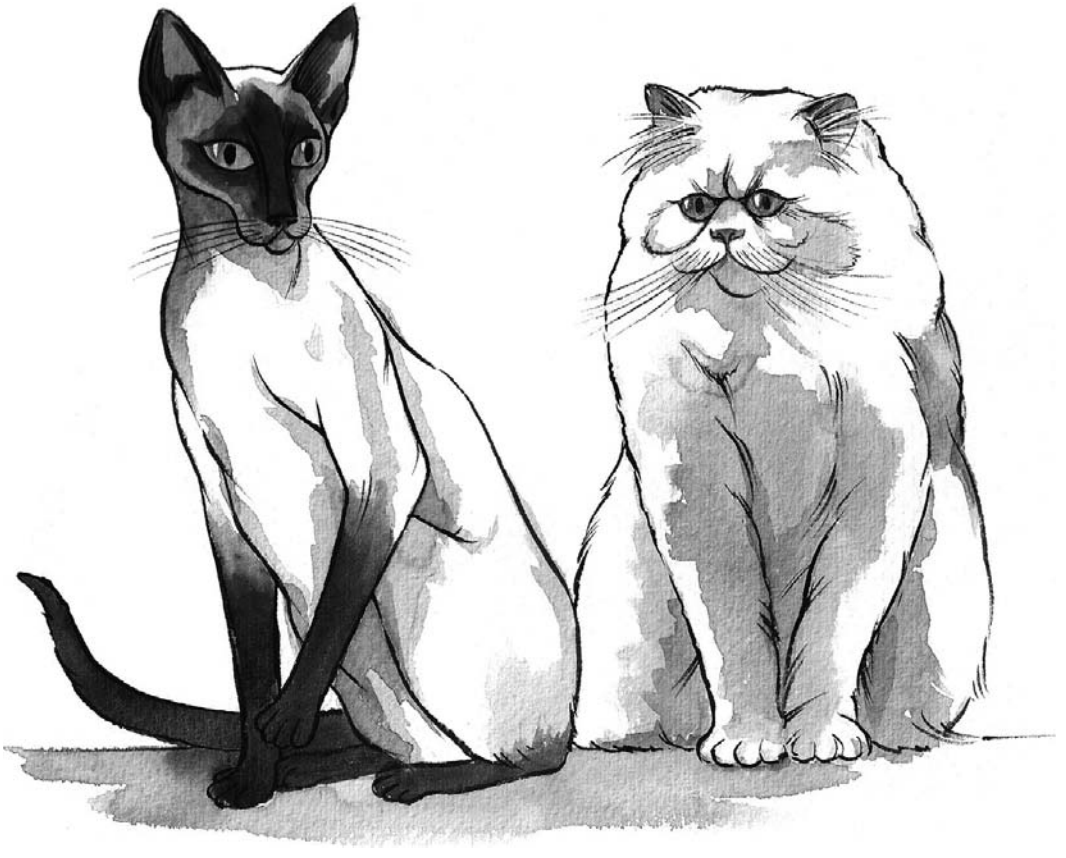
The final strategy is the humane and effective management of the feral and semi-feral cat populations. This is a huge challenge that must be tackled; dialogue with all groups, including those involved in wildlife conservation, is necessary. Options for the management of these free-roaming cat populations are described in Chapter 15.

## Acknowledgements

I am grateful to the Department of Veterinary Medicine at the University of Cambridge for providing the facilities to write this chapter, and to David and Lily Gouldstone for reading the first draft.

# 11 Breed and gender behaviour differences: relation to the ancient history and origin of the domestic cat

Benjamin L. Hart, Lynette A. Hart and Leslie A. Lyons



*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

When going through the adoption process for a new puppy there is typically a focus on breed identification with an eye on what to expect when the dog grows up in terms of behaviour as well as body shape and size. Talk to someone who is thinking of adopting a kitten and typically little attention is given to breed or breed composition. Instead, thought is given to hair coat length, colour and pattern along with a concern about an appropriate place from which to adopt a kitten (Karsh & Turner, 1988).

The overwhelming practice in selecting a kitten is to adopt a generic type, commonly referred to as a domestic shorthair (DSH) or longhair (DLH). It appears as though not much thought is given to the behavioural profile of the cat as an adult. The logic seems to be 'a cat is just a cat'. In other words, you get what you get. Contrast that with someone who adopts a Jack Russell Terrier dog knowing that the behaviour – reactive and snappy – will be quite different from the Golden Retriever they had before.

Puppy adopters commonly select a breed based on what they expect in the way of behaviour as the puppy grows up; knowing the breed, one can predict the future behaviour to some extent (Hart & Hart, 1985, 1988). While people adopting kittens do not seem to consider the future behaviour of the kitten, they are certainly affected by the behaviour of their cat as adulthood is reached. The behaviours that many cat caregivers find desirable include being affectionate towards the human family members and socially outgoing; and you can add in being good at litter box use. Behaviours that are universally undesirable are being aggressive towards human family members, overly fearful of visitors and urine marking in the house. What astute cat people realise is that some behavioural differences among cats are genetically based. And, when it comes to purebred cats, there are striking differences in behaviour – at least between some breeds – as there are in dogs.

Until just recently, only one study had compared the behaviours among breeds. Studying the Persian and Siamese breeds, along with the generic DSH, the study examined the cats' behaviours directed towards their owners; the study combined direct observations of the cat's interactions with the owners with the owners' subjective assessments of the cats' personalities (Turner, 2000a). While the behaviour of both purebreds was more predictable, and more human-oriented than that of the DSH, using this methodology, relatively few differences were found between the two purebreds.

In this chapter we discuss a new study using statistical methodology to see what behaviours may or may not have a genetic basis by virtue of behavioural differences and similarities among 15 popular breeds of cats. We also go over some of the ancient and more recent history of cat breeds, linking this to modern-day cat breeds. We further discuss some recent insights into behavioural differences between neutered males and neutered females. As in dealing with any genetic study of behavioural differences, it must be emphasised that the early experience and current environment of a cat are important behavioural determinants along with genetic influences.

From the practical standpoint, even without a focus on adopting a purebred, it may be useful to know about breed differences in behaviour in order to get a perspective on genetic-related variability in behaviour. For a person interested in adopting a kitten, regardless of the kitten being a purebred or not, it can be valuable to understand the degree to which male cats differ from female cats in behavioural patterns that relate to their suitability as family pets.

A point to be made in discussing behavioural profiles of cat breeds is that while the behavioural differences in dog breeds had their origins in their working roles, such as guarding homes, herding sheep or retrieving game fowl, cats virtually never were selected to perform in a working role for humans. However, the breeds analysed in this study are known to reflect genetically distinct groupings of cats, originating from different populations (Lipinski *et al*., 2008; Kurushima *et al*., 2013); thus, it is likely that the different genetic backgrounds account for many differences in their behaviours.

The artificial selection seen in body style can influence selection for behaviour. For example, the Persian, with its long, dense coat, had to be selected for an activity level and behaviour that would allow it to endure extensive grooming by the caregivers. One breed selected for being very affectionate as well as having an appealing, warm-looking body is the Ragdoll. Pretty much the same goes for the Burmese: they were selectively bred, starting with the thin, moderately affectionate, Siamese. The breeders made choices for a rounded head, an almost stocky body, and a more affectionate temperament than the Siamese.

## Data-based breed and sex profiles

The information here, outlining a few of the more interesting results on breed-specific behaviour of cats, is from a just-completed, data-based study involving systematically gathered data from many feline authorities (Hart & Hart, 2013). The design of the study was derived from that used in developing breed profiles of dogs (Hart & Miller, 1985; Hart & Hart, 1988). The authorities were 80 feline veterinary practitioners who had seen many cats of all breeds and types and who had heard cat owners complain and boast about their pets. Of primary concern was to acquire a relative comparative ranking of cat breeds, not expecting that breeds could be scored on an absolute scale. However, authorities were expected to converge in ranking breeds on various characteristics such as affection to family members or being friendly to visitors.

The authorities were interviewed over the telephone for about 30 min, after previously scheduling the interview. They were chosen randomly from a directory, taking into account the goal to have about equal representations of men and women and regions of the United States. Each authority was assigned to rank 5 breeds of purebred cats, randomly chosen from the master list of 15 breeds, plus the DSH and DLH, on each of 12 behavioural traits. The master list of purebreds included the Abyssinian, Bengal, Persian, Ragdoll, Siamese, Burmese, Manx, Norwegian Forest Cat, Sphynx, Cornish Rex, Oriental, Maine Coon, Tonkinese, Exotic and Russian Blue.

The 12 characteristics chosen for ranking were considered to be of interest to cat owners. These were: activity level, affection to human family members, aggression to human family members, aggression to other cats, fearfulness of visiting people, being friendly to visitors, playfulness, vocalisation, use of the litter box, urine marking (spraying) in the house, scratching furniture and predation on song birds.

As mentioned, early experience and current environment can influence behaviour as well as genetics. By surveying a large number of authorities, each of whom has heard

from a large number of cat owners, the statistical approach used averages out the experiential and environmental differences, and significance testing reveals the degree to which actual genetically related differences among breeds come through.

The study was designed at the outset with input from a statistician. The rankings were drawn from the 80 authorities on each of the 12 characteristics, and then processed by computer, and endpoint analyses involved ranking by least-squares means. With the provision that some characteristics differentiate between breeds better than others, highly significant differences were found, across breeds in general, on each of the 12 traits ($p < 0.001$). For each characteristic, the breeds were ranked from the lowest to highest after adjusting the least-squares means to a range of 1 (lowest) to 10 (highest).

## Behavioural characteristic ranks

Looking at a sample of the ranking of breeds, we can see the fruits of the labour of cat breeders in persistently selecting for behaviour. The complete set of profiles for the breeds portrayed in this study are published elsewhere (Hart & Hart, 2013). A sample of the breed rankings is shown below for some behavioural traits.

### Activity level

A cat that uses the home as a three-dimensional forest is clearly different than a quiet, calm breed. Making the best use of the artificial 'jungle' at home, the Bengal and Abyssinian rank highest on activity level. The Persian and Ragdoll are the least active and pretty much lie around as if content to stay back in the safari lodge. Figure 11.1 portrays the ranks in activity levels for all breeds that were studied.

### Affection towards human family members

This is a characteristic where the Ragdoll comes out at the top rank. At the low end on affection is the Bengal, which, as will be explained below, is a hybrid between the domestic cat and the wild Asian Leopard Cat.

### Aggression towards human family members

This is a trait where the Bengal and Ragdoll trade places, with the Bengal highest and the Ragdoll lowest.

### Litter box use

While clearly of interest to cat owners, this trait might not be expected to differ among breeds, but it does, just not as prominently as activity level. Ranking the lowest in the use of the litter box is the Persian and at the top is the Tonkinese.

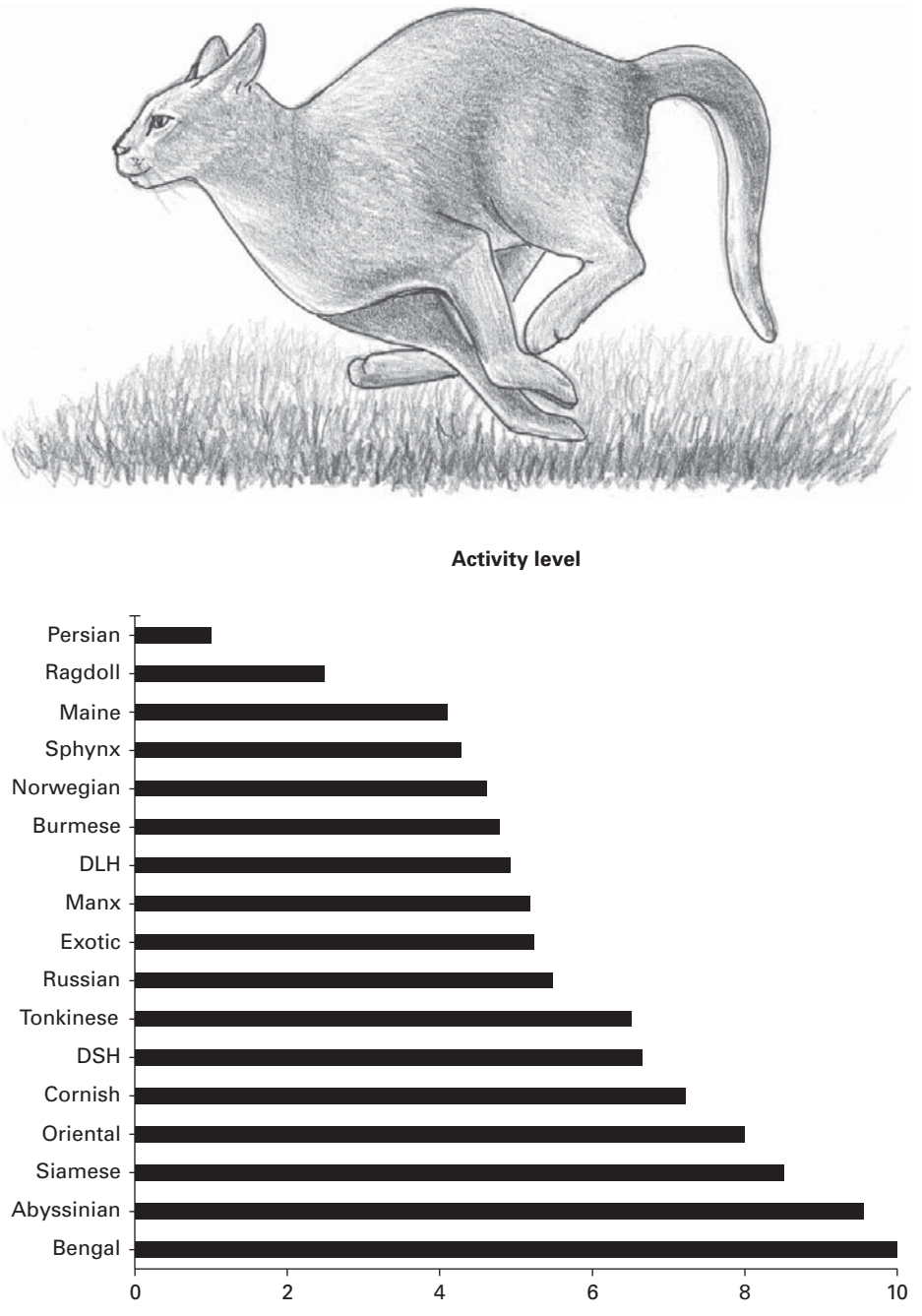



**Figure 11.1** Ranking of cat breeds from 1 to 10 on activity level by adjusted least-squares means. The lowest ranking is 1 and 10 is the highest. Statistically significant differences are typically found between the two or three breeds at the top or bottom and the remaining breeds. From Hart and Hart (2013), reprinted with permission.

### Urine marking (spraying)

This behaviour is the most common behavioural problem of cats for which medical treatment is sought (see Chapter 14). This is related to normal territorial behaviour, especially in males. And while the behaviour is largely eliminated in males neutered either as adults or before puberty (Hart & Barrett, 1973; Hart & Eckstein, 1997), urine marking in the house does occur in about 10% of neutered males overall. However, breeds differ in the degree to which the neutered males are likely to urine mark in the house. While the breeds are fairly closely clustered for the most part, the Bengal stands out with the highest ranking, and the naked Sphynx with the lowest rank.

## Sex differences: who ever thought males could be the gentler sex?

Well, the astute cat observers knew this all along. While the role of breed membership may or may not be useful for those wishing to adopt a kitten, the role of sex can be useful in virtually all instances. In the telephone interviews of feline veterinary authorities, before they were asked to rank breeds, they were asked to rank spayed females versus neutered males on each of the 12 traits upon which the breeds were to be ranked afterwards. The sex comparisons were independent of breed designation.

A picture roughly along the lines of previous findings on dogs (Hart & Hart, 1988), where males (neutered) are the more aggressive and less affectionate sex, might have been expected, but could not have been more wrong. Neutered male cats far outranked spayed females in being more outgoing and affectionate. Females far outranked males in being more aggressive. Not surprisingly, male cats far outranked females in the likelihood of urine marking in the house.

For most cat owners the choice of sex can be a bit complex. Selecting an affectionate, non-aggressive neutered male, where he is the only cat, could be a logical decision. Being the only cat means that he is less likely to urine mark than if other cats are around. Introducing a non-aggressive, outgoing male cat to a multi-cat home also has its appealing points, but because inter-cat interactions are the main causative factor in urine marking (Pryor *et al*., 2001a), this could be bringing on trouble. Not an easy decision. Do not forget that cats differ, genetically, in the tendency to urine mark, where the Bengal is highest and the Sphynx, the lowest. So this consideration can be part of the decision.

## Ancient origins of cat breeds

Estimates of the beginning of domestication of the cat vary depending upon the dating procedure, but generally place this event as far as 8000–10,000 years ago after humans stopped their lifestyle of hunting and gathering and adopted a more agriculture-oriented living (Clutton-Brock, 1993; Driscoll *et al*., 2009a). The domestication was particularly prominent in the Fertile Crescent (Gupta, 2004; Vigne *et al*., 2004, 2012; Vigne, 2011). As settled humans learned to grow and improve grains as their dietary staple, their

stores were soon discovered by rodents, and pursuing the rodents were small wild cats. One can easily see how many of these cats eventually became household pets and the process of domestication began. The actual genetic domestication process, as revealed by recent phylogenetic work, stems from a single domestication event in the Near East (Driscoll *et al*., 2007; Lipinski *et al*., 2008).

These early-domesticated cats, which were attached to their humans, spread to virtually all parts of Asia and Europe, mostly along trade routes between ancient civilisations. Eventually, genetically distinguishable groups of cat types were found in Asia, Western Europe, East Africa and the Mediterranean basin. The cats found in North America are closely linked to European cats. The Southeast Asian breeds form a grouping that is at the opposite end of the genetic spectrum from the Western Europe and North American breeds (Lipinski *et al*., 2008; Kurushima *et al*., 2013).

An interesting aspect of cat domestication is that as global migration continued, many developing breeds remained quite similar to their wild felid ancestors in form and function. It is generally believed that, compared with the dog and other common domesticated animals, the modern cat is not as fully domesticated in behavioural terms, as demonstrated by cats of many breeds being self-sufficient in hunting skills and even surviving without direct human support – so-called feral cats (Clutton-Brock, 1999; Dobney & Larson, 2006; Driscoll *et al*., 2009a; Vigne, 2011).)

One can trace the development of certain breed body styles to various regions of the world. A small subset of cats that had a similar body style, and that had undergone intensive selection for maintaining the signature body style, became the ancestral purebred or pedigree cats which were then recognised by the cat fancy associations. Most recently, breed development has generally reflected selection for simple, single-gene variants derived from the initial breeds.

Within the family of cats that spread throughout the world, a wide range of genetic variability, referred to as degree of heterozygosity, is found. The Burmese has the lowest heterozygosity, reflecting the most intense inbreeding. This is contrasted with the Ragdolls, where heterozygosity is among the highest in recognised breeds (Lipinski *et al*., 2008; Kurushima *et al*., 2013).

Although not among the very lowest in heterozygosity, the Persian is believed to be the oldest identifiable cat breed (Cat Fanciers' Association, 1993). This breed, and its somewhat recent shorthair relative, the Exotic, has undergone what was undoubtedly extreme selection for a brachycephalic, or stub-nosed, head type and a bulky body type. Even with the ancient Persian origin of the Persian breed, it is a bit surprising to find that it is genetically clustered with cats from Western Europe; the modern Persian cat has lost its genetic link to its region of origin. In contrast to the Persian, the Siamese, with its narrow head shape, referred to as dolichocephalic, has retained its phylogeographical identity, and has been used as the foundation stock for other dolichocephalic breeds, in particular, the Oriental (Lipinski *et al*., 2008; Kurushima *et al*., 2013).

While one can point to the intriguing ancient history in the development of cat breeds, two examples of recent developments of breeds reveals the effort of

intense selection, and searching for appropriate cross-breeding partners, to satisfy the whims of the breed developers. These two examples come from – where else but – southern California. One avid cat fancier was evidently captivated by the looks of the spotted Asian Leopard Cat she had seen on a trip to the jungles of Southeast Asia. After the trip she obtained a female Asian Leopard Cat from a pet shop specialising in exotic animals, and brought home a male domestic black cat as a potential mate. The offspring were sterile when bred with each other, but the female offspring were bred again to domestic male cats and produced fertile offspring. When a male Asian Leopard Cat, sent from a zoo in India, was brought in, further breeding brought out the distinctive leopard-like rosettes and stripes, giving the appearance of a small wild cat (Johnson, 1991). The small Asian Leopard Cats (*Felis bengalensis*) are fairly fractious and difficult, if not impossible, to tame. Selection for the exotic coloration of the Leopard Cat in the development of the Bengal undoubtedly brought with it selection for a low level of affection, high levels of aggression to humans and other cats, as well as a high degree of activity (Figure 11.2).

A contrast with development of the Bengal is the origin of the Ragdoll breed, attributed to a cat fancier who had breeding Persians but was attracted to one of the offspring of a neighbour's cat that had a very docile predisposition. She decided to breed this docile neighbour's cat to one of her Persians, and to her delight, the offspring had an exaggerated tendency to go limp in your arms just like a child's toy ragdoll. So she continued with this breeding experiment, using additional crosses with cats of the Burmese and other breeds, but always selecting for docility, and a love of being handled. The nick-name "Ragdoll" stuck and is the official breed identification. The behavioural profile of the Ragdoll could hardly be more different from that of the Bengal, ranking tops in being affectionate and lowest with regard to aggression to family members and other cats (Figure 11.3).

## Conclusion

In terms of understanding something about the most favoured companion animal in human history, we now can appreciate that domesticated cats have been with us since early humans first started farming on a regular basis. As human ancestors started to move about the world, and trade routes developed, they took with them their favourite cats; eventually genetic lines of cats became differentiated according to regions of the world.

Subpopulations gave rise to different body types and different behavioural characteristics, all reflecting the whims or desires of the breeding enthusiasts of the area. In the body type category, we have thin cats with narrow, dolichocephalic heads and bulky cats with stubby, brachycephalic heads. We have long-haired robust cats suitable to live in the coldest countries and delicate cats with no hair. We have wild-like cats that could be mistaken for the Asian Leopard Cat and easy-going cats equivalent to the ragdoll of the cat world. In the behavioural

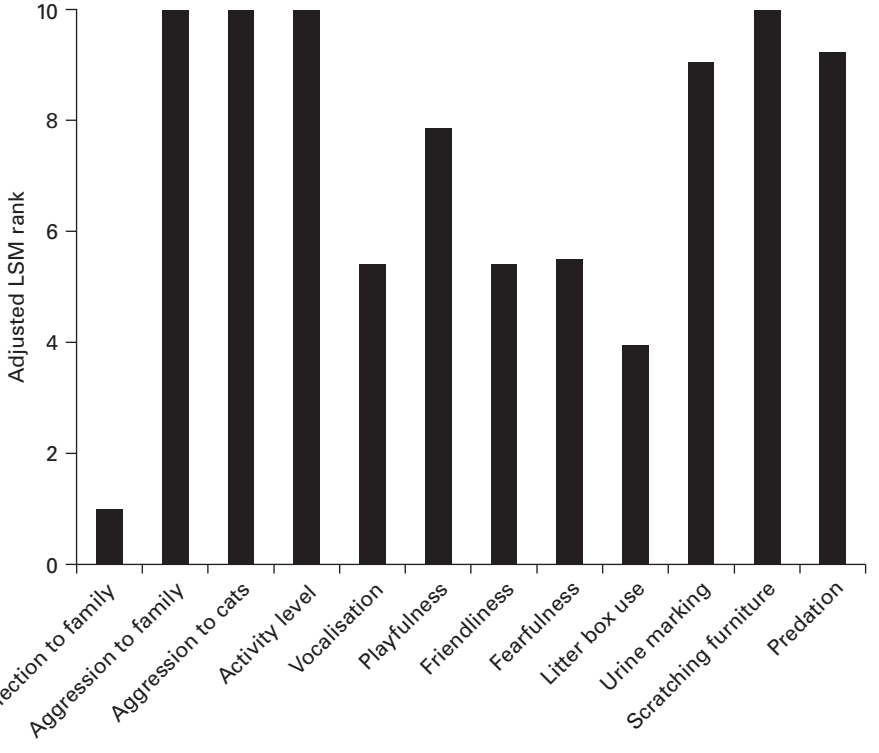



**Figure 11.2** Behaviour profile of the Bengal breed reflecting rankings from 1 to 10 in comparison with other breeds, by adjusted least-squares means with a ranking of 1 being the lowest and 10 the highest. From Hart and Hart ( 2013), reprinted with permission.

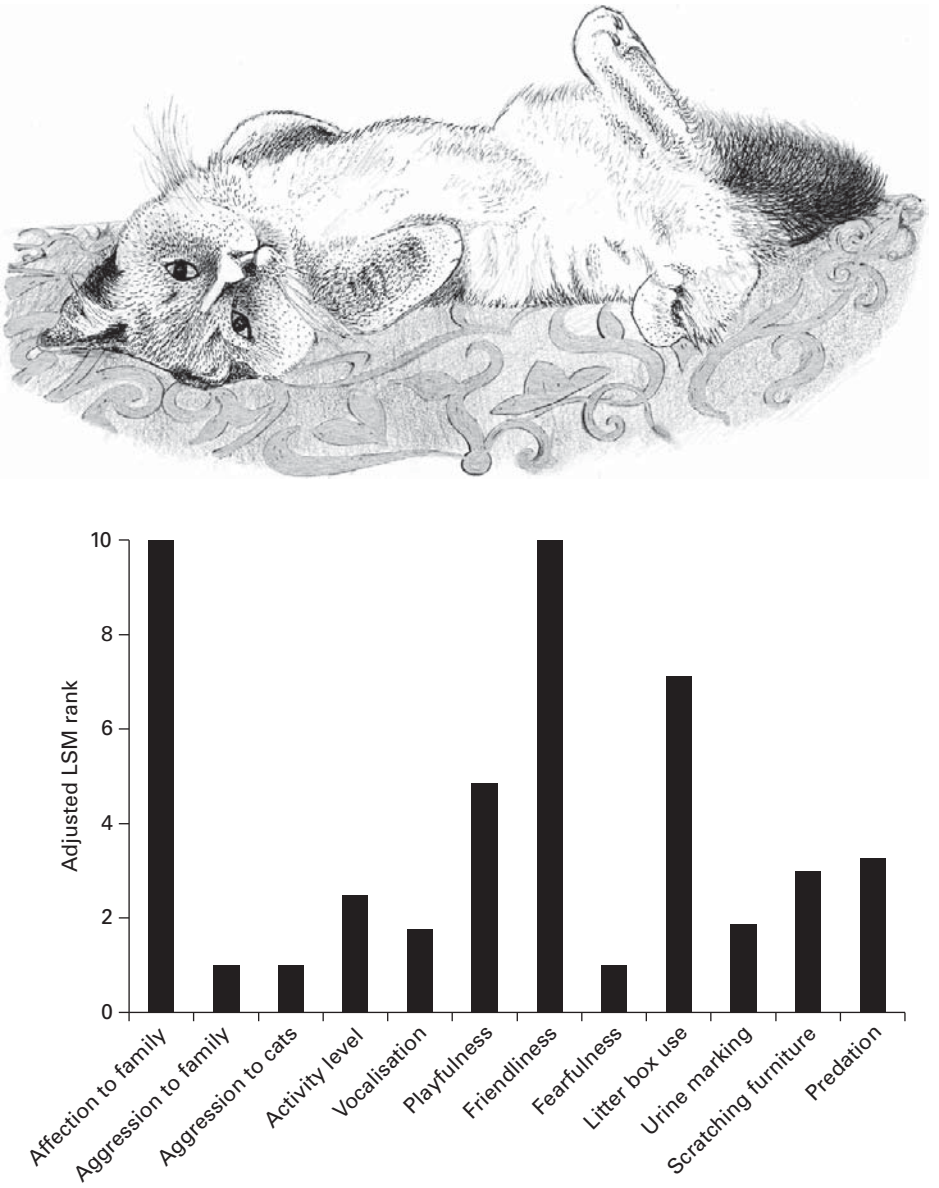



**Figure 11.3** Behaviour profile of the Ragdoll breed reflecting ranking from 1 to 10 in comparison with other breeds, by adjusted least-squares means with a ranking of 1 being lowest and 10 the highest. From Hart and Hart (2013), reprinted with permission.

area we have affectionate, non-aggressive, visitor-friendly cats and we have overly active, non-affectionate cats with an aggressive edge. Given the potential for relative ease in developing body types and behavioural characteristics, we can expect breed development to continue, with surprises in both body form and behaviour along the way.

## Acknowledgements

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# 12 Showing cats

Anne Gregory,[1] Steve Crow[2] and Hilary Dean[3]


[1] All-breed GCCF Judge, Director on the GCCF Board.
[2] GCCF Judge, Chairman of the GCCF Genetics Committee, Vice-Chairman of GCCF.
[3] Secretary Guild of GCCF Judges & Stewards, Director on the GCCF Board.

*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

The whole concept of different breeds of cat is a relatively modern one extending back only about 150 years. Other domesticated animals have a breed history much older; dogs and horses in particular were deliberately domesticated to 'serve' humans and were, to some extent, selectively bred from very early in their relationship with people to fit their needs. Thus the idea of selecting for different physical 'types', whether size, mass, speed, or certain mental abilities or characteristics is something human beings have pursued, albeit in a somewhat random way, probably for several millennia. By the eighteenth century this practice in some domestic species was quite refined, with a large number of recognisably different types of dogs, horses and, following the agricultural revolution from the mid eighteenth century onwards, of various farm animals such as cattle, sheep, pigs and fowl, all developed to meet different needs in human society. Deliberate selection had not yet been applied to the domestic cat, but by the latter half of the nineteenth century there was a growing understanding of basic genetics and as a result people realised they could select for, perpetuate and even improve certain attractive or distinctive features in domestic animals. Mendel's findings on the principles of heredity were initially ignored, but by the beginning of the twentieth century were gaining acceptance. It was discovered, without the reasons being completely understood, that by breeding like to like or mating together closely related animals, offspring could exhibit the features particularly valued and sought after. Although the domestic cat has had a relationship with humans for at least 4000 years, this relationship has principally been one of exploitative captive, where the cat provided an effective control of rodents and other vermin in both urban and rural environments. In performing these functions the cat was regarded as extremely useful and gradually also respected as a companion animal (see Chapter 7). However, as far as breeding was concerned, the domestic cat was left very much to its own devices. Indeed, Charles Darwin (1859) was dismissive in his comments about distinct breeds: '[c]ats, from their nocturnal rambling habits, cannot be matched, and, although so much valued by women and children, we hardly ever see a distinct breed kept up; such breeds as we do sometimes see are almost always imported from some other country, often from islands'.

However, over time, the domestic cat had in fact exhibited a number of genetic mutations affecting colour, pattern and coat length. The original natural pattern of the cats' ancestor, *Felis sylvestris libyca*, is a black mackerel tabby, but, as with all species of animal, genetic mutations occasionally occur and, if these provide any advantage to the animal concerned in its environment, they may be reproduced and persist down the successive generations. The world wide consensus regarding coat colours and length which has been in progress for some years has revealed that most of the mutant genes of the cat are of considerable age. The first to occur were probably the non-agouti form, i.e. black self, followed by the blotched or classic tabby, the spotted tabby and the ticked, consisting of the agouti ground but with little or no overlying pattern. All of these occur in other species of cat, either large or small. It is reasonably certain that other mutations such as the dilute gene, the piebald (white spotting gene), orange,

dominant white and longhair genes have been around for hundreds of years. The inhibitor (silver) gene could also be an old mutant, but it is difficult to assess its age. Certain mutants have high frequencies in some parts of the world, which could be indicative of their place of origin. Orange cats are more common in the Far East than in Europe, pointed cats originated in Siam and the longhaired gene appears to have occurred first in Russia and travelled further via trading routes to Persia and Turkey.

During the nineteenth century when many of the aristocracy and wealthy middle classes travelled extensively in Europe, Asia Minor and beyond, it became fashionable to bring home exotic pets including cats. Careful breeding took place to continue the colour, pattern and coat length and people were then keen to 'show off' their prized possessions.

The earliest recorded 'Cat Show' took place in England at the St Giles Fair in Winchester in 1598 with prizes awarded for the 'best ratter' and 'best mouser'. However, the first organised cat show where the judgement was for the type, coat, conformation, pattern and colour of the cats exhibited was held at Crystal Palace in 1871. The organiser was Harrison Weir, a Fellow of the Royal Horticultural Society, artist, writer and self-confessed ailurophile. There were three judges, including Weir himself, and 170 cats.

## How breed standards are set

Across the world, judges assess cats on their closeness to the perfect cat described in the relevant 'Standard of Points' drawn up and published by their relevant governing or registration body. Weir drew up the first Standard by which cats should be judged in the UK, which he called 'Points of Excellence'. The different features of the cat were awarded points according to their importance, with a total of 100 points overall for the 'perfect cat'. This system of allocating points has continued to this day in all registration bodies, thereby giving judges the criteria for their placings. Table 12.1 compares the allocation of points for Siamese cats for the first show at the Crystal Palace with the current standard issued by the Governing Council of the Cat Fancy (GCCF; note that such abbreviations are explained in a summary Glossary at the end of this chapter) in the UK. It is fascinating to note and compare the weightings.

## The development of cat showing and setting standards

Weir's show in 1871 was the foundation stone for Cat Fancies throughout the world and in Britain a popular new hobby was born. After a cat show at the Alexandra Palace in 1887, a number of fanciers decided to set up a club for exhibitors and breeders, so the National Cat Club was born with Harrison Weir as its first president. It kept a register of cats and granted licences for small clubs to stage shows. In 1898, Lady Marcus Beresford set up The Cat Club, which also kept a register and granted licences for shows. Standards of Points were issued for judges, but there were problems due to the

**Table 12.1** Scale of points for Siamese

| 1871 – Harrison-Weir's Points of Excellence | | 2010 – GCCF Standard of Points | |
|---|---|---|---|
| Head | 10 | Head 15; Ears 5 | 20 |
| Eyes | 15 | Eye Shape & Set 5; Colour 15 | 20 |
| Size & Form | 10 | Body 15; Legs & Feet 5 | 20 |
| Tail | 5 | Tail | 5 |
| Colour | 20 | Body Colour | 15 |
| Markings | 20 | Points Colour | 10 |
| Fur | 10 | Coat Texture | 10 |
| Condition | 10 | | |
| Total | 100 | Total | 100 |

**Table 12.2** Scale of points for the Smoke Persian

| Silver & Smoke Persian Cat Society 1903 | | GCCF Standard 2010 | |
|---|---|---|---|
| Head & Expression | 20 | General shape of head; forehead; set of ears; nose length; width & stop | 25 |
| Eye Colour | 15 | Eyes; size, shape & colour | 15 |
| Shape | 10 | Body conformation, shape, legs, tail etc | 20 |
| Tail | 10 | | |
| Coat & Condition | 20 | Coat & condition; colour; shading & its distribution, texture & quality | 40 |
| Colour of undercoat | 10 | | |
| Absence of markings | 15 | | |
| Total | 100 | Total | 100 |

great rivalry between the two clubs, with exhibitors obliged to register with both in order to show their cat under their several rules and standards. By 1902 Harrison Weir became disillusioned with some members of the Cat Fancy who appeared to think more of winning cups and trophies than caring for their cats (a sentiment often echoed by cat judges today!). He was also disappointed that the shorthaired English cats (today referred to as British Shorthairs) were declining in numbers while Angoras and Persians were becoming more and more popular because of their long coats. He therefore retired from clubs, judging and shows.

In 1903, Frances Simpson's *The Book of the Cat* was published and immediately became the 'bible' for cat fanciers. She was encouraged in her work by Harrison Weir and acknowledged his support in the introduction. She included standards for various breeds, preceding them with an illustration featuring the 'points' of the cat (Figure 12.1). She felt there were basically just two types of cat, the Longhair or Eastern and the Shorthair or European. She states, 'The term breed is, even here, used advisedly, for whatever the outer covering or coat, colour or length of fur, the contours of each and all is practically the same' (Simpson, 1903). Table 12.2 illustrates a comparison from her book of the Standard of Points for a Smoke Persian in 1903 compared with the current GCCF Standard published in 2010.

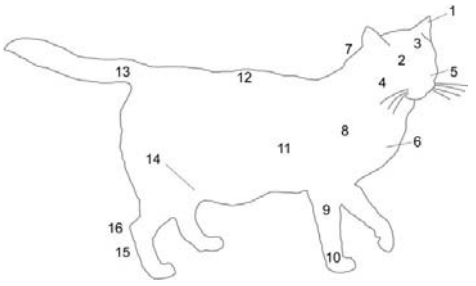


**Figure 12.1** The points of a cat.

By the turn of the century more and more Breed Clubs were formed, including the Silver & Smoke Persian, The Blue Persian Cat Society, The Shorthair Cat Club and the Siamese Cat Club. Each issued a Standard of Points for the various breeds they represented and became responsible for choosing judges. Frances Simpson felt the Standards of Points were meant for exhibitors and breeders as guidelines, they were not for judges. She claims, 'I venture to assert that a judge is no judge if he requires anything besides his own personal conviction, experience and common sense when called upon to decide the various points in the different breeds' (Simpson, 1903, chapter 5, p. 68).

## The formation of the Governing Council of the Cat Fancy

In March 1910 representatives from the various clubs were invited to a meeting in London and The Governing Council of the Cat Fancy was born. The GCCF now had all rights for registration, issuing of stud books and transferring cats between owners in the UK. More and more cat clubs were formed and many more shows licensed. Each club affiliated to the GCCF could send delegates to the Council Meetings, which were held four times per year, and it was here that judges recommended by the Breed Clubs and any changes to the Rules and Standards of Points were approved. Today, the GCCF is the premier registration body for breeding and showing pedigree cats in the UK with the health, welfare and well-being of all cats its mission as it advises, educates and supports all cat owners.

## The development of cat showing in the twentieth century

During the major part of the twentieth century the breed clubs were responsible for choosing and training their judges and for maintaining their Standards of Points. Their delegates would attend the quarterly Council Meetings to represent their views. Then, in the late 1980s the Governing Council voted to set up Breed Advisory Committees (BACs), with representatives from the constituent Breed Clubs to administer all aspects of their relevant breed(s) and also to monitor and train judges and candidates within

the GCCF Judge Appointment Scheme. This effectively took away a great deal of the power previously held by the judges and gave a wider group of owners and breeders more responsibility for making decisions regarding their breed.

## How are judges trained?

At first, judges were not trained; organisers chose people they felt had the knowledge and experience to make informed judgements on the cats they were presented with. At Weir's first show there were 170 cats judged by himself, his brother John Jenner Weir and the Reverend J. Macdona.

Frances Simpson (1903, p. 70) had very definite ideas about judging. She states, 'I think that judges are born, not made and people who have not a keen power of observation and a faculty of coming rapidly to a fixed conclusion can never hope to become satisfactory or competent judges'. She writes with some detail about her methods of judging, which would have been valuable information for those aspiring to join the ever-growing number of cat judges.

After the introduction of Breed Clubs, it became their responsibility to select judges from the influential breeders in their ranks. Those wishing to become judges worked as stewards for the senior judges at shows, learning from observation and gaining experience until they were invited to become a judge themselves.

This manner of training prospective judges continued well into the second half of the twentieth century until the BACs were set up in the late 1980s. The Executive Committee of the time drew up a document containing the Philosophy and Principles of the GCCF Judge Appointment Scheme together with the Constitution and Rules of Procedure.

Under this new system, the breeds at a show were grouped into seven sections: Persian, Semi-longhair, British, Foreign, Burmese, Oriental and Siamese. Candidates began their training as Stewards by working with Full Judges of the appropriate breed(s). They had to cover a minimum number of engagements, forwarding completed Stewarding Certificates to the Secretary of their BAC. The BACs met a minimum of twice a year when the progress of candidates would be discussed and feedback given.

The next stage was for the candidate to become a Probationer Judge of the breed. They were then allowed to judge the Breed Classes for kittens as well as mixed 'side' classes with a variety of cats within the section. Tutorials were held with full judges and BACs would organise annual breed seminars which candidates were expected to attend. After a minimum of two years plus two or three assessments with full judges, often chosen by the BAC, the candidate could apply for Full Judge status. Often BACs were not satisfied the candidate was ready for promotion and would require further judging and assessments before reapplying. With some revision, this system has continued within the GCCF until the present day. It is a long, hard process and certainly weeds out those candidates lacking the required commitment to the task.

Other registration bodies across the world have similar systems in place. Very often their cats are placed in just four groups consisting of Persians & Exotics; Semi-Longhaired

Breeds; Shorthaired Cats; and Oriental Breeds. In some bodies' grouping, the Persians and Semi-Longhaired Breeds are combined and the Exotics included within the Shorthair section. Training can be by stewarding or becoming the clerk to a judge. There is also a system of parallel judging of the same exhibits with discussion between the candidate and their tutor to assess competency. Attendance at seminars by candidates is mandatory and there are frequently written examinations about the breed standards, basic genetics and the history of the organisation in addition to the practical assessments. As these judges become trained across a section rather than by individual breeds it is often a shorter route to becoming an all-breed judge.

A group of judges and BAC Officers from the GCCF Board of Directors is working on the process of training judges at this present time, hoping to streamline the complicated process. They have completed a more educational and supportive stewarding scheme administered by the Guild of GCCF judges and stewards.

As GCCF judges who have worked with a number of stewards and probationer judges, personal experience tends to agree with Frances Simpson that someone with the 'eye' to appreciate the particular features and quality of a breed is 'born'; it is very hard to teach someone how to 'see' a cat if they do not have that capability. It is extremely easy to pick out a clear winner from a group, but challenging to rationalise placings when the class consists of a group of 'middle of the road' exhibits.

## Cat breeds introduced in the twentieth century

With the popularity of cat breeding and showing in the twentieth century and particularly since the Second World War, some of the naturally evolved breeds with physical characteristics somewhere between the heavy-boned, cobby cats of northern Europe and the more sinuous, fine-boned cats from the warmer climates of Asia have been developed by breeders to give a definite 'look' unique to the individual breed; they include the Russian Blue and Abyssinian breeds which were at the first cat shows but have since been selected to produce more refined wedge-shaped heads, lithe, muscular bodies with slender legs and oval paws. Today this 'Foreign' section of 'moderate' cats is the largest in the Fancy and is midway between the short, massive head of the Persian and the long, triangular wedge of the Siamese.

A new phenomenon has also occurred, with breeds deliberately created either by selecting an individual which has exhibited a rare mutation as found with the waved coats of the Cornish, Devon, Selkirk Rex and LaPerm; or where two or sometimes more, existing breeds have been crossed to create a completely new breed, as in the case of the Asian or the Tonkinese. Another group in this category includes those where a longhaired or shorthaired version of an existing natural breed has been deliberately developed into a separate breed, as in the case of the Somali, which was finally recognised in 1962 as a semi-longhaired variety of the Abyssinian, or the Exotic developed in the 1960s as a shorthaired cat of Persian type. (See also Chapter 11 with regard to the Bengal and Ragdoll breeds in the USA.)

The constant desire by breeders and cat owners for something new and different encourages this behaviour, which in itself may be perfectly acceptable, but can be resisted by those traditionalists who wish to keep cat breeds pure and who regard new colours, patterns or coat lengths with some suspicion.

## What effect has showing had on the physical appearance of the domestic cat?

Harrison Weir's opinion, 'It would be well to hold "cat shows" so that the different breeds, colours, markings, etc. might be more carefully attended to' (Weir, 1889), had the immediate effect of highlighting the more desirable coat colours, patterns and quality. Gradually the longhaired Angora and Persian cats became more popular with their impressive long coats that took daily grooming to maintain.

The Points of Excellence or Standards for judging that Harrison Weir drew up for the first cat show proved as important for the development of pedigree cats as the establishment of the registering bodies themselves. The primary purpose of standards for each approved breed was to promote sound breeding practices by highlighting the characteristics of the breed that can only be achieved in this way. Breeders were provided with a model of the 'perfect cat' they could aim to reproduce for exhibition. The standards also provide the basis for uniformity in judging, although here personal interpretation will always play a role.

As breeders worked to refine and develop distinct and individual breeds based on their naturally occurring differences, variation in body type and coat texture became more pronounced and even exaggerated. This tendency has been driven mainly by the desire to create or maintain purity within a breed, facilitated by inbreeding to fix the desired differences upon which the breed was originally based, but also to improve certain features such as definitive type, depth and tone of colour, clarity of pattern and length and texture of coat. This process has accelerated since the late nineteenth century by the desire to win at shows and gain titles for what are regarded as the best examples of each breed.

## Cat show format, classes and awards

Just as different bodies have different training programmes for their judges, so there are huge differences across the world in the organisation of shows, classes and awards. Some shows have all the cats penned in breed order with the judges going from pen to pen, others use the ring judging method. We will outline the systems used by the world's most senior cat registration bodies, the Cat Fanciers' Association (CFA) based in the USA and the GCCF based in the UK.

Both bodies have championship competition for adult cats and premiership competition for neuters; all classes where cats are competing for titles are split into male and female and whether they are intact cats or neuters. The classes for kittens are similar to

the adults, with opportunity for Best of Breed but without titles awarded. In CFA, kittens can be shown from 4 months and become adults from 8 months whereas in GCCF, kittens can be shown from 14 weeks and enter title classes from 9 months. For those breeds that have not yet achieved championship status but have been recognised for registration and given a breed name, they may enter Miscellaneous then Provisional competition in CFA or progress through Preliminary and Intermediate status in GCCF. It is successful competition at these stages that provides the evidence required for championship status to be approved.

## The ring system used by CFA

In CFA, a cat show is composed of a number of separate shows, running concurrently throughout the show hall in different judging 'rings'. A ring may be classified as 'All-Breed' or 'Speciality'. In the latter, only cats of similar coat length or group will compete. The cats are brought by their owners to the different rings for judging. As shows have multiple rings, the exhibitor must listen carefully to announcements if they are to ensure their cat is in the right place at the right time! As exhibitors may have vast distances to travel with their cats, it is usual in CFA for a show to take place across two days. An average show in the USA would have six rings per day with an upper limit of 225 cats.

## CFA titles and awards

Once an adult, a CFA-registered cat begins its career in the Open Class for its breed or colour grouping, where it needs to gain first place and a Winner's Ribbon. Once it has been judged in its first ring, the cat then competes in the other rings under different judges, hoping to be similarly successful. Once a cat has been awarded six Winner's Ribbons it becomes a Champion or Premier. In large shows, a particularly successful cat could gain its title in six rings in one day.

Next, the ring judge considers the Champions and Premiers competing for their Grand titles and makes their placings. This is followed by Best of Breed or Division and then the Best Champion/Premier of the Breed from all the relevant cats. When each judge has judged all the cats, kittens and neuters in their different classes, they hold a 'Final' during which they will present rosettes to the 10 top winners from those judged in their ring.

Every cat receiving the Best Champion/Premier ribbon will receive a point towards its Grand title for every Champion or Premier it has defeated in that breed. In order to gain a 'Grand' title, a champion will need 200 points in the USA or 75 points in smaller regions like the UK; premiers require 75 points in the USA or 25 in the smaller regions to gain their Grand title. Additionally, each cat must also have won at least one Best Cat or one Second Best Cat of its breed or colour or must have achieved at least one 'Final' placing. The required points must have been awarded by at least three different judges.

The above process is repeated by all the judges in all the rings, but as each ring is independent, a cat chosen as 'Best' in Ring One may not achieve that distinction in other rings. To summarise, therefore, each ring in a CFA show is a show in itself with the presiding judge responsible for awarding the prizes, choosing their winners and their Best Cats. Top winning cats in CFA may continue showing to collect their points in order to compete for Regional or National awards.

In CFA, household pets may compete whether random-bred or pedigree pets. They are judged without regard to sex, age, coat length or colour but for their personality, good health and vitality. They receive a Merit Award.

## The GCCF show format

GCCF cat shows are one-day events and are organised by the member clubs under licence. Shows can be for a single breed, groups of similar breeds or all-breeds together. Sometimes two or more member clubs hold 'back to back' shows in a large venue to share expenses and enable cats to compete for more than one certificate on the day.

GCCF shows are laid out in breed order. Each breed has its own classes with judges moving along the rows of pens, proceeding from cat to cat in class order. It is usual for exhibitors either to leave the show hall during Breed Class judging or to remain in the area close to the stalls around the perimeter in order to leave space and a quiet atmosphere for judging. A GCCF all-breed show of around 500 cats would require perhaps 40 judges. Show managers engage judges for the different breed and title classes; at the beginning of each show season they are given the list of classes that have to be included in show schedules and also a list giving the qualifications of each GCCF judge. The breed class judge considers all cats of the appropriate breed (including titled cats) for Best of Breed. The best of breed cats, kittens and neuters in each section then compete for Best of Variety and those winners are eligible for Best in Show.

## How are GCCF titles obtained?

Once a cat reaches 9 months of age it can enter its appropriate breed class to compete for a Challenge or Premier Certificate. It requires three certificates from three different shows and three different judges for the cat to become titled.

Once a Champion or Premier, the cat must then enter the Grand Champion or Premier class. Again, it must win three certificates at three shows under three different judges in order to gain the title. Cats of breeds within the same section are grouped for the Grand Classes so at this level, cats will start to compete across different breeds to win this title, which is different from the awards in CFA.

Cats with a Grand title are then eligible to enter the Imperial Classes. These require five certificates from five different judges with cats competing across their complete section of breeds.

A new GCCF title initiated in June 2010 was the Olympian. A cat competes for this prestigious title against Imperial Grand Champions across all seven sections and therefore must be of exceptional quality. This title has three levels – Bronze, Silver and Gold – each requiring five certificates.

The GCCF holds its own annual Supreme Show where Grand titled cats and above can compete for a 'UK' award. It requires two of these certificates for a cat to add the coveted 'UK' to its list of titles.

Household pets can also compete at GCCF shows either in the non-pedigree or pedigree pet sections. They are judged on presentation, condition, temperament and personality and are grouped into various colours and also according to their coat length.

The Household Pet titles begin with 'Master Cat' and progress in a similar fashion to those in the Pedigree Section to the ultimate title of UK & Olympian Gold Imperial Grand Master Cat.

## Other features of CFA and GCCF shows

Both bodies strive to make their shows interesting for exhibitors and visitors. CFA has introduced Feline Agility for cats that love to follow a feathered stick or dangling toy. This class is open to any cat and it is frequently a household pet that becomes the overall winner on the day. GCCF shows have miscellaneous classes such as 'Breeders' or 'Adolescent' where cats compete against other breeds and are entered under different judges. This can be a valuable choice for exhibitors wishing to know a particular judge's opinion.

The CFA has Junior Showmanship and the GCCF its Young Exhibitors Scheme (YES!), enabling young people to learn more about their cats and their hobby. In both bodies this has proved a successful initiative, encouraging a healthy future for the Fancy.

## What has been the influence of breeders and judges with regard to the physical characteristics of our pedigree cats?

Pedigree cat breeds in the UK suffered serious decline during the two world wars and particularly the Second World War when many breeders were forced to give up breeding because of lack of food (no rations for cats) and the destruction caused by the bombing. Since then there has been a relative explosion of new breeds both in Britain and elsewhere, particularly the United States. These have appeared, either having been 'discovered' as a natural population somewhere in the world, or more often as a result of hybridisation between existing breeds (as mentioned above). During the same period a much greater understanding of genetics has developed, with pioneers such as Pat Turner and Roy Robinson increasing knowledge and understanding through research and experimental breeding. This body of knowledge has encouraged a more scientific approach to pedigree cat breeding and identified some of the origins of genetic-based health problems in certain breeds.

No breed remains still or fixed in type; all must continue to evolve, change and develop as breeders continue in their efforts to improve colour, coat and type in their aim to achieve the ideal described in the Standard of Points. The latter has become more detailed and refined across the years, influenced both by breeders and the interpretation put upon the standard by judges at cat shows. As breeds have improved in type, as colours have improved in richness and vibrancy of tone and patterns in clarity, so the relevant Standard of Points has been revised and become more demanding in terms of the ideal. The vast majority of judges are, or have been, involved in breeding pedigree cats, often for a considerable number of years; they know their particular breed(s) intimately, having very valuable personal knowledge and understanding of their particular breed and what constitutes the best type and quality. Many breeders become judges to share this knowledge and experience and to safeguard the purity and integrity of the breed they are involved with.

The breeding of cats to a high standard of perfection is far from simple; it is a life's work for many people, with each peak of attainment a stepping stone to the next. As the quality of the breed improves, the task of breeding the superlative animal becomes more difficult over time. Winning at shows is the pinnacle in terms of the prestige it confers upon a breeder, expressed in the recognition granted to particular cats which achieve high titles for meeting the criteria expressed in the Standard of Points.

Generally speaking this is or can be a good thing. Over time, it encourages breeders to reduce or eliminate genes that have a detrimental effect on what is deemed to be the most attractive and desirable type, conformation, colour and tone or coat length and texture. However, there is a certain tension between the ideal that breeders are trying to achieve, the results of which they exhibit on the show bench, and the judges of those cats who assess and reward them according to their own interpretation of the Standard of Points. If judges like the cats breeders show and award them high placings and certificates enabling them to achieve prestigious titles, then exhibitors are generally happy. However, if a breeder or small group of breeders find the cats they show do not win, they have the choice of either to try showing under different judges who may have a slightly different interpretation of the current Standard, or to try to breed cats of the type that a particular judge or group of judges appears to prefer and reward. This can then encourage selection for cats of more extreme type with longer or shorter faces, larger or smaller ears, larger, bolder or more slanted and deep-set eyes, cobbier or more svelte body conformation, etc., depending on the breed concerned. Where this can lead, and indeed has in some instances, is the breeding of cats approaching the extreme ends of the type spectrum; either to be cobby, thicker-set Persians with even more brachycephalic like heads, or long, elegant, fine-boned Siamese with long, narrow wedges and huge ears set low giving their heads the appearance of 'Concorde'.

## What problems have arisen from those exaggerated characteristics and how are these problems being dealt with?

The dangers of exaggeration are the production of genetic as well as general health and welfare issues. Too much inbreeding and selection to exaggerate desirable features and 'fix' them in a breed also risks doubling up on harmful recessive mutations which

may go on to cause hereditary diseases. Exaggerated type can also be responsible for physical health problems such as breathing difficulties from too short noses with small nose leathers and nostrils of reduced size; blocked tear ducts leading to watery eyes as a result of breeding for excessively flat faces in Persians. At the other extreme, squints and deep-set small eyes caused by breeding for long narrow wedges, skull depressions on the forehead, bumps on the back of the skull where the bones have not fused smoothly or fragile bones from selecting for very fine legs, etc. have caused problems in the Siamese and Oriental breeds. Constant inbreeding also tends to reduce the size of the cat over successive generations, causing a lack of general 'hybrid vigour' and the cat's natural ability to resist infection and disease. See also Chapter 11.

The desire to produce something different, something more extreme and even unique remains a powerful influence on breeders, particularly if this difference is rewarded on the show bench. To combat the dangers of pursuing extremes, as has happened to a much larger extent in other species, cat governing bodies have sought to provide guidelines and advice and in some cases impose sanctions upon breeders. The understanding of genetics and the cat genome that has increased significantly in the past two decades, along with the availability of DNA testing for genetic anomalies, has helped greatly in this endeavour. All cat registration bodies world wide take advice from geneticists (and have some form of genetics committee within their organisations) and the veterinary profession. The GCCF has a well-established structure to enable its Genetics Committee and Veterinary Sub-Committee to advise the Board and Breed Advisory Committees on new breeds applying for recognition and on health and welfare issues relating to existing breeds.

In January 2010 the GCCF published its General Breeding Policy, which sets out clear guidelines for all breeders of pedigree cats to help them breed responsibly. It warns of the dangers of excessive inbreeding and refuses the registration of parent/offspring and full sibling matings on its active breeding register. The use of available DNA and other tests to help identify and eventually eliminate genetic diseases is strongly encouraged. The Policy also takes a clear stand by stating it will not recognise certain breeds of cat which are based on a genetic mutation that has known detrimental effects on the cat's health, welfare and quality of life. This Policy is in the public domain on the GCCF's website. It is also a requirement for each Breed Advisory Committee to write a Breeding Policy to guide, educate and support their breeders.

Outcrossing is a controversial topic within most registration bodies. An obvious benefit is the addition of hybrid vigour in the early generations and if regular outcrosses are permitted as part of a managed breeding programme, this genetic variability can be maintained at a healthy level. Counter to this is the case for genetic 'purity' as the definition of a cat breed; some breeders are not just resistant to new breeds and outcrossing, they oppose the addition of new colours or patterns to be introduced into their own breed. Several of the recently recognised breeds are not regarded as 'proper' pedigree breeds by some diehards who believe they are just crossbreeds and will not necessarily breed true. Recent efforts by the GCCF to introduce an agreed outcross for all recognised pedigree breeds in the UK is meeting with some resistance from those who believe that the so-called purity of breeding lines is more important than regularly

introducing genetic variation to increase hybrid vigour and prevent serious inbreeding with its detrimental effects. However, responsible BACs are working hard for the benefit of their breed(s) and doing everything possible through literature and seminars to promote healthy breeding. A very recent example of this programme was demonstrated by the Persian Smoke & Tipped Breed Advisory Committee, which, at the GCCF Delegate's Meeting in February 2012, successfully applied for the dilute series of green-eyed silver and golden Persians to be recognised. This is a huge victory for the said BAC. Although these cats are recognised by major bodies across the world, including CFA, FIFe and TICA (see the Glossary at the end of this chapter), efforts in the past to gain GCCF's acceptance had been doomed to failure. However, following a very positive presentation at a seminar, their persistence was finally rewarded. This is a logical step to enable these cats to be shown and encourage breeders to outcross and thus enlarge the gene pool. Breeders working with this programme have reported healthy litters where the size, substance and growth of the cats have all been much improved.

Reading back through show catalogues and reports in cat press, there is some evidence that fashions change both for certain breeds or for particular colours or coats. To some extent at least, this relates to lifestyle choices, changes in society, living arrangements and work/life balance over time. Many people do not have the time to care for and regularly groom longhaired or even some semi-longhaired breeds; other breeds, such as Siamese and Bengals, are thought to be noisy and more demanding (see also Chapter 11), which may be a consideration for people living in close proximity to others. Cat registration bodies and individual breed clubs are taking an increasing responsibility for encouraging prospective owners to investigate the different characters of cats across the breeds and select which particular breed will fit best into a specific environment and/or lifestyle. Figure 12.2 showing the analysis of breeds registered by the GCCF in 2009 and 2010 shows a marked variation across just one year.

## What are the attitudes of cat bodies to hybridisation and 'man-made' breeds?

A Chinese proverb claimed that man domesticated the cat in order to pet a tiger; one can never stop people experimenting or seeking the new and different. Cat fanciers across the world have for years aspired to have a house pet with the distinctive markings and a special coat quality usually found in a wild species. The pursuit of this desire has led to some beautiful breeds, but problems have also arisen with temperament and the ability of the offspring to settle in a normal home environment as a pet; the early outcrosses need special carers who are aware of the kittens' needs and take great care to socialise them. The only hybrid breed recognised by the GCCF in the UK is the Bengal cat, a striking and handsome breed that was the result of matings between the Asian Leopard Cat and Egyptian Maus, Abyssinians and Ocicats, among others. Problems were inherent from the start as the F1 males are usually sterile and males in the F2 and F3 generations were also frequently found to have fertility problems. On the behavioural front, it is not until the fourth generation that the kittens can really be

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**Analysis of Breeds Registered**

| Breed | 2009 | | 2010 | |
|---|---|---|---|---|
| | Number Registered | Rank | Number Registered | Rank |
| British Shorthair | 5415 | 1 | 5204 | 1 |
| Ragdoll | 2665 | 3 | 2686 | 2 |
| Siamese | 2696 | 2 | 2310 | 3 |
| Maine Coon | 2076 | 4 | 2191 | 4 |
| Burmese | 1702 | 7 | 1736 | 5 |
| Persian | 1755 | 6 | 1494 | 6 |
| Bengal | 1996 | 5 | 1355 | 7 |
| Birman | 1384 | 8 | 1237 | 8 |
| Oriental Shorthair | 988 | 9 | 938 | 9 |
| Norwegian Forest | 621 | 11 | 623 | 10 |
| Exotic Shorthair | 674 | 10 | 607 | 11 |
| Tonkinese | 310 | 15 | 367 | 12 |
| Russian | 333 | 14 | 366 | 13 |
| Sphynx | 242 | 17 | 352 | 14 |
| Devon Rex | 349 | 13 | 338 | 15 |
| Abyssinian | 287 | 16 | 322 | 16 |
| Asian (including Tiffanie) | 380 | 12 | 286 | 17 |
| Egyptian Mau | 172 | 19 | 194 | 18 |
| Selkirk Rex | 231 | 18 | 176 | 19 |
| Snowshoe | 92 | 26 | 141 | 20 |
| Somali | 112 | 24 | 140 | 21 |
| Siberian | 145 | 20 | 138 | 22 |
| Cornish Rex | 143 | 21 | 113 | 23 |
| Ocicat | 108 | 25 | 112 | 24 |
| Balinese | 132 | 22 | 110 | 25 |
| Korat including Thai | 127 | 23 | 107 | 26 |
| Oriental Longhair | 30 | 30 | 62 | 27 |
| Turkish Van & Vankedisi | 81 | 27 | 59 | 28 |
| RagaMuffin | 30 | 31 | 57 | 29 |
| Singapura | 49 | 28 | 56 | 30 |
| LaPerm | 49 | 29 | 24 | 31 |
| Manx | 5 | 32 | 8 | 32 |
| Other Breeds | 38 | | 21 | |
| Total | 25,417 | | 23,930 | |

**Figure 12.2** Analysis of breeds registered by the GCCF in 2009 and 2010.

considered domestic, which leaves a considerable welfare issue. The Bengal Cat Club states on its website, 'The goal in developing the domestic Bengal cat breed was to preserve a strong physical resemblance to its beautiful wild ancestor and, at the same time, the new domestic breed was designed to be a pleasant and trustworthy family companion'.

From personal experience, the vast majority of Bengals met on the show bench are both handsome and friendly cats, but they are sometimes noisy and have a tendency to pace which can intimidate the cats of other breeds penned nearby or opposite. The GCCF recognised the Bengal in the 1990s but has since made a statement, 'After careful consideration, it was decided to make a policy statement that, with the exception of the outcross to the Asian Leopard Cat which has produced the Bengal, the GCCF would not recognise any other outcross to a non-domestic cat'. Breeders have outcrossed the domestic cat with Margays, Bobcats, Lynx, Jungle Cats, Servals, Geoffroy's Cats, Fishing Cats and the Indian Desert Cat but these are registered with other bodies.

## How has cat showing produced benefits for cats and raised welfare standards?

As cat showing and breeding has developed in the last 140 years so has the direct involvement between the owners and breeders of cats and the veterinary profession grown stronger. Many of those early shows were breeding grounds for the dreaded feline enteritis and cat 'flu', with large numbers of exhibits becoming ill or dying shortly after the show. In 1901 the National Cat Club show arranged for all exhibits to be examined by veterinary surgeons on entrance to the show and this practice of having Duty Vets at GCCF shows has continued to this day. Disease contracted at shows continued to be a real danger to the cats exhibited and it was not until after the Second World War that a vaccine was developed against enteritis and even later before effective vaccines were available for cat 'flu'. Today, every cat entering a show has to have a current certificate of vaccination against FIE, FVR and FCV or be rejected from entry. Regular vaccination is now commonplace across the cat population in the UK and has improved the health, welfare and well-being of all cats, saving many lives each year.

The close relationship between the Cat Fancy and the veterinary profession has been sustained and grown considerably, with the setting up of supportive organisations such as the Feline Advisory Bureau in the UK giving valuable advice to all cat owners and breeders. Research scientists working in the fields of cat genetics and cat diseases have also contributed enormously; a mutually beneficial two-way cooperation has encouraged breeders to supply DNA and other samples from affected and non-affected cats to recognised laboratories across the world, which has helped to perfect tests for genetic anomalies as well as vaccines or preventative interventions for bacterial, viral or fungal infections. A number of Breed Advisory Committees in the GCCF have Registration Policies insisting upon independent DNA testing by a veterinary practice on a uniquely identified cat indicating a negative or 'normal' result for a condition that may be prevalent in a breed before a cat can be registered on the Active Breeding

Register. In this way, responsible breeders can totally eliminate life-threatening diseases such as Pyruvate Kinase Deficiency from their breed in a matter of five years.

As already stated, when breeding to modify the shape of any species to produce distinct breed types a danger arises that selection for exaggeration to 'fix' a certain 'look' will produce deformities. Most registration bodies with concern for health and welfare have a Veterinary Defect List published for judges and breeders. The GCCF, working with their Veterinary Sub-Committee, originally voiced their concerns to Council in June 1985 and in 1986 produced such an illustrated and descriptive list as a Preface to the Standard of Points. This list included not only the defects which could lead to health problems, monorchidism and cryptorchidism, etc., but also squints and kinked tails. This list has been regularly reviewed and amended since its initiation, with the latest edition published in 2010. In addition to the faults mentioned, all judges have the right to withhold prizes on any exhibit they feel is not in excellent physical condition or that appears undersized for its age and breed. A far cry indeed from the early days when exhibits could be sent off to a show in a basket lined with straw, by train, with the hope they would be met by the show manager, fed at the show and returned without mishap!

Strict show rules demand that exhibits are in good health, free from parasites or any sign of illness. Veterinary surgeons at vetting-in have published guidelines to follow as they give each exhibit a health check and vaccination certificates are also examined to ensure they are up to date. Failure to comply with the rules results in the exhibit being disqualified and could mean all exhibits from that household are refused entry to the show.

From the first cat shows in the nineteenth century to the present day, the pursuit of their hobby has driven the desire for breeders and owners to increase their knowledge and maintain the highest standards of health and well-being for their cats. Even though their motives may be driven by the determination to win the highest accolades and have the reputation for breeding the 'best', the ultimate benefit has been for the cat.

Local visitors to a show are often amazed at the number of different pedigree breeds shown as well as household pets, which compete in their own section and are judged on their condition, temperament and presentation. These visitors have the opportunity to chat with owners and breeders, learning valuable tips on good animal husbandry, grooming and diet, etc. The fact that neutered cats can win the highest accolades in the Fancy including Supreme Exhibit at the GCCF's annual show has done much to encourage the routine neutering of cats not used for breeding. Bodies such as The Cat Group (see the Glossary) recommend early neutering, offering advice to breeders and their veterinary surgeons. This has given breeders the security of knowing that kittens sold on the non-active register will not be used for breeding by unscrupulous new owners pretending to purchase a pet.

Throughout the world, whatever the registration body, their member clubs take the welfare of their particular breed or of cats living in their area very seriously. An enormous amount of work is done by advising and supporting cat owners who may have problems or by rescuing and rehoming cats. Rehoming can be necessary for a number of reasons, including changes in family or financial circumstances, moving

to a new home unsuitable for pets or where a cat is neglected or abused (see also Chapter 10). Where there has been a national disaster, cat bodies across the world provide funds to support rehabilitation and rescue of those cats affected. Although opinions may differ regarding a certain breed's type and conformation and the relevant standards differ across the world between the various feline bodies, a close-knit relationship exists as far as support for the cat and cat welfare are concerned. At the time of the first cat show, Harrison Weir wrote, 'it is to be hoped that by these shows the too often despised cat will meet with the attention and kind treatment that every dumb animal should have and ought to receive at the hands of humanity'. We are sure he never envisaged just how popular the cat would become across the world so that now it is acknowledged as 'number one pet' and it is certain that cat shows have played an important role in realising this achievement.

## Glossary

- BAC – Breed Advisory Committee: in the GCCF, a BAC exists to work in the interests of the cats of its Breed List by monitoring the selection, training and performance of the judges on its list and the candidates within its scheme and by reviewing its Standards of Points, Registration and Breeding Policies and amending them if and when required with due consideration to the health and future of the breed concerned.
- CFA – Cat Fanciers' Association: a registration body based in the USA, the oldest cat registration body in the world. www.cfa.org.
- FAB – The Feline Advisory Bureau: a charity dedicated to promoting the health and welfare of cats. www.fabcats.org.
- FIFe – Federation Internationale Feline: a worldwide Cat Fancier Society and registration body. www.fifeweb.org.
- GCCF – Governing Council of the Cat Fancy: the UK's premier cat registration body. www.gccfcats.org.
- The Cat Group: a collection of professional organisations dedicated to working on cat welfare from slightly different perspectives. For member organisations see:
  - TICA – The International Cat Association: international cat registration body, www.tica.org.

# 13 Individual and environmental effects on health and welfare

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## Introduction

Individual states of health and welfare result from complex interactions between the individual and the environment it inhabits. Recent research has resulted in a paradigm shift in our understanding of these relationships, with identification of new individual vulnerability factors that change disease risk, the effects of inhabiting environments far removed from the animal's natural history, and the central role of the interaction between humans and animals on the welfare of each.

This chapter will describe some of these issues from the perspective of domestic cat health and disease. Beyond the implications for cat health and welfare, how these factors influence cats also serves as an example of factors affecting health and disease in other species, with the cat serving as the 'canary in the coal mine'. Environmental factors affecting cat behaviour and welfare in confinement, in homes, or in cages while housed in shelters, research facilities and veterinary clinics and how to optimise the environment by minimising perceived threat through provision of resources, control and predictability will be outlined.

## Evolution of the domestic cat

The modern domestic cat (*Felis silvestris catus*) is the product of 11 million years of natural selection in a world free of people, and 12,000 years of natural selection in a world increasingly dominated by humanity (Driscoll *et al*., 2009b). The domestic cat, as a subspecies of the wildcat (*Felis silvestris*), evolved from, and still is, a solitary hunter of small prey. It is also the prey of larger carnivores.

Although cats are increasingly kept as pets, often confined to the indoors in many parts of the world, they have been described as 'exploited captives' (Clutton-Brock, 1999) that have not yet been truly domesticated. Defined as the exploitation of a species by humans for economic reasons, domestication typically involves controlling animals' breeding, providing their food, and restricting their movement.

While controlled breeding is critical to domestication, animals bred in captivity are not necessarily domesticated. In fact, wildcats are improbable candidates for domestication because of their specialised diets (obligate carnivores), relatively solitary social system, and defence of exclusive territories (making them more attached to places than people; see Table 13.1). Additionally, their utility to humans is debatable; even as mousers, terriers and ferrets generally outperform cats. For all these reasons, there is little reason to think that early civilisations sought out wildcats to tame as pets. It seems more likely that cats exploited human settlements, eventually diverging from the wild form (but see Chapter 7). Thus, unlike other domesticated species, the domestic cat appears to have resulted more from natural than intentional selection (although some of this surely has occurred).

The selection process has favoured more plasticity in the social behaviour of domestic cats versus wild cats. While gregariousness has not been reported in wild cats, domestic kittens socialised to other cats, humans, dogs, etc., during the sensitive period

**Table 13.1** Key features of species that influence domestication. Bold type indicates traits of cats. Adapted from Driscoll *et al.* (2009b)

| Feature | Favourable | Unfavourable |
|---|---|---|
| **Social structure** | Dominance hierarchy | **Territoriality** |
| | Large gregarious groups | **Family groups or solitary** |
| | Male social group affiliation | **Males in separate groups** |
| | Persistent groups | Open membership |
| **Food preferences** | Generalist (herbivorous feeder or omnivore) | **Specialist (carnivore)** |
| **Captive breeding** | **Polygamous/promiscuous mating** | Pair bonding prior to mating |
| | Males dominant over females | Females dominant, or males appease females |
| | Males initiate | Females initiate |
| | Movement or posture mating cues | Colour or morphological mating cues |
| | Precocial young | **Altricial young** |
| | Easy divestiture of young | Difficult divestiture of young |
| | High meat yield per food/time | **Low meat yield** |
| **Intra- or interspecies aggressiveness** | Non-aggressive | Naturally aggressive |
| | Tamable/readily habituated | **Difficult to tame** |
| | Readily controlled | **Difficult to control** |
| | Solicits attention | **Avoids attention/independent** |
| **Captive temperament** | Low sensitivity to environmental change | **High sensitivity to environmental change** |
| | Limited agility | **Highly agile/difficult to contain** |
| | Small home range | **Large home range** |
| | Wide environmental tolerance | Narrow environmental tolerance |
| | Non-shelter seeking | **Shelter seeking** |
| | Implosive herd reaction to threat | Explosive herd reaction |
| **Interaction with humans** | **Exploits human environments** | Avoids human environments |

of socialisation from about the age of 2–7 weeks are more likely to live comfortably in groups than are kittens raised by their mother alone. Moreover, this sensitive period for developing social preferences appears to be distributed across the family Felidae. A study of 16 species of small felidae from 5 lineages found that this phenomenon was not concentrated in the domestic cat lineage, but was widely distributed across the species studied (Cameron-Beaumont *et al.*, 2002). This finding suggests that early life events as well as a genetic 'tendency to tameness' may explain the recent evolution of domestic cats. Once this trait was established, the global spread of domestic cats may have obviated any need for domestication of other small felids (Faure & Kitchener, 2009).

So are domestic cats truly domesticated? The criteria for complete domestication including dependence on humans for food, shelter and controlled breeding are not satisfied for many cats. Understanding the processes and attributes of domestication is essential to the study of animal welfare. The extent to which domestication violates the

environmental engagement decision rules of ancestral species can result in negative subjective experiences (suffering) when a mismatch between an animal's current environment and the environment in which its decision rules have evolved occurs (Cameron-Beaumont *et al*., 2002). In this sense, we may consider the environment of domestic cats in the home to be similar to that of zoo animals, with the confined space, proximity of conspecifics and other predator and prey animals, combined with limited resources and opportunities to express species-typical behaviour potentially influencing the cat's perceptions of control and threat, which in turn determine its welfare.

## Pet keeping

Housing cats indoors has become common veterinary advice in the United States. The American Association of Feline Practitioners Statement on Confinement of Owned Indoor Cats – December 2007 (http://www.catcenter.org/pages/knowledgebase/documents/38_indoor_vs_outdoor/pdf%201807%20aafp%20guidelines_position_sgmf3wwu.pdf) takes the position that: 'Veterinarians are encouraged to educate clients and the public concerning the dangers associated with allowing cats' free-roam access to the outdoors. Free roaming cats may be exposed to injury, suffering, and death from vehicles, attacks from other animals, human cruelty, poisons, and traps. Additionally, these cats have an increased potential to be exposed to feline-specific and zoonotic diseases. Lastly, adherence to this policy also reduces predation of native wildlife populations, a goal and policy of the AVMA and the AAFP'. This is not the official policy, nor the position of most European veterinarians, and depending upon how the policy is instigated, might even be considered cruel to the cats affected (see Turner, 2012).

While reducing the risk for some health problems of cats, confinement has long been known to increase the risk for others. In 1925, Kirk recognised that 'too close confinement to the house' increased the risk of lower urinary tract signs (LUTS) and obesity (Kirk, 1925). Subsequent epidemiological studies have found that indoor housing is associated with increased probability (odds ratio) for a variety of common disease problems in cats, including odontoclastic resorptive lesions (~4.5), obesity (1.6–15.8), type 2 diabetes mellitus (1.4–4.6) (Slingerland *et al*., 2009), hyperthyroidism (4–11.2) and behavioural disorders (Buffington, 2002; Slingerland *et al*., 2009). The observation that these disorders also occur in cats that are not housed exclusively indoors suggests that it may not be the indoor environment itself, but some variable features of the cat's surroundings that influence their risk for these illnesses.

A leading candidate feature of the cat's surroundings that may influence disease risk is the cat's perception of control and predictability. The perception of or actual lack of ability to control their surroundings is perhaps the greatest stressor in the lives of captive animals. Captive animals have little or no control over who their social partners are, how much space they can put between themselves and other animals, what types; amounts and availability of food and water they can consume; where, when and how they can eliminate; or the quality or quantity of environmental stimuli including lights, noise, odours and temperatures (Morgan & Tromborg, 2007). Predictability means

accurate expectations about when activities occur and who performs them. Inability to accurately predict events in captive environments may be stressful; given a choice, animals choose predictability over unpredictability, especially over aversive events (Weiss, 1971, 1972; Morgan & Tromborg, 2007).

## Stress and stress physiology

Evolutionary success depends upon reproductive success. Reproductive success in turn depends upon the ability to perceive and respond to environmental threats to sustain life long enough to ensure transmission of genetic material (Dawkins, 1990). To succeed, animals must act in constantly changing environments, so a process called homeostasis developed to permit regulation of internal environments within the rather narrow ranges required for survival.

When animals interact with their environments, they collect a constant stream of new information through their sensory systems (olfactory, gustatory, auditory, tactile, visual and pheromonal). These signals are integrated by the central nervous system (CNS) (Freeman, 1998) and acted upon (or not) in a constant reiterative cycle with a time constant of milliseconds (Damasio, 1999). When no threat is perceived, the initial course of action progresses; when a threat is perceived, however, different actions result.

Threats, a type of stressor, are environmental events that activate the stress response system (SRS) of the CNS (McEwen, 2008) to restore homeostasis. External environmental threats can be classified as (1) physical, such as blood loss, heat, cold or noise; (2) psychological, such as learned responses to previously experienced adverse conditions; and (3) social, such as territorial disputes. Stressors can be further categorised as either acute (single, infrequent, time-limited) or chronic (frequent, prolonged or continuous exposure). The stress response includes both physiological and behavioural features intended to (1) reduce exposure to negative environmental conditions and enhance the prospects of a return to normality (homeostasis), (2) adjust to or tolerate the conditions, (3) maintain emotional equilibrium, and (4) preserve social relationships (Pacák & Palkovits, 2001). The systems that permit successful responses to threats have been selected for over several hundred million years, and are complex, interactive and redundant. They may have developed initially as local defence responses to noxious environmental stimuli, and have been built upon and expanded as the vascular, immune, endocrine and nervous systems developed increasing complexity (Ottaviani & Franceschi, 1998). The threat potential of many environmental events also varies widely across individuals based on their unique life histories, the context in which the event occurs, and the expected outcome of the event for the individual (McEwen, 2007).

Responses of the SRS may be activated peripherally by environmental factors ('bottom-up'), or centrally by perception of threat ('top-down'). Most sensory input from the internal and external environment reaching the brain is received in the CNS by the thalamus, and is then forwarded to the cortex for further processing before transmission to the motor systems. Threatening information can also be transferred directly to the emotional motor system, and thence to the SRS in the hypothalamus. Stimulation

of the SRS by either internal or external stimuli can result in activation of variable combinations of peripheral neural, hormonal and immune responses. The pattern of activation depends both upon the nature of the threat and individual animal factors (Pacák & Palkovits, 2001).

Activation of the SRS results in release of corticotrophin-releasing factor (CRF) from the hypothalamus, which acts both as a neurotransmitter to stimulate neural activity in the sympathetic nervous system and as a hormone to induce release of variable combinations of hormone-releasing factors from the pituitary gland (Neeck & Crofford, 2000; Neeck, 2002). One of these is adrenocorticotropic hormone (ACTH), released from the anterior pituitary, which stimulates release of glucocorticoids from the adrenal cortex (LeDoux, 2000; Van Bockstaele *et al*., 2001). Activation of the sympathetic nervous system organises the immediate responses to threat by activating orienting and vigilance behaviours, as well as the longer behavioural responses such as 'freeze, flight, fight, fright, faint' (Bracha, 2004). Release of glucocorticoids both facilitates the physiological and behavioural response to the stressor and inhibits SRS activity through a series of negative feedback loops.

Adjustment or changes in the behaviour, physiology and structure of an organism that result in greater suitability to an environment are called adaptation. Adaptation can result from genetic or phenotypic changes. Genetic adaptation occurs at the population level over generations, whereas phenotypic adaptation occurs in individuals through physiological acclimatisation and behavioural adjustment. Individual adaptation is largely phenotypic because confinement environments change too quickly for genotypic adaptation to occur. The ability to cope successfully is a function of the many component variables of the confinement environment, including its physical dimensions and complexity.

Control and predictability are important determinants of an animal's ability to adapt to environments because they permit behavioural responses that increase adaptation skills, which in turn facilitate successful responses to subsequent stressful situations (Morgan & Tromborg, 2007). Learning to predict significant events also facilitates adaptation. In nature, animals attach a great deal of significance to cues that signal the approach or intentions of others, as well as environmental events such as sunset and sunrise or changing seasons. The process of forming anticipatory associations (which underlies classical conditioning) likely evolved to predict important negative or positive events. Animals are said to have adapted when they learn to disregard unimportant events and to take action for important events (Tarjei, 1989).

Processes also developed to permit animals to respond to threats to homeostasis. Threats to homeostasis result in activation of allostatic (maintaining stability through change) processes that promote adaptation and attempt to restore homeostasis through alterations in physiological processes and behavioural strategies. Acute activation of the SRS helps individuals cope with sudden, unexpected events. In contrast, persistent activation of the SRS, resulting from variable combinations of the sensitivity of the SRS and the threatening nature of the environment (Broom & Johnson, 1993), may produce chronic wear and tear on the body (McEwen, 2007, 2008). The wear and tear to body systems, called allostatic load, can result in illness.

When environmental events are so intense, prolonged, noxious or novel that they exceed the adaptive capacity of the SRS, poor health, suffering and reduced life expectancy can result (Broom & Johnson, 2000).

## Sickness behaviours

The actions of the SRS include effects on immune function. One of the consequences of immune system activation is development of sickness behaviours through release of pro-inflammatory cytokines. Sickness behaviours refer to a group of non-specific clinical and behavioural signs that occur in response to infection; they have been found in all animal species studied (Dantzer & Kelley, 2007). Sickness behaviours are thought to reflect a change in motivation of the animal from pursuing usual activities, such as foraging or social behaviours, to one that promotes recovery by inhibiting metabolically expensive activities and favouring ones that promote healing (Dantzer *et al*., 2008). Although sickness behaviours are usually thought of in the context of responses to external organisms, psychological stress recently has been associated with immune activation and pro-inflammatory cytokine release (Marques-Deak *et al*., 2005). Moreover, a recent review has linked sickness behaviour, cytokine activation, mood symptoms and chronic pain (Raison & Miller, 2003).

We have found that cats also appear to exhibit sickness behaviours in response to environmental disturbances. Stella *et al*. (2011) recently reported that colony-housed cats, both healthy and those afflicted with feline interstitial cystitis or, as recently suggested by Buffington (Goldstein), 'Pandora Syndrome' to acknowledge the systemic nature of the syndrome), exhibited increased sickness behaviour in response to unusual environmental events that occurred during routine management of the colony. These events included transient (one-week) discontinuation of contact or interactions with the cats' primary caretaker, changes in time of day of routine husbandry, unfamiliar caretakers, and a delay of 3 h in feeding time (one-week duration) during a study of feeding choices. Such disturbances are comparable to those that typically occur in veterinary clinics, research facilities and shelters, as well as in homes.

The most common sickness behaviours observed were vomiting of hair, food or bile, decreased appetite, and eliminating outside of the litter tray. In cats, such behaviours are often considered to be normal (vomiting), finicky (decreased appetite) or unacceptable (not using litter tray) by owners and veterinary professionals. Other less commonly observed sickness behaviours included excessive or decreased grooming, fearful or aggressive behaviour, decreased affiliative interactions with conspecifics and human caretaker and decreased play behaviour. These results suggest that veterinarians and other caregivers may need to consider the possibility that these signs might have resulted from external as well as internal events when a cat is evaluated clinically for the cause(s) of these signs (Buffington, 2002). Furthermore, these behaviours are not unique to cats; similar behaviours have been reported in other species in response to environmental disturbances (Dantzer & Kelley, 2007; McEwen, 2008).

The motivational state of the sickness behavioural response has a physiological basis and should be considered in welfare assessments as well as other motivational states

such as fear, hunger and thirst. Seeking of rest, withdrawal from the environment and caring for one's self are adaptive responses to infection that are as normal as arousal and escape are in response to a threat (Dantzer & Kelley, 2007). However, when this motivational state is caused by chronic environmental disturbances with which the individual is unable to cope, it is a sign of impaired welfare and should be addressed. Thus, daily monitoring of cats for the occurrence of sickness behaviours offers cat caretakers a practical, non-invasive method to assess stress responses and, thus, gauge overall welfare.

## Early life experiences

Converging evidence from a number of fields suggests that the SRS also may be sensitised to the individual's surroundings by experiences occurring early in life. In cats with 'Pandora Syndrome' (feline idiopathic cystitis), we have found anatomical evidence (small adrenal cortices) of response to a stressor by the pregnant queen that affected her offspring (Westropp *et al*., 2003). In addition to these effects, neurological changes in central stress circuits also are likely to have occurred (McEwen, 2007; Buffington, 2011).

Evidence from clinical, epidemiological and experimental observations has led to the development of theories about why and how environmental cues attempt to match the physiology of the developing organism to its post-natal environment. The 'developmental origins of health and disease' (Gluckman & Hanson, 2006a) hypothesis proposes that when a pregnant female is exposed to a sufficiently harsh stressor, the hormonal products of the ensuing stress response cross the placenta and affect the course of foetal development (Meaney *et al*., 2007). The biological 'purpose' of transmitting this response to the foetus may be to induce the development of the foetal stress response and associated behaviours toward enhanced vigilance in a threatening environment and so to increase the probability of survival (Matthews, 2002; Gluckman & Hanson, 2006a). As Gluckman and Hanson (2005) described, the foetus may use cues from its environment to make predictive adaptive response 'decisions'. That is, if a threatening or nutrient-limiting environment is perceived from maternal signals, the developmental trajectory of the foetus may change to enhance reproductive fitness in the predicted environment.

The effects of stressors on foetal development seem to depend both on the timing and magnitude of exposure to products of the maternal SRS in relation to the activity of the developmental 'programmes' that determine the maturation of the various body systems during gestation and early post-natal development (Gluckman & Hanson, 2005). In the case of the adrenal gland, for example, if the developing foetus is exposed before initiation of the developmental programme, there may be no effect. During the critical period while the adrenocortical maturation programme is running, however, studies in rodents (Cadet *et al*., 1986; Fameli *et al*., 1994), carnivores (Braastad *et al*., 1998) including domestic cats (Westropp *et al*., 2003) and primates (Challis *et al*., 1974; Leavitt *et al*., 1997), all have found reduced adrenal size in the affected offspring. If a

sufficiently severe stress response occurs after the critical period of adrenocortical development, adrenal size and subsequent adrenocortical responses to stress may be increased (Matthews, 2002).

Studies have found that a variety of chronic illnesses can result from a mismatch between the predicted and actual environment an organism inhabits (Gluckman & Hanson, 2006b; Godfrey, 2006). For example, variable combinations of clinical signs referable to other organ systems such as the gastrointestinal tract, skin, lung, cardiovascular, central nervous, endocrine and immune systems have been identified in cats with Pandora Syndrome (Buffington *et al*., 2006a, 2006b). Cognitive function also is affected by both genetic (Matzel *et al*., 2006) and developmental (Chwang *et al*., 2006) influences. Impaired coping in stressful situations, increased fear and anxiety-related behaviours, and dysregulation of the hypothalamus–pituitary–adrenal axis all have been found in adults exposed to adverse early life experiences (Weinstock, 1997, 2005; Dickerson *et al*., 2005; Kosten *et al*., 2006). Studies of enduring effects of stressful developmental experiences on health have now been published in a wide variety of mammalian species, including rodents, carnivores, primates and human beings (Zhang *et al*., 2006; Fumagalli *et al*., 2007; Owen & Matthews, 2007).

Sensitisation is not restricted to the developmental period (Tsankova *et al*., 2006) but it does appear to be more likely to occur during this time of growth and maturation of the neuroendocrine systems. Sensitisation of the SRS may be part of a more general 'survival phenotype', which includes smaller (or larger) size at birth. Although the phenotype does not appear to affect reproductive capacity, it has been associated with a variety of adverse clinical outcomes (Gluckman & Hanson, 2005) including metabolic syndrome, obesity, psychological disorders and recently, irritable bowel syndrome (Bengtson *et al*., 2006).

Recent research suggests that one mechanism underlying the sensitisation of the SRS involves a process called epigenetic modulation of gene expression (Weaver *et al*., 2004; see also Chapter 2). This general biological process mediates such commonplace events as sex- and organ-specific patterns of gene expression that lead to the final phenotype of the organism by silencing genes not appropriate to the particular tissue environment. Epigenetic modulation of gene expression is now a prominent candidate mechanism for the identified differences in stress responsiveness found in patients exposed to adverse early life experiences (Fowden *et al*., 2005; Seckl, 2004). Even when sensitisation of the SRS occurs, it may be unmasked only by another adverse experience sometime later in life, possibly by another round of epigenetic modulation of gene expression. Once expressed, these alterations in gene expression may be quite stable, and resistant to current medical interventions.

## Welfare

Animal welfare has been defined as the animal's state as regards its attempts to cope with its environment (Broom & Fraser, 2007). Coping pertains to the process of reducing stressor-induced physiological activation by performing behaviours that either

alter the stressor or reduce the emotionality associated with the stressor (Carlstead *et al*., 1993; Broom, 1996).

Welfare is a characteristic of the individual that varies on a continuum from poor to good. It is not a static state, but will change across the day, seasons, reproductive states and life stages of an animal. The welfare of each individual should be monitored regularly and appropriate modifications made as needed. Impaired welfare can be considered a chronic imbalance between positive and negative experiences resulting in chronic stress and failure to cope. It is now assumed that, similar to humans, chronic stress may induce mental suffering in animals with or without physical health problems.

Animal welfare is assessed by evaluating three categories: physical health, affective states and the ability to live naturally. Physical health and biological functioning can be assessed by measuring disease, injury, rates of survival, growth and reproduction. Study of affective states has been primarily focused on identifying and quantifying negative (pain, fear, distress) affective states (Broom, 1998; Fraser & Duncan, 1998). Such studies are difficult because affective states cannot be observed directly, thus physiological changes (increases in heart rate and/or cortisol) and behavioural responses (vocalising, flinching) are often measured as proxies or indirect evidence of the affective state of the animal. Animals should be able to live a reasonably natural life and express species-typical behaviours (Broom, 1988). Study of domestic animals' wild counterparts should inform animal care personnel of 'normal' species-typical behaviour and provide a starting point or goal for the captive population. Environmental enrichment becomes important in achieving these goals.

## Environmental enrichment

Environmental enrichment (EE) has been defined as 'a concept which describes how the environments of captive animals can be changed for the benefit of the inhabitants' and as 'a process for improving zoo animal environments and care within the context of their inhabitants' behavioural biology and natural history. It is a dynamic process in which changes to structures and husbandry practices are made with the goal of increasing behavioural choices to animals and drawing out their species appropriate behaviours and abilities, thus enhancing animal welfare'(Young, 2003). The connection between EE for captive animals and domestic cats may not be apparent until one considers that owners confine many cats to spaces much smaller than their natural home ranges, often keeping cats in cages, indoors or allowing access to small outdoor spaces (which may contain perceived threats). Cats kept in these environments live akin to zoo animals and, as with zoo animals, environmental quality can exert important effects on their health and welfare (Buffington, 2002).

The goals of EE are to: (1) increase the range, number and diversity of normal behaviour patterns; (2) reduce the occurrence of abnormal behaviours; (3) increase positive utilisation of the environment; and (4) increase the ability to cope with challenges in a more normal way (Young, 2003). These goals are intended to create and sustain a perception of control and predictability about the surroundings that

**Table 13.2** Types and subtypes of environmental enrichment for cats (adapted from Young (2003))

| | |
|---|---|
| **1. Social** | A. Contact |
| | a. Other cats (pair, group, temporary, permanent) |
| | b. Other species (human, dog, other pets) |
| | B. Non-contact |
| | a. Visual, auditory, cooperative device |
| | b. Human, dog, other pets, wildlife outside |
| **2. Occupational** | A. Psychological (puzzles, control of environment) |
| | B. Exercise (climb, scratch, run and play, time out of cage) |
| **3. Physical** | A. Enclosure |
| | a. size |
| | b. complexity (climb/perch/scratch, hide/resting opportunities) |
| | B. Accessories |
| | a. Internal |
| | i. Permanent (furniture, bars) |
| | ii. Temporary (toys, ropes, substrates) |
| | b. External (hanging objects, puzzles) |
| **4. Sensory** | A. Visual (tapes, TV, images, windows) |
| | B. Auditory (music, vocalisations) |
| | C. Other stimuli (olfactory, tactile, taste) |
| **5. Nutritional** | A. Diet form (e.g. canned, dry), processing, sensory properties |
| | B. Delivery (frequency, schedule, presentation) |
| | C. Type (novel, variety, treats) |

permits animals to thrive. Five major types and subtypes of EE have been identified (Table 13.2) and the authors have applied these to the domestic cat situation (see also Chapter 10).

A consistent, predictable (by the cat) daily routine is essential, particularly when the cat is confined to a cage. As mentioned above, we have found that changing the time of daily husbandry and feeding resulted in increased sickness behaviours, indicative of a stress response, in our colony-housed cats (Stella *et al*., 2011, 2013). This is probably true of cats in homes as well as in cages.

Environmental enrichment concepts and needs are similar for cats housed in shelters, research facilities, veterinary hospitals, boarding facilities or inside homes. We recommend that both the macro (the room or indoor home of the cat) and the micro (the individual cage or restricted area of the cat) environments be enriched (see Chapter 10).

## Social interactions and environmental enrichment

Free-living domestic cats tend to live in small groups consisting of related females and their young, where females will pool their kittens into crèche groups and all young are alloparented. Males are more solitary, tending to live on the margins of the group. They typically hunt in larger home ranges and do not provision the female or young with

food. In a study of households with two cats (Barry & Crowell-Davis, 1999), some 50% of time was spent out of one another's sight, even though they were most often within 1–3 m of each other. Cats thus may be unusually susceptible to health and welfare effects of indoor restriction because of their solitary behavioural strategies.

Cats do not appear to develop conflict resolution strategies to the extent that more gregarious species do, so they may attempt to circumvent agonistic encounters by avoiding others or decreasing their activity (Bernstein & Strack, 1996). These cats may prefer to have separate food and water sources, litter box and resting areas to avoid competition for resources, and to avoid unwanted interactions. Unrelated cats housed together in groups also appear to spend less time interacting with conspecifics than related ones do (Bradshaw & Hall, 1999). Published guidelines for introducing new cats into a home or group-living system are available (Bohnenkamp, 1991).

Human beings are perhaps the dominant feature of many cats' environment. Repeated interactions between the cat and human occur, eventually allowing each to make predictions about the other's behaviour. The quality (positive or negative) of the resulting human–animal relationship likely determines the quality of the cat's (and the owner's) life (Figure 13.1). Moreover, the human mostly determines the number and nature of interactions and hence the quality of the relationship. Unfortunately, most research on the human–animal relationship to date has focused on the outcome of the relationship for the owner rather than for the animal (Bernstein, 2005; Virues-Ortega & Buela-Casal, 2006; Walsh, 2009).

Research in livestock has identified the most aversive human behaviours toward animals to include hits, slaps, shouting and fast speed of movement. In contrast, positive interactive behaviours included pats, strokes, resting the hand on the animal, talking to the animal and slow deliberate movement (Coleman *et al*., 1998; Pajor *et al*., 2000). Helping caretakers understand that these same behaviours are likely to affect cats similarly may improve interactions, and thus the relationship.

Avoiding punishment behaviours may be even more important in cats than in other animal species with which humans interact. Possibly because of their heritage as a relatively solitary species, cats do not appear to have developed many behaviours typical of interactions between members of more gregarious species. As with other

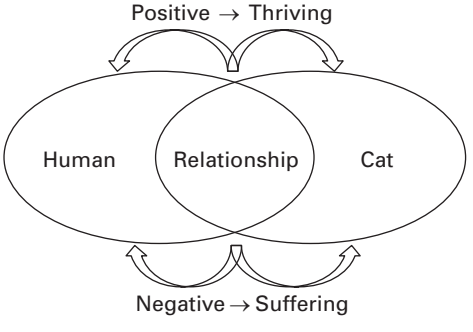



**Figure 13.1** Effect of the quality of the human–cat relationship on both participants in the relationship.

animals, use of a soft voice (and avoiding sounds that resemble hissing), indirect eye contact (to avoid predatory gazing), displaying slow blinks and movements, and letting the cat initiate and control the extent of contact during initial interaction (Turner, 1991) reduces the probability of creating a perception of threat in the cat.

A familiar, trusted person appears to be essential for effective cat management. Cats adapt more quickly and easily to new environments when they see the same friendly person each day. Studies have shown that animals can easily learn to discriminate between two people (Davis *et al*., 1997; Davis & Taylor, 2001). If animals are able to recognise and discriminate among the humans they regularly come in contact with, then these same persons can become predictors of salient events (food, pain) in animals' lives. This is a classical conditioning response, in which the person becomes the conditional stimulus or predictor of the salient event, and can be used to improve the animals' welfare.

Given time constraints in many environments, the quality of human–animal interactions may be more important than the quantity of interactions. When a familiar person takes some time to pet, talk to and offer food treats daily, the cat is more likely to respond positively when that person enters the room. The person also becomes familiar with the usual affect and behaviour of the cat, and so can quickly recognise any changes in behaviour that may signal a change in health or welfare. This is true in home environments as well as in more confined situations. The more threatening the environment, the more important a familiar person becomes to the cat.

When cats' perception of safety becomes threatened, they appear to respond in an attempt to restore 'control'. During such responses, some cats become aggressive, some become withdrawn and some become ill. Conflict among cats can develop because of threats from other animals (including humans) or from cats outside the cage or house. With a little practice, one can recognise the signs of conflict; in this way, caretakers can act to reduce the intensity of the conflict. Of course, some conflict within a group is normal, regardless of species. The goal is to reduce unhealthy conflict in order to attain a more manageable level for the cats involved.

## Macro environment

Macro environmental factors that may be associated with stress in cats include lighting, sound, odours and temperature (Morgan & Tromborg, 2007). These environmental factors will affect cats differently depending on whether they are housed in cages or areas where they are unable to control or move away from a factor they find aversive.

Cats are more sensitive to light brightness than humans are; this should be considered in housing facilities because light intensity can affect the cat's welfare. The auditory frequency range of cats (and most species) exceeds that of humans, making assessment of the welfare implications of high-frequency noise difficult. We recommend sound pressure levels be kept to a minimum ($< 60$ dB – quiet conversational level; reasonably accurate dB meters are freely available for many 'smart phones' currently) based on observations of cats successfully maintained in environments in this range. This level is

still well above sound pressure levels in nature, which range from 20–37 dB in savannah habitats to 27–40 dB in the rain forest. Almost all mammals depend more on olfactory cues (macro-osmotic) than do most primates, including humans. Therefore, aversive odours can be an additional source of chronic stress for confined animals. For cats, potentially objectionable odours include dogs (a natural predator), other cats, alcohol (from hand rubs), cigarettes, cleaning chemicals (including laundry detergent but not bleach, they seem to like this odour), some perfumes and citrus scents. Cats prefer the ambient temperature to be much warmer than many species. The thermoneutral zone for domestic cats is 30–38 °C (National Research Council, 2006). Most cat housing areas are not this warm, and most homes and laboratory housing for cats are maintained closer to 22 ± 2 °C (National Research Council, 1996).

## Micro environment

Micro environmental factors that can be potential sources of stress for cats include food (type and presentation), elimination facilities, hiding and perching opportunities, and outlets for the expression of species-typical behaviours. The type and presentation as well as the availability of these features of the environment can be either a source of stress or enrichment.

### Food and feeding

Free-living cats – as opportunistic predators of small prey – typically eat frequent small meals throughout the day, spending a large portion of their day engaged in food acquisition. Providing one or two large meals a day in a bowl requires minimal effort on the cat's part to feed itself. Commercial dry cat food is of a very different composition and texture than the 'wild' diet of the cat. This may lead to under- or over-eating and boredom in the confined cat. Cats with free access to food usually prefer to eat several small meals throughout the day as opposed to one to two large meals, and most will hunt for prey when given the option (Bradshaw & Thorne, 1992). Although free access to food may allow for frequent feeding sessions, this feeding strategy removes the opportunity for the cat to express natural predatory instincts (Morris, 2002), and may contribute to development of obesity and other health problems (Kienzle & Bergler, 2006). Because cats evolved as solitary hunters of small prey (Morris, 2002), separate feeding containers out of sight of other cats' food facilitates 'solitary' feeding and reduces the risk of conflict over resources.

Cats sometimes display strong food preferences based on foods encountered early in life, although usually these can be modified by later experience (see Chapter 2). Some cats also develop decreased preference for foods that have formed a large part of their diet in the past, the so-called 'monotony effect', and display preferences for novel foods (Bradshaw, 2006). Although some owners perceive their cats to be 'finicky' eaters, evidence suggests that food refusal also is a common feline response to environmental threat (Stella *et al*., 2011). However, Turner and Stammbach-Geering (1990) and Turner

(1991) have also found evidence that cats reported to be 'finicky eaters' got that way because their owners 'gave in' to the cats' whims, which the cats, in turn, rewarded with more social interaction with the owners at other times of the day.

Available evidence confirms that currently available commercial diets adequately meet the nutritional needs of domestic cats (Hoyumpa Vogt *et al*., 2010; Hewson-Hughes *et al*., 2013). Meeting nutrient needs in ways that best mimic cats' natural preferences can provide additional enrichment. For example, caretakers can accommodate cats' natural predatory habits and increase their daily activity by offering food in puzzle toys, such as balls or other devices designed specifically for cats to release dry food or treats when physically manipulated (Ellis, 2009).

Cats also seem to have preferences for water that can be investigated. Water-related factors to consider include freshness, taste, movement (water fountains, dripping faucets or aquarium pump-bubbled air into a bowl) and shape of container (some cats seem to resent having their vibrissae touch the sides of the container when drinking).

## Elimination facilities

As with food and water containers, litter boxes should be located in safe, quiet areas to ensure that the cat's access to or from the box cannot be blocked by another animal, and away from machinery that could come on unexpectedly and disrupt the normal elimination behaviour sequence. Placing litter boxes in quiet, convenient locations could help improve conditions for eliminative behaviour. If different litters are provided, it may be preferable to offer them in separate boxes, as individual preferences for litter type have been documented (Borchelt, 1991; see also Chapter 14). Covered litter boxes may trap odours and prevent the cat from having a safe vantage point for the approach of other animals during elimination, making them a less desirable option for many cats. For group-housed cats, provide a box for each cat (or cat group) plus one additional box, out of sight of each other (Neilson, 2004). Most cats display a preference for unscented and finely particulate litter material (Horwitz, 1997), making clumping litter a desirable option.

## Physical environment

The physical environment should include opportunities for climbing, scratching, hiding and resting. Cats seem to prefer to monitor their surroundings from elevated vantage points, and seem to welcome provision of climbing frames, hammocks, platforms, raised walkways, shelves or window seats (Rochlitz, 1999). Cats seem to prefer soft resting substrates, such as pillows or fleece beds (Crouse *et al*., 1995), in warm areas, such as safely heated beds or sunny windows. Caretakers of multi-cat households or group-caged cats need to provide enough space to permit each cat to keep a social distance of 1–3 m (Barry & Crowell-Davis, 1999), horizontally as well as vertically, in spaces shared with other cats. Although some cats rest together and allogroom and rub each other, most cats use common resting, perching and hiding locations at different times of the day (Bernstein & Strack, 1996; see also Chapter 6). Hence, caretakers of

more than one cat need to provide safe, comfortable and private locations for each cat to avoid creating competition for scarce resources.

Cats are a prey as well as a predator species, so climbing for observation and safe vantage is an important feline behaviour. Understanding this behavioural need permits the caretaker to perceive the cat's climbing proclivity as natural and to enjoy providing acceptable opportunities for cats to climb, while protecting areas they do not want the cat to access.

Scratching and marking are species-typical behaviours in the cat; thus, appealing, appropriate objects need to be provided to confined cats as outlets to express these behaviours. Scratching behaviour maintains claw health and leaves both visual and pheromonal territorial marks (Landsberg *et al*., 2003).

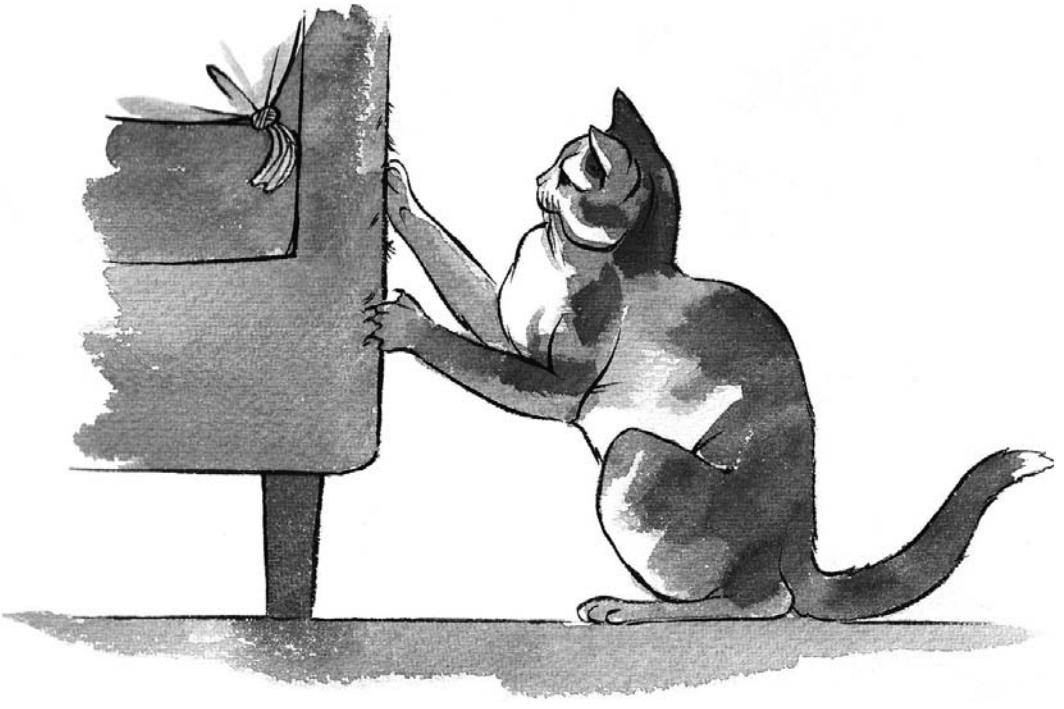
## Conclusions

The effectiveness of environmental enrichment efforts depends on identification and accommodation of various parameters of the cat, the housing situation and the caretaker. Cat factors include the animal's genetic and epigenetic heritage and prior individual experience. Housing factors include the number of cats and other animals in the household or housing area and the feasibility of modifying the environment. Caretaker factors include the strength of the human–cat bond, the ability to identify modifiable factors, and the willingness to commit the financial resources and time to create and sustain an enriched environment. Due to the lack of controlled trials, it currently is not possible to prioritise the importance of any of these suggestions for environmental enrichment, or to predict which would be most appropriate in any particular situation.

While more precise recommendations based on research will be welcome, the benefits of enriched environments, based on recognition of and opportunities to engage in species-typical behaviours, provide a compelling goal for improving the relationship between cats and their surroundings, which include humans.

# 14 Feline behavioural problems and solutions

Benjamin L. Hart and Lynette A. Hart



*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

Over the last decade or so, cats have moved into the position as the most common companion animal. The reasons are fairly obvious: they are known for being fastidious in eliminative behaviour – no necessity to take them on walks for elimination; they cuddle up next to us as we sit on the sofa; they can welcome visitors and they can even take care of the occasional vermin problem, should one arise. Cats have become ever more intimate family members, and they are an important source of emotional support for human family members. They provide 'affection and unconditional love' (Zasloff & Kidd, 1994). This is important for people who are depressed or isolated from others, those with special needs such as those restricted to a bed, and those caring for another person in a demanding role such as caring for a relative with Alzheimer's (Hart *et al*., 2006).

The onset of a behaviour problem that interferes with the emotional support role of an otherwise loving cat, or even makes the cat intolerable to keep in the home, is particularly tragic. Fortunately, many behaviour problems that put the human–animal bond aspect of a companion cat at risk can be resolved or even prevented. The most serious of the problems is house soiling and this constitutes the most frequent category of behavioural problems in cats for which cat experts are consulted. Problems centring around aggressive behaviour are not as frequent as with dogs, but can become serious at times. A common problem for many cat owners is furniture scratching. Cats are increasingly kept indoors nowadays, especially in the USA and in urban areas, and eating house plants can be an issue both for the owners, who do not want their indoor garden messed up, and others whose cat may munch on a house plant or two that is poisonous.

In this chapter we will discuss the reasons behaviour problems arise and the ways to resolve and prevent the problems, at least in many instances. Keep in mind that many of the behaviours that come across as problems to owners are actually normal to the cats – usually reflecting an inherited predisposition of the wild ancestral cat where the behaviours had survival value.

## House soiling

House soiling, whether urination or defecation or both, can have behavioural causes that are dealt with in this chapter, or medical causes, such as lower urinary tract disorders, intestinal disorders or even arthritis interfering with use of a litter box. These medical causes may need to be ruled out as part of the diagnostic evaluation. In the context of house soiling that has behavioural causes and behavioural solutions, it is necessary to differentiate between inappropriate elimination and urine marking: both are dealt with separately below.

### Inappropriate urination and defecation

One of the concepts that plays a role in feline problem urination is that cats are attracted to use a spot that already has some faecal and urine odour, because this indicates – in nature – a toilet area where faeces and urine are deposited (Hart *et al*., 2006). In nature,

**Table 14.1** Differentiating inappropriate urination from urine marking

| Behavioural signs | Inappropriate urination | Urine marking |
|---|---|---|
| Posture | Squatting posture<br>Emptying bladder | Standing, not emptying bladder; can be squatting at times |
| Litter box usage | Usually stops using box | Continues to use litter box for normal urination and defecation |
| Target areas | Attractive substrate such as carpet; planter soil | Vertical targets most often; may have behavioural significance |
| Preliminary signs or precipitating factors | Signs of aversion to litter such as straddling box, shaking paws, not covering | Preceded by identifiable stimuli such as agonistic interactions with feline housemates or outside cats |
| Defecation behaviour | Often accompanied by inappropriate defecation | Defecation not used in marking |

cats virtually all carry at least a light load of intestinal parasites. And the parasites reproduce by leaving ova in the faeces of the cats. When the faeces are a few days old the ova hatch into infective larvae that latch onto whatever is passing by. If the passerby is a cat, the larvae can attach to the hair and subsequently be groomed off and swallowed; the cat is thereby infected or re-infected with the parasite.

An outdoor toilet area, with some smell of faeces and urine, indicates a place for a cat to eliminate, somewhat concentrating eliminations in an area away from sleeping and resting places. If the cat goes to the area, and digs a hole, covers over the droppings and then gets out of there, intestinal parasite infestation or re-infestation is minimised. However, if the toilet area is used too much, and faecal droppings become too concentrated and infective larvae too numerous, the associated strong odour would tend to drive away cats because this indicates a 'parasite minefield'.

Translating this concept to the urban home scene, an appropriate toilet area – the litter box – should have a small bit of faecal and urine odour (which we cannot smell), but not a strong odour that drives the cat away. This explanation is meant as an 'ultimate' explanation and involves no implication that the cat understands the parasite part; the cat is just showing that a strong odour is aversive.

The typical history of inappropriate elimination is that the cat changes its toilet area, the litter box, to another part, or parts, of the house. The litter box is no longer used some or all of the time. The problem may be with urine, faeces or both. When just urination is involved, inappropriate urination should be distinguished from urine marking. Table 14.1 outlines the differences between the two types of problem urination. The main differentiating criterion is that urine marking typically is on vertical surfaces (or on objects left behind on the floor), using a small amount of urine, whereas inappropriate urination is never on a vertical surface and involves a large, bladder-emptying amount of urine.

Inappropriate urination can stem from aversion to the litter box or, for outside cats, inclement weather or harassing dogs or other cats. The problem could also result from attraction to inappropriate places or substrates, such as a carpet. The cat may use a litter box for defecation, but urinate in other places, or vice versa, or both urinate and defecate outside the box.

The most common cause of inappropriate elimination – faeces, urine or both – is not cleaning the litter of solids and (clumped) urine frequently enough. Some authorities mention that behaviours such as straddling the box (to avoid touching the litter), shaking the paws after touching litter, digging outside the box on the floor, or not covering faeces and running from the box are markers of an emerging house-soiling problem (Borchelt, 1991). These behaviours are often linked with a litter box that is cleaned too infrequently, but aversions can also be related to introduction of a new type of (disliked) litter, changing the depth of the litter, use of a box liner or use of an electric self-cleaning box.

The resolution of inappropriate elimination is based on the cause of the problem. For an aversion to the litter box, the recommended approach is to clean the litter box daily and change soiled litter weekly. Because the litter box itself absorbs odours, this cleaning prevents the parasite landmine effect but retains the toilet area signature odour. When unsure of the suitability of the litter material, a litter preference test is recommended. This indicates what the cat prefers. Up to five cardboard trays, cut down from boxes as temporary litter boxes, can contain samples of material such as current litter, sand, plain clay litter and different types of clumping litter. It is generally recognised that cats prefer finely granulated clumping litter, and certainly clumping litter makes it easier to remove urine from the litter box. The unscented litter is recommended because scented litter has been associated with an increased likelihood of house soiling (Horwitz, 1997). For multi-cat households, there should be a sufficient number of litter boxes. A recommended rule of thumb is one more box than the number of adult cats in the household. And, different cats may prefer different types of litter. The litter boxes should be positioned to provide easy access by all cats. The regular litter boxes should be cleaned with mild, unscented detergent; bleach, ammonia, pine oil cleaners and other strongly smelling agents should be avoided.

For cats that normally eliminate outdoors, the appeal and accessibility of the toilet areas can be enhanced by eliminating aversive elements such as harassing dogs and effects of inclement weather. A roof over the normal toilet area might be provided for weather protection. If a sandy litter area is provided with commercial sand, then this should be cleaned frequently as is done with an indoor litter box; thus the outdoor toilet area will have a characteristic odour, but not come across to the discriminating cat as a parasite landmine.

Once the litter box has been made as attractive as possible, the previous area(s) in the house should be cleaned thoroughly and then made unavailable with plastic covering, or booby traps such as sticky (two-sided) tape or a motion sensor alarm if necessary. Keep in mind that a cat's odour detection is probably up to 100,000 times more sensitive than a human's, and the cleaning is unlikely to eliminate the toilet-area smell to the degree that the cat cannot detect an odour.

Finally, for some problem cats, it may be necessary to temporarily confine the cat in a smaller space where there is a high probability it will use the litter box, such as a bathroom or utility room with a tile or vinyl floor. Once the cat is regularly using the litter box, it can then be gradually allowed access to the rest of the house. Because confinement can be aversive to cats, this option should be instituted as a last resort.

Experience with litter box use may also play a role when one is adopting a kitten or older cat from a source where the cat is already using a litter box. One should give some thought to helping the cat get started in litter box use in the new location by adopting the familiar litter box and some of the familiar litter along with the cat. If that is not possible, at least one should use the same litter material. The litter type can be changed gradually by mixing the old type with the new type.

## Urine marking (spraying)

Urine spraying on vertical surfaces, and occasionally on horizontal surfaces, is urine marking. Although often thought of as normal for intact toms, and possibly females in oestrus, this problem occurs in about 10% of castrated male cats and less than 5% of spayed female cats (Hart *et al*., 2006).

Urine marking is a reflection of normal territorial marking of cats living in nature, where males presumably repeatedly mark target objects which are most commonly trees. Urine marks are not particularly deposited on the borders of home ranges, but rather all over the ranges with the exception (normally) of the sleeping areas. From the urine marks alone, the sex and reproductive status (oestrus) and the degree of familiarity of the urine depositor – familiar or unfamiliar – can be determined by a cat investigating the urine marks (see Chapters 4 and 5). Cats at lower, more natural densities are territorial and the odour left on the tree is the resident cat's olfactory signature which can be read by other cats passing through. If a tree has not been marked for quite a while, the odour fades. In nature, this could mean to a cat passing through, looking for a territory, that the previously occupied territory is open. What this means is that the marking targets must be freshened up, lest the cat find himself having to unnecessarily defend the territory. Marking targets do not constitute a border, but involve just a few prominent trees or bushes within the territory.

Urine marking is activated in most males by testosterone at the time of puberty and maintained, in most males, by ongoing androgen secretion – take away the androgen by gonadectomy and the response is deactivated. However, for about 10% of males the response, once set into action at the time of puberty, is not sensitive to androgen withdrawal by castration. A point that is misunderstood by many cat authorities, including veterinarians who perform the operation, is that the age of the cat at time of castration – from long before puberty to well into adulthood – makes no difference with regard to the predisposition of the neutered male to urine mark (Hart & Cooper, 1984; Hart & Eckstein, 1997; Hart *et al*., 2006). It is perhaps counterintuitive that the experience a male has in urine marking prior to neutering has no predictive power as to whether the cat will continue to urine mark or not, or to take up the behaviour as an adult, if neutered before puberty.

Translating the above background to the urine marker in the home, the culprit has selected target areas to mark. These are typically vertical surfaces, such as walls or furniture. On occasion, selected targets may have particular olfactory characteristics, such as the owner's clothes, where the marking is on a horizontal surface. Stereo speakers and electrical appliances may be targets, possibly because they give off

volatiles from electrical insulation that evoke marking. As in nature, the target areas are hit repeatedly to keep the olfactory signature fresh.

The criteria involved in the diagnosis of urine marking, as opposed to inappropriate urination, are outlined in Table 14.1. The most important diagnostic criterion is deposition of urine on a vertical surface, a criterion often missed by cat owners and sometimes even by veterinarians (Bergman *et al*., 2002). In contrast to the occasional cause of inappropriate urination by urinary tract disease, no evidence suggests that lower urinary tract disease causes urine marking (Tynes *et al*., 2003). The most common precipitating factors for the onset of urine marking are: agonistic interactions with other cats, either in the same household or with an outside cat; the introduction of a new cat to the household; moving to a new home; making an outdoor cat an indoor cat; owners returning from a trip; a major change in household schedule; and onset of the cat breeding season (Pryor *et al*., 2001a).

The resolution of a urine-marking problem involves several approaches. If the problem cat is a gonadally intact male, neutering has about a 90% likelihood of stopping the behaviour, either rapidly or gradually over a month or two (Hart & Barrett, 1973).

Attention to litter box hygiene makes sense, as with inappropriate elimination. One study reveals that this may reduce the marking by about half in 70% of females and resolve the problem in about 30%. There seems to be no effect of this approach in males (Pryor *et al*., 2001a).

Because urine marking in nature requires that the cat renew the signature urine odour frequently, previously marked areas should be made unavailable or the cat deterred with the use of sticky upside-down carpet runner or other double-sided sticky tape. Aluminium foil may work in instances where a cat does not like walking on the foil.

Attention to the predisposing factors for urine marking, such as inter-cat aggressive encounters, should be addressed by separating living areas for the fighting cats that seem to evoke marking. If the trigger is the sight of a cat through the window, then blocking the window at critical times should be considered.

A different approach in the efforts to control urine marking is the development of a so-called feline pheromone (Feliway®) aerosol that has some similarities to cheek gland secretions of cats. When applied to prominent areas, the aerosol spray allegedly induces 'friendly' behaviour which in turn is claimed to reduce marking. Clinical trials suggest the effect in reducing urine marking ranges from modest to almost total resolution of the problem behaviour (Frank *et al*., 1999; Hunthausen, 2000; Mills & Mills, 2001; Ogata & Takeuchi, 2001).

While one or a combination of the above approaches may reduce or occasionally completely resolve the urine-marking problem, experience reveals that for inveterate urine-marking males, the use of an anti-anxiety, serotonin-boosting drug is usually required (Hart *et al*., 2006). Depending upon desires of the cat owner, behavioural approaches might be attempted and, if not successful, add the drug. Most cat owners seem to feel the situation is more urgent and wish to combine the behavioural approaches and drug treatment.

A series of anti-anxiety formulations have been employed over the years, including progestins, diazepam and buspirone, but the current medications are the selective

serotonergic reuptake inhibitors, fluoxetine and clomipramine (Pryor *et al*., 2001b; Hart *et al*., 2006). Results with fluoxetine reveal that achieving at least a 90% reduction in marking frequency may take 16 or even 32 weeks of treatment in some cats. Eventually almost all cats seem to respond (Hart *et al*., 2005).

The remaining clinical problem in the drug treatment is a recurrence of marking, to 50% or more of baseline, in most cats even after as long as 32 weeks of treatment (Hart *et al*., 2005). Some cats may have to be kept on treatment indefinitely, with periodic attempts to withdraw the drug along with health evaluations every 6 months or so. Both fluoxetine and clomipramine seem to involve few side effects with long-term treatment, but regular monitoring for liver function is recommended. Although not tested, it stands to reason that recurrence of marking after drug withdrawal would be less likely if the provoking factors causing the marking are controlled during drug withdrawal. Cats seem to respond to a second series of fluoxetine treatment as well as to the initial series, and thus clinicians may take a cat off treatment to test for recurrence with confidence that, if the marking recurs, it is likely to be controlled again. Also, cats do not seem to become refractory to the dose as initially used, even after several months of treatment (Hart *et al*., 2005).

## Aggressive behaviour

Although aggression is not uncommon among cats in a household, it is not nearly as common a complaint as problems with elimination. Cats do not usually respond to discipline in interactions with people or to the rituals reflecting a dominance–subordination relationship with other cats, which, in dogs, can maintain peace. In contrast to dogs, aggressive episodes towards other cats or people are much more likely to involve females (spayed) than males (neutered). Neutered males are the more affectionate, 'peace-loving' gender in this species (Chapter 11; Hart & Hart, 2013). Like other problem behaviour areas, differences in aggressive tendencies are also related to breed membership (Chapter 11; Hart & Hart, 2013).

Different authorities have classified feline aggression; the following classification is fairly typical and does offer some guidelines for diagnosis and treatment. While some types of aggression are directed just at other cats, namely territorial and inter-male, another type may be directed to both cats and people, namely, fear-related, and still other types just at people: play-related, redirected and petting-evoked. As will become evident, management by the caregiver is often the most successful treatment (Hart *et al*., 2006).

### Territorial aggression

This is a common type of aggression typically displayed to new cats introduced into the home, as the resident cat tries to drive away the intruder. The new cat, of course, may be aggressive in return. The cats may eventually adapt to each other or the aggression may continue indefinitely. Not only do cats show individual, social partner preferences,

and rejections (Kerby & Macdonald, 1988), their initial socialisation status to other cats during kitten-hood also plays a role in maintaining peace in the household (see Chapter 6). Sometimes territorial aggression may occur after one cat, resident in the household, has been absent for a time and returns; it may then be treated as a stranger. Territorial aggression may also be seen in a resident cat's responses to a neighbourhood cat that comes on its property. This is also a type of aggression that emerges among cats raised in the same house, even among littermates or mothers and offspring. In such instances the behaviour appears to be a manifestation of the behavioural process that underlies dispersion, seen in the wild ancestor of domestic cats. This type of aggression differs from fear-related aggression in that the cat does not avoid encounters.

The resolution of territorial aggression involves a gradual process when introducing cats to each other. This may be accomplished by first separating cats within a household, using separate feeding stations and litter boxes, but where they can still see and smell each other. Fights should be avoided because they may increase attacks by one cat while evoking some fearful behaviour of the other.

### Fear-related aggression

This behaviour may be displayed towards either other cats or humans, especially visitors to the house. It is recognised by the typical signs of defensive aggression: an arched back, or a crouched stance with flattened ears and dilated pupils. The latter posture should not be mistaken for a submissive posture because the cat if approached may very well attack. Generally the behaviour is displayed if the cat cannot hide from or avoid contact with human visitors. This type of aggression is usually seen when the fearful cat cannot escape. To the degree that the aggression keeps the fear-producing stimulus – other cats or people – away, it is reinforced.

Dealing with this problem can be as straightforward as avoiding the fear-producing situations. Resolution will usually involve some sort of gradual desensitisation to the fear-provoking stimuli until they are desensitised. While the use of an anti-anxiety drug, such as fluoxetine, may seem logical, no clinical trials have evaluated its feasibility. A potential confounding issue for fear-related aggression between cats is that an anxiolytic may increase aggression in a fearful cat that previously just avoided the other cat.

### Inter-male aggression

While this type of aggression could be called inter-cat aggression because female cats fight as well as males, this label specifically refers to the strong tendency of gonadally intact males to get into serious, injury-producing fights with other males away from the home. Classically, the male comes back from an outing with wounds, or even an abscess, from fighting with other males. This is a much more common occurrence in intact male cats than dogs, reflecting the absence of a predisposition of the cats to avoid a fight through ritualistic expressions of dominance or submission related to the encounter. Castration has about a 90% probability of eliminating this problem

in adult males, or in preventing the problem if the neutering was done before puberty (Hart & Barrett, 1973; Hart *et al*., 2006).

As mentioned above, some aggressive or aggression-like behaviours in cats typically just involve human family members. These are play-related aggression, redirected aggression and petting-evoked aggression, and are discussed below.

### Play-related aggression

This may be a problem when the stalking, pouncing, biting and scratching are directed toward a moving person. The behaviour may be a combination of the cat's active, aggressively playful personality, and a bit of play-deprivation when the owner has been gone for long periods of time. Hand-reared cats may be more predisposed to this type of behaviour, especially if the adopting caregiver encouraged play biting. This can especially be a major problem with young children or the elderly.

Not surprisingly, in dealing with this problem it is best just to avoid situations that provoke the behaviour. If necessary, using a toy on a string, play can be directed away from the person's legs. The cat can be regularly engaged in play sessions using appropriate toys, such as a fishing pole with a stuffed sock, for cats that have a strong drive for play. As another alternative, when attacked the cat should not be pushed away with the hands, which will just provoke more play, but instead try an aversive deterrent such as discretely using a water spray at the beginning of the attack. If using this approach, an acceptable outlet of playful behaviour should be arranged first.

### Redirected aggression

This term, derived from classical ethology, refers to a cat that has been highly aroused and is in an aggressive state – commonly from having seen another cat in an antagonistic context – and directing an aggressive attack towards a person that touches or closely approaches the aroused cat. The cat is otherwise affectionate and the owners may not be aware of what aroused the aggression and may interpret this as an unprovoked attack upon themselves. This problem is generally successfully dealt with by avoiding interacting with the cat when it is aggressively aroused. Wait until the cat is calmer, perhaps when it is eating or grooming.

### Petting-evoked aggression

This is an odd, but not uncommon, behaviour where a cat that is being held suddenly turns and digs in the claws or bites the person holding and petting it. Usually, but not always, there are warning signs such as restlessness, tail-twitching and ears furled back. In dealing with this problem, avoid the behaviour by not holding the cat for too long. In addition to being aware of the warning signs, the owner can learn how long a particular cat can be held before the behaviour is likely to occur. But remember: cat bites and scratches need to be thoroughly disinfected once they break the skin!

## Scratching furniture

This problem arises from cats scratching the 'wrong' object. In nature, a scratched tree trunk serves as a visible marker to other cats, and the secretions from the glands in feet wiped on the scratched area are a chemical marker, meaning in cat language 'the territory is occupied'. Recall that the wild ancestor is solitary and chases away all feline intruders sighted. However, the marking needs to be freshened up to convey the ongoing message that the territory is actively occupied. This is the same reason that urine marks need to be freshened up frequently. Chemical signals, whether from foot secretions or urine deposits on trees, quickly fade away.

Because territory marking is such a powerful predisposition, cats often choose a tree-like place to scratch in human homes, such as the corner of a couch. Once a place is chosen, cats tend to stay with it – territorial markers need to be renewed. The texture of the object influences whether it is used; the cat must be able to drag the claws down. Scratched objects, whether a tree or couch, also serve to remove an old outer claw when the replacement new claw underneath is ready.

Resolution of problem scratching is not to prevent it, but to direct the scratching to an acceptable target, which is usually a scratching post which should take the place of a tree trunk. The first step is to place the chosen scratching post with a proper, scratch-friendly covering in about the same prominent spot as the scratched furniture. One possibility is to fasten some upholstery from ruined furniture to the new post to encourage scratching there, because it has the appealing odour that needs to be renewed. Sometimes people ask if rubbing the cat's feet on the new post may get the point across. The answer is yes, but not because the scratching place has been demonstrated, but because rubbing some secretions from the paws encourages scratching on the post. After the post is being used regularly, gradually move it to the side of the room over a period of several days. Cats tend to stay with the same scratching object.

Then, after the cat has an appealing post to scratch, the scratched piece of furniture should be made unavailable by moving it aside or covering it with something like a heavy plastic – hopefully temporarily. The scratched furniture can be made aversive with a motion-sensor alarm or sticky tape. No scratching attempts at the prohibited areas should be allowed once the new appealing object is available. When adopting a kitten the new caregiver can ask to take the scratching post, if the kitten is using it. This gives the cat a previously marked object to use in the new home. As an aside, taking along the scratching post, which the kitten has been using, along with the litter box from the natal home can give the new home a jump start in feeling welcoming to the new kitten. While generally frowned upon, if not illegal, questions do arise as to the use of declawing as a last resort. Some cat books and magazine articles have claimed that declawing may lead to cystitis, asthma, skin disorders and weakening of forelimb muscles, as well as gangrene, shattered bones and infection from the surgery. Also, it is claimed that declawing adversely affects cat social relationships, climbing, fighting and that declawed cats are more likely to bite people and become a danger to people. Surveys, however, indicate that medical and behavioural problems are rare, provided that the surgery is performed correctly (Morgan & Houpt, 1989; Landsberg, 1990).

## Eating grass and plants

With the new emphasis on keeping cats indoors all the time, owners soon become aware of the propensity of some cats to munch on houseplants. Thus, this behaviour can be a serious problem for those who want to enjoy a home with many plants. Before addressing this issue as a problem behaviour, some comments about plant eating are in order.

Both cats and dogs are frequently observed to eat grass and other plant items that presumably have little nutritional value. The explanations have been that plants provide fibre or that the animal is feeling ill and eating grass induces them to vomit. New findings reveal that, contrary to popular opinion, 10% or fewer of cat and dog owners notice that their pets regularly show signs of illness prior to plant eating and only about 20% notice their pets regularly vomiting afterwards (Sueda *et al*., 2008; Hart, 2008, 2009). Type of diet is not related to plant eating, which does not support the dietary fibre idea. These findings all point to plant eating as being perfectly normal and wild felids and canids regularly eat grass which is seen in 5–10% of scats of wolves and cougars.

The perspective favoured by the authors is that grass eating mostly occurs in normal dogs and cats, and is not associated with illness or a dietary need, but reflects an innate predisposition, inherited from wild ancestors, the function of which is intestinal parasite purging. In nature, animals are always exposed to intestinal parasites, so canids and felids living in the wild have presumably evolved their own anthelmintic, or parasite-purging, treatment, basically the same as that well studied in chimpanzees (Huffman & Caton, 2001). An interesting possible secondary function, which may be more relevant on the domestic scene, is that grass and other plants that a cat ingests from time to time may help expel fur balls that develop from a cat's grooming. The grass stems and leaves may wrap around the fur balls and carry them through the intestinal tract much as is envisioned as happening with intestinal worms.

Given that the assumption that plant eating by cats is normal behaviour – more-or-less the same as grooming or purring is normal – then there is no problem behaviour. However, two aspects of plant eating fall into the category of potential problems. One is when the frequency of plant eating noticeably increases. In nature, if an intestinal parasite load happens to build up for some reason, there may be a feeling of intestinal discomfort. The cat then responds to the intestinal discomfort by increasing the level of plant eating, which should increase the purging effect on intestinal parasites. Now on the domestic scene, gastrointestinal discomfort is more likely to come from a type of bacterial disturbance or hair ball than parasite build-up – the cat cannot distinguish one possibility from the other, so the default is to act like a cat in nature, and try self-medicating with the readily available herbal medicine – grass. While not losing sight of the perspective that grass eating is the first, and only, type of herbal medicine attributed to a cat, we as concerned caregivers should use a persistent increase in plant eating as a good reason to seek modern medical attention and give the cat credit for being smart (Hart, 2008, 2009; Sueda *et al*., 2008).

The second problem can arise when cats are strictly indoors, and have some spontaneous drive to eat plants, at least occasionally. What plants the cats might eat

can be a cause for concern. If the home has one or more poisonous plants, which are actually quite common, these could be eaten, causing anywhere from mild to severe gastrointestinal disturbance, with vomiting, diarrhoea and/or anorexia (Hart, 2008, 2009). Lists of common poisonous plants are available online. One solution is to provide grass gardens for the cats. Even with no houseplants around, it is still a good idea to give a house cat a personal grass garden. After all, why not go along with nature and let the house cat exercise what comes as naturally as grooming, at least for some individuals.

## Conclusion

In Chapter 11 the authors presented the perspective that of all domestic animals, the cat has retained the basic nature of its wild ancestor. This includes an array of robust behavioural predispositions that resulted from natural selection in its native environment. These behaviours are expressed by cats living in our homes, and influence their toileting behaviour, territorial marking with urine, scratching household furniture, aggressive interactions with other cats and human family members, and eating plants in their environment. These behaviours can be serious problems for the human caregivers of the cats. Understanding the reasons for the problem behaviours, and the strategies for the resolution of the problems, as presented here, relies on reference to the functions of the various behaviours in nature and in the wild ancestors of the domestic cat.

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# VI

# The Future

# 15 Cat population management

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*The Domestic Cat: The Biology of its Behaviour* (3rd edition), ed. D.C. Turner and P. Bateson. Published by Cambridge University Press. 

## Introduction

The almost ubiquitous presence of domestic cats in human society is evidence that people value this species highly, both as companions and as biological control of pests. In some countries, including the UK, USA and China, they have out-competed other species in becoming the most common household pet (Bernstein, 2005). However, the presence of cats can also give rise to a range of problems to humans and other species and they may experience welfare problems themselves. As cats can survive and reproduce successfully outside of human care, or indeed with human care but without human intent, their populations and the problems these present may increase to a level deemed unacceptable to society and hence the motivation for 'cat population management'. The global number of domestic cats is a notoriously difficult figure to estimate; Jarvis (1990) suggested 400 million cats globally; however, an unpublished report to the World Society for the Protection of Animals (WSPA) in 2007 used published data on pet statistics and questionnaires of non-governmental organisations and veterinary surgeons to gather information from 194 countries, leading to an estimate of 272 million cats worldwide of which 58% were thought to be 'stray' or 'feral' (see the discussion that follows regarding these terms).

Feral cats are commonly perceived as *the* focus for population management. The term 'feral cat' is probably most appropriate to describe an unowned and unsocialised cat that is not suitable for placement in a home as a pet, as opposed to the biological term feral to describe a domestic animal 'gone wild' (Slater, 2005). Indeed, many of the problems described in the following section regarding disease, nuisance and predation are more closely related to unowned cats because they are less likely to be neutered, vaccinated or fed than owned cats. However, to consider feral cats as a separate population is to misunderstand the fluidity of the cat population. Many owners report that their cats left home and did not return and many apparently unowned cats are adopted into households; for example Chu *et al*. (2009) found that 34% of owners reported obtaining their cats as 'strays', while Schneider (1975) found that 25% of cats left their homes within one year. Cats Protection, a UK non-governmental organisation, provides cat sterilisation support in response to public requests. In 2011, 34% of these requests concerned stray cats, with the remainder identified as being pets and of those identified as pets, around 28% had been originally sourced as stray (this figure does not include those obtained from a formal rescue establishment or group; Cats Protection Neutering Team, pers. comm.). Similarly, to consider feral cats as the only population of concern is to ignore the potentially much larger population of semi-owned cats that live in colonies with one or more carer and owned cats that roam freely. Apart from in the USA and Australasia where indoor cats are more common, most owned cats are allowed to roam freely and hence distinguishing an apparently unowned cat from an owned roaming cat can be difficult. Due to the fluidity of the cat population and the narrowness of the term 'feral', in this chapter we will focus on 'roaming' cats as the target for population management. These roaming cats are not confined but may well be owned, completely unowned (including classic ferals and recently abandoned owned cats), or fall in-between these two states as semi-owned cats (also termed 'colony' cats).

## Problems of cat populations

Cats can present a public health risk by transmitting zoonotic diseases (a disease that is transmitted to humans from non-human animals). A major European project, CALLISTO (2012), is underway to assess current knowledge of the risk of zoonotic disease transmission from companion animals and make recommendations for mitigation. The rabies virus causes perhaps the most well-known and feared zoonotic disease; it can infect all mammals, including cats and humans, and is almost invariably fatal without post-exposure treatment. No cat-adapted rabies strains are known and the transmission chains (number of secondary infections resulting from a primary infection) resulting from rabid cats appear to be short; to date no evidence indicates that populations of cats can act independently as a reservoir for rabies. However, where rabies maintained by wildlife or dog populations is endemic, cats can be infected by rabid animals and hence can act as a vector of rabies to humans. Thankfully vaccines against rabies are very effective and this risk can be easily avoided through regular vaccination.

Another well-known zoonotic disease related to cats is toxoplasmosis, caused by an infection of the parasite *Toxoplasma gondii*. Toxoplasmosis can be mild or even undetected in people with normally functioning immune systems; however, the symptoms can be severe in high-risk groups with impaired immunity, including developing foetuses, infants and elderly people. Cats are the primary hosts for *T. gondii* and shed oocysts in their faeces; humans may accidently ingest oocysts after cleaning cat litter trays or with contaminated soil on unwashed fruit or vegetables or after gardening. However, most people are infected through eating undercooked meat containing tissue cysts. These transmission routes can be avoided by wearing gloves and careful washing of hands after gardening or cleaning litter trays, washing of fruit and vegetables and avoiding undercooked meat.

The impact of roaming unowned cats on the health and welfare of owned cats in regard to the transfer or transmission of parasites or disease may be another area of concern. However, for diseases such as feline immunodeficiency virus (FIV) and feline leukaemia virus (FeLV), research indicates these diseases are of a similarly low prevalence in both owned and unowned cat populations (Gibson *et al*., 2002; Lee *et al*., 2002; Luria *et al*., 2004). Where other infectious diseases are present (e.g. feline calicvirus (FCV), feline herpesvirus (FHV)) the risk of transmission to owned cats can be minimised by owners ensuring their cats are regularly vaccinated. Studies suggest that managed colonies, where sterilisation is combined with other health measures, pose a limited health risk to other cats (Slater, 2005).

The impact of cats on wildlife through predation is an issue that can become quite polarised when debating the need for cat population management. Cats are clearly adept predators. However, the impact of cats as compared to other predators or other threats such as habitat destruction may be overstated (see Chapter 5). In general, the impact of cats on wildlife should be assessed objectively at each location as opposed to making generalisations from one location to another. See Fitzgerald and Turner (2000) for a more detailed discussion of cat predation.

Nuisance behaviours may also be cited as a motivation for wanting to manage cat populations. Cat mating behaviours and fighting can be loud and disruptive for people living nearby. Similarly, cats foraging in bins can be noisy, but more likely it will be the trail of refuse that causes consternation. However, the welfare problem experienced by the cats themselves may be just as commonly mentioned; in a questionnaire study of the general public in Texas, cat welfare was stated as the most important problem after nuisance behaviours (Ramon *et al*., 2008). One study of a relatively small roaming cat population in Texas found adult feral cat survival to be 0.56 over the 14-month study period; mortality was due to traumatic events, the majority road traffic accidents but also dog attacks and by gunshot (Schmidt *et al*., 2007). Kittens tend to have a higher mortality: for example, just 25% survived to 6 months of age in populations of roaming cats studied in the USA; just under half of these deaths were known to be due to traumatic events, mostly attacks by dogs; however, the other half were suspected to be due to disease (Nutter *et al*., 2004). In countries where unowned cats are collected and sheltered for rehoming, different welfare concerns are related to confinement, especially for those cats that are used to roaming freely and have no prior experience of captivity or close contact with humans. The fate of these cats may also present a significant ethical challenge as many will be euthanised due to lack of available homes (see Chapter 10 for further discussion of feline welfare).

## Is management of cat populations obligatory?

Many wild animal populations will experience welfare issues of similar prevalence to those found in roaming cat populations, so some may question the obligation to intervene in their populations. Cats are usually defined as domestic animals; however, they appear similar to their wild ancestors and their ability to survive and reproduce outside the care of humans suggests they have maintained many of the behavioural and physiological capacities suited to the wild, or at least a new kind of 'humanised urban wild'. This may be because, unlike dogs and typical farm animal species, until recently, humans have had very little control over cat reproduction. Even now, purposeful cat breeding or sterilisation to prevent breeding is only common in some countries. As a result, cats may occupy differing status in national psyche and hence the legal obligation to cats may vary. For example, in the UK, the guidance for how cats should be cared for in order to comply with UK animal welfare legislation applies to all cats (DEFRA, 2009); however, in New Zealand the equivalent code only applies to 'companion cats' (MAF, 2007), while feral cats are covered under the Biosecurity Act. Unfortunately, in many countries, cats (and often all other animals) do not benefit from any legal protection of their welfare at all and, as a result, can suffer unrestrained cruelty in the name of population control.

The decision of whether to engage in population management may therefore be influenced by national or local public opinion of cats and the level of concern over their welfare as much as any objective measure of the problems caused by their populations. However, it is important to state that regardless of the perceived status

of cats in society, as sentient beings they have the capacity to suffer and any attempt to manage their populations must be done humanely.

In the rest of this chapter we will discuss the preparation and operation of actual cat population management. An initial stage of assessment allows for thoughtful preparation and selection of population management options. Despite significant financial investment in cat population management, research on this subject is still relatively limited and hence we will be referring to peer-reviewed published literature, unpublished data and reports from current programmes to illustrate real-life application of cat population management.

## Assessing and monitoring cat populations

A core principle of managing any population is to start with a clear understanding of the problems presented by the population and the root cause of these problems. For example, if the problem is the number of roaming cats brought into shelters that are then euthanised for want of a good home, the key question for the assessment phase is where do these particular roaming cats come from? What is the *source* of these cats? Are they born as kittens of already unowned roaming cats, are they kittens of owned cats that are later dumped, or owned adult cats that are lost or abandoned? And why are they neither adopted from the shelter nor reclaimed by their owners if they turn out to be roaming owned cats? Taking time to study the population and answer these questions will help the population management programme be more efficient at addressing the key problems by focusing on the right subpopulation of cats.

It is quite possible that answering these questions confidently cannot be achieved completely at the assessment phase. However, it is important that some of the methods used for assessment are repeated as the programme progresses in order to provide an evaluation of its success. Thoughtful evaluation and subsequent refinement of the programme will lead to a greater understanding of these important questions about root cause and hence the opportunity to resolve the problems presented by the cat population more efficiently.

The methods available for assessment and continued monitoring and evaluation will fall roughly into two groups: those that aim to gather information and perspectives from the people involved and those that focus on the cat population itself. Cat owners and people who feed cats regularly are common target groups for assessment; household questionnaires or focus groups (in-depth interviews of a small group of people carefully selected to represent the target group as best as possible) are just two of the available tools to access these groups. Non-government organisations that shelter and rehome cats and the government organisations responsible for managing animal populations and zoonotic diseases are two other important target groups, and these may be best approached through interviews with key people within these organisations. When looking at the cat population itself, useful statistics may well be available from non-government and government organisations about cat populations, including the number and type of cats relinquished to shelters and the proportion of these that cannot be

rehomed, and the number and type of complaints received about cat populations. These statistics may also be detailed enough to highlight particular geographical areas that are problematic. The roaming cat population itself can also be observed directly to provide an assessment of population size and animal welfare. Further details on methods for assessing cat population size, and monitoring its change over time, can be found in 'Humane cat population management guidance' by the ICAM Coalition (2011).

It is clear from the number of potential target groups discussed as relevant for the assessment that working on cat population management is not akin to working in a vacuum. Many stakeholders have opinions on what should happen to cats. Some of them may already be actively trying to manage the cat population, either because they hold a legal responsibility for this role or out of an interest in cat welfare or reducing the impact of their population on other animals. Hence it is wise, both for the assessment phase and ongoing management and evaluation, that a multi-stakeholder committee is developed to avoid duplication of effort and maximum support for the programme.

## Population management

Our definition of the term 'cat population management programme' is a comprehensive or 'holistic' approach to improving the welfare of roaming cats and reducing the problems presented by their populations in the most appropriate way for a particular situation. Such a programme of work is comprised of a variety of tools or elements, but the level to which each element is utilised will differ between locations. No single approach will suit all situations. Assessment, as described in the previous section, will provide a picture of the local situation and an indication of what combination of elements is likely to be the most successful; it appears the greater the variety of elements and ingenuity of matching the approach to the locality, the more successful the programme tends to be.

The information on root causes provided through the prior assessment will also lead to development of the aims of the population management programme. For example, where the semi-owned cat population is found to be successfully raising kittens to adulthood, and hence a significant source of the next generation of roaming cats, a valid aim could be to reach and maintain a target proportion of sterilised semi-owned cats (the term 'sterilised' is used here to mean preventing reproduction; 'spay' or 'neuter' are alternative commonly used terms). Where unwanted kittens of owned cats are found to be a significant source of roaming cats, a valid aim could focus on owners and improving their responsible cat-owning behaviour, specifically by increasing the sterilisation of owned cats and reducing abandonment; this may be further refined by targeting a specific group for sterilisation such as young female cats if it is found that many owned cats are only sterilised after their first 'surprise' litter. Concurrently, improving veterinary knowledge and practice to encourage early sterilisation and thus make more sterilisation pre-emptive will also help owners to achieve these aims. Achievement of these aims would lead to the desired impacts, such as reducing the size of the roaming cat population, improving roaming cat welfare and reducing the number of nuisance complaints.

## Elements of a management programme

### Reproduction control

Both surgical and non-surgical methods for reproduction control are available (see also Chapter 10). Currently, non-surgical treatments (contraceptive or sterilisation) are predominantly aimed at the owned cat population as the level of monitoring and supervision required is, at present, incompatible with a large unowned cat population. As the methods and products available for non-surgical reproduction control continue to be developed and tested, their application for wider-scale use in general population control will become more appropriate (and indeed preferable due to the potential considerable reduction of costs and required infrastructure), but at the present time, surgical techniques are still the accepted method.

Surgical sterilisation (castration of males and spaying of females) is used throughout the world as a permanent measure in controlling reproduction. It requires trained veterinarians and ancillary staff as well as considerable infrastructure and resources which can make the costs involved prohibitive (direct costs to owners getting their cats sterilised or investment costs in undertaking a population management programme). If a veterinary infrastructure is already in place then it should be encouraged to offer a sterilisation service. Working in partnership with local authorities or an animal welfare organisation, vets' involvement can be instrumental in the long-term success of a population management programme.

In Rome, Italy, national legislation which endorsed the sterilisation of roaming cats saw the local Veterinary Public Services collaborating with the associations of cat carers to undertake a successful cat population management programme (Natoli *et al*., 2006). The veterinary profession also plays a key role in encouraging and promoting responsible ownership by making affordable sterilisation (as well as vaccination and parasite control) available, which helps address one of the root causes of the roaming cat population. In addition, it can be influential in dispelling misconceptions and commonly held beliefs such as allowing cats to have one litter before they are sterilised. In Barcelona, Spain, the city council's Department of Animal Welfare provides a sterilisation clinic for feral and stray cats, and fiscal grants are provided to animal welfare organisations that deliver the work in their city districts (Plataforma Gatera, pers. comm.).

In roaming cat populations, sterilisation programmes are generally delivered by the method of TNR (trap–neuter–return), sometimes also referred to as CNR (capture–neuter–release). Roaming cats are humanely trapped, surgically sterilised and returned back to the same environment from where they were collected. TNR programmes exist throughout the world but the degree to which they are successful will rely on how thoroughly and efficiently the method is applied to a cat population. Well-intentioned attempts at TNR are often thwarted because the number of cats trapped, neutered and returned is very small in proportion to the population. Sterilising 1 or 2 cats each month from a colony of 40 or 50 is unlikely to see any impact in the overall numbers as reproduction will outpace sterilisation. This shortfall may be for a number of reasons: financial, veterinary capacity or poor trapping technique.

**Table 15.1** Population parameter values for two example populations of cats. The estimates of juvenile annual survival listed by the authors have been converted to the probability of survival from birth to recruitment, $S_j$ (animals are defined as *recruited* when they have joined the breeding population and hence able to have their first offspring). Budke and Slater (2009) give a midpoint value of 2.52 kittens born per year to a fully recruited female, using their reported litter size of 3.6 and 50 : 50 sex ratio the number of female kittens per litter, $K$, is calculated as 1.80 per litter and number of litters per year, $L$, as 1.40

| Example number | 1 | 2 |
|---|---|---|
| Data source | Nutter *et al*. (2004) and Schmidt *et al*. (2007) | Budke & Slater (2009) |
| Age at first reproduction, $r$ | 0.875 | 0.70 |
| Adult annual survival, $S$ | 0.56 | 0.70 |
| Survival to recruitment, $S_j$ | 0.20 | 0.51 |
| Litters per year, $L$ | 1.40 | 1.40 |
| Litter size, females per litter, $K$ | 1.75 | 1.80 |

The rate at which a cat population can grow in size and hence the proportion of that population that needs to be sterilised to achieve stability or reduction depends on how well they survive and reproduce. Survival and reproductive success can vary significantly; to illustrate, Table 15.1 presents two examples taken from a combination of the results reported by Nutter *et al*. (2004) and Schmidt *et al*. (2007), who describe observing similar populations of 'feral' cats in the USA, and (by selecting the midpoints of their 'low' to 'high' ranges) from Budke and Slater (2009), who report parameters from cat populations studied in a range of locations. Using such data, one can estimate the population growth rate and the percentages of females that would need to be sterilised to stabilise the population; the formulae used to do this are available at www.cambridge.org/9781107025028.

The population of cats illustrated by example 1 in Table 15.1 has an estimated annual growth rate of 1.01 and example 2 has a rate of 2.11, more than double that of the first population. To stabilise the population in example 1 would require just 1% of unsterilised females to be sterilised per interval (time between successive breeding seasons, usually shorter than one year in cats), leading to 3% of the female population being sterile at a stable population size. The corresponding values for example 2 are 41% and 76%. Clearly even quite a low rate of sterilisation would reduce the size of a population with example 1 parameter values, but whether that reduction would be sustained depends on whether the low rates of juvenile and adult survival are inherent to that location or the consequence of density dependence, with this population being close to its carrying capacity. The traumatic events identified by Nutter *et al*. (2004) as sources of mortality are not density-dependent although some of the unidentified sources may be; if some cases of mortality are density-dependent the survival rates may increase as the population size decreases, requiring a greater sterilisation rate for further reduction in population size. In example 2, survival rates are much higher and may be typical of a population well below carrying capacity. As Budke and Slater point out, the effort required to stabilise a large population of that type would be

considerable. Even if the population is reduced to a low density, the same trapping effort has to be maintained because the same percentage still needs to be sterilised each year. Ideally, when planning a management programme, estimates of the effort required based on parameter values taken from a population of well-resourced cats living in or near the location where management is planned will give the most conservative or 'worst case' scenario of what will need to be done.

It is also worth considering that a rapidly growing population will become very much larger before being stabilised by a programme of sterilisation. Although such a 'transient response' to an intervention can be easily simulated using a matrix model of population growth, it is difficult to predict accurately because the degree to which density-dependence affects survival and reproduction is unknown. The pragmatic solution is to use a sterilisation rate much greater than that estimated to stabilise the population and monitor the population to determine whether this rate is sufficient to prevent excessive population growth. Over the long term the rate can then be adjusted to converge to the value estimated to stabilise the population at the desired level.

## Examples of TNR programmes

In Porto, Portugal, a pilot TNR campaign undertaken by the local animal welfare organisation, Animais de Rua, saw a colony of cats drop from 45 in 2005 to 10 by 2009 (Animais de Rua, 2009). Dependent on the proportion of cats sterilised and the mortality rate of cats, it may take a number of years before a noticeable reduction in the population occurs due to attrition without replacement with new kittens. However, it is also possible that other cats could migrate into the colony location or owners, seeing that a colony of cats is being well managed, will abandon their animals there. In Rome, Italy, a survey of 103 cat colonies was undertaken to assess the effects of a 9-year sterilisation programme conducted by the Veterinary Public Services. While it showed a general decrease in cat numbers, the percentage of new cats (those that were either abandoned or spontaneously arrived) accounted for 21% of the population (Natoli *et al*., 2006). This is an example of where ongoing monitoring and evaluation showed that using just one element in isolation may not be the most efficient option; additional elements may include education of local cat owners with the aim of improving their responsible ownership behaviour and concurrently improving the provision of accessible sterilisation services for owned cats.

Another example of the importance of combining TNR with other elements to ensure the greatest success was shown by a programme based on a university campus in Florida, USA. This programme used an adoption scheme for kittens and tame adults combined with TNR of adult cats not suitable for adoption, leading to a 66% decrease in the cat population over 11 years (Levy *et al*., 2003).

Being able to identify sterilised cats from non-sterilised cats is vital in TNR programmes. Time, resources and money can easily be wasted by repeatedly trapping and anaesthetising the same cats over and over again, not to mention the unnecessary stress and potential harm this can cause to the cat. While several identification methods are

in current usage, ear tipping is the predominantly favoured practice. This is where the tip of a cat's ear is removed under general anaesthetic at the same time as it is being sterilised. The amount removed will vary between 3 and 10 mm depending on the size of the cat; what is essential is that the method used is clearly artificial and can be viewed from a distance. It provides a highly visible indicator (even from a distance) of the cat's status as having been sterilised. It both reduces repeated trapping and acts as a symbol to the community that the cat is part of a well-managed colony. Care must be taken to ensure that owned cats are not sterilised and ear-tipped as part of a TNR programme without the owner's consent. Efforts must be made to notify the local community that a sterilisation programme is underway and any cat that is trapped should be checked for signs of ownership (collar, tattooing, microchipping).

If time or resources are limited, prioritising the cats that are to be sterilised is essential. Targeting females should be the priority as fecund females will be the limiting factor to population growth as opposed to intact males. The use of manual traps will enable trapping precision. If automatic traps are used, it must be accepted that a high proportion of the catch will be males; in situations where resources are limited this will lead to a choice between releasing male cats unsterilised (if the sex can be determined) or accepting that females will not be targeted for sterilisation and their sterilisation proportion is likely to equal that of males.

Additional animal welfare benefits arise in reducing the levels of reproduction. For example, mortality rates for kittens in roaming cat populations are as high as 75% (Nutter *et al*., 2004) so reproduction control removes the potential for this significant animal suffering. Adult cats may also benefit; in Alachua County, Florida, body condition scoring of the subject cat colony one year after a sterilisation programme showed a marked improvement in their general condition (Scott *et al*., 2002).

A further welfare advantage for roaming cat populations is the opportunity a TNR programme offers for disease monitoring, control or prevention. In areas where rabies is present, for example, a vaccination component can be incorporated into the programme. Additionally, vaccinating against other diseases or administering anti-parasitic treatments can have a significant impact on the welfare of the roaming cats (Fischer *et al*., 2007) and could lower the risk of disease transmission to the owned cat population.

A TNR programme also provides infrastructure and opportunity to test for disease prevalence in the roaming cat population and remove or treat sick animals. An example of this is where it has been used to test for the prevalence of FIV and FeLV; however, controversy exists over the merits of this. Cats that have been vaccinated against FIV can show a false-positive for the disease if subsequently tested and kittens can show a false-positive as a result of passively acquired maternal antibodies; therefore, repeat confirmative testing is recommended, which may not be practical in roaming cat populations. The American Association of Feline Practitioners (2009) has produced guidelines about testing efficacy. Additionally, several studies (as noted previously) have indicated that FIV and FeLV are of low prevalence in the roaming cat population and, therefore, not least for reasons of economy, cats showing symptoms of these diseases could be managed in the same manner as cats displaying any other form of disease or injury, without the need for blanket testing.

Several available resources cover in great detail the practical aspects of setting up and running a TNR programme (Neighborhood Cats, 2004; Feline Advisory Bureau, 2006; Alley Cat Allies, 2010). They provide in-depth information about the intricacies of TNR. This includes types of traps and methods of trapping (automatic traps activated by cats stepping on a footplate or manual traps where the trap is triggered remotely); appropriate surgical techniques (flank or midline spaying); insights into cat behaviour and how they react to being trapped and released and how any potential trauma can be minimised or mitigated; and the appropriate long-term measures for managing a colony by involving the community as a whole and, for example, setting up cat cafés (purpose-built feeding sites that attract cats to specific areas and reduce the instances of conflict between cats and people).

## Engagement of cat carers

In many locations, a population of cats is 'looked after' by one or more carers; members of the public who have taken it upon themselves to provide food for the cats in their community. As a result, the cats are often provided with an abundance of food. It is unlikely that carers could be prevented from providing food for the cats; even in areas where this is prohibited by law, compassionate carers will disregard such legislation. However, if involved in the management of the population, carers can use this provision of resources as an opportunity to monitor the welfare and sterilisation status of the cats and act when needed, hence incorporating them effectively into the programme. When a programme of removal was underway at the University of Florida campus, carers openly disregarded policies not to feed the cats and interfered with attempts to trap and remove them. When this was replaced with humane interventions, it had the full support of the carers and many assisted in the management of the programme (Levy *et al*., 2003). On the island of Isabela in the Galapagos Archipelago, the non-governmental organisation Animal Balance found, on their first attempt to conduct TNR, no cats on the streets; the 'feral' cats had all been encouraged and confined indoors by their carers for fear of what would happen to them following a history of poisoning cats on the island.

A TNR programme needs to be monitored and sustained in order to maintain a reduced population size or to achieve extinction, as well as to ensure the welfare of the cats. Local carers can be key to achieving this; it should be their responsibility to monitor the cats once they have been sterilised and returned and to provide at least a minimum level of care for the colony. As well as providing food and in some cases shelter, this should also include seeking veterinary attention in cases of injury or disease and ensuring that any new cats (those that have arrived subsequent to the initial TNR intervention via either migration or abandonment) are also sterilised. While their involvement is crucial, a carer should not be saddled with this responsibility alone. It is essential that support is also provided by the local authorities, the wider local community, the veterinary community and local animal welfare organisations.

## Education

Increasing public understanding about the purposes of a management programme is essential, but alone will not help address the root causes of a cat population problem unless where the cats are coming from is sustainably addressed. Whether through the active or passive abandonment of owned cats or allowing unsterilised owned cats to roam, the source of the roaming cat population will always stem from the complacency or ignorance of the human population. Developing the concept of owner responsibility and actual responsible behaviour is a key aim and fundamental to the success of a management programme. As cat owners, people need to understand the role their cat can play in the roaming population and their responsibility both towards the cat itself and the impact it can have. Owners have a duty of care to ensure the health and welfare of their cats; fulfilling that duty is likely to require ensuring their cats (both sexes) are sterilised and vaccinated, but, additionally, understanding that the abandonment of cats, either actively or passively, is unacceptable. Vets, local authorities and animal shelters (among others) have a vital role to play in providing the support needed to promote and engender this responsibility.

Effective education in responsible cat ownership may also lead to an increase in the number of cats being adopted from shelters as well as increased support for shelters and other welfare programmes (see Chapter 10). Additionally, if the infrastructure is there, it may encourage the registration and identification of cats. For the wider community (which also includes cat owners and carers) awareness of roaming cat issues should be raised and a general understanding of the role a population management programme plays. They need to be aware of how and why such a programme is beneficial and that the health and nuisance concerns they associate with roaming cats can only be sustainably addressed with buy-in from the community. Veterinary professionals clearly have a very important part to play in disseminating information and raising awareness as they tend to be the most trusted source of information for animal owners. Opportunities for development within the profession are also available, such as improving sterilisation techniques, training veterinary students in the rationale behind population management programmes and understanding the veterinary profession's role in promoting responsible ownership. Public health departments and local authorities need to understand the long-term benefits of a sustainable population management programme and the role they play in enabling its success through accurate, unbiased public information, appropriate legislation and consistent enforcement.

Outlets for raising awareness can include incorporating concepts of animal welfare into school lesson plans; making information available to target audiences via traditional routes such as leaflets and flyers or by taking advantage of more modern mediums such as social media; engaging support from print, broadcast and internet media outlets and developing community-based awareness campaigns. While education is a fundamental factor in ensuring the long-term success of a population management programme, its impact can take some time to become apparent. To ensure that appropriate messaging and information is being used and that it is getting the desired results, methods of monitoring and evaluating public awareness, understanding, acceptance and compliance are essential.

## Legislation

Appropriate legislation is another essential element for the sustainability of a cat population management programme, but has far broader implications as well.

Legislation can be used as an instrument for good or as an excuse to hide behind. Legislation that is too prescriptive is unlikely to have the foresight to allow for advances in intervention tools and can make the implementation of good animal welfare practices difficult; however, legislation that lacks clarity can leave the door open for any number of ill-considered interpretations. A balance needs to be struck between allowing best practice in animal welfare to evolve and establishing clear boundaries dictating what is and is not acceptable in the broadest terms. For legislation to be at its most effective and sustainable it should deliver a framework that gives authorities the power to act when required; is deemed appropriate and reasonable by the community; and ensures that the responsibility to improve animal welfare is ubiquitous. In legislatures where a system of primary and secondary legislation is used, it is always pertinent to look towards secondary legislation where possible as this is often easier to adapt and change and requires less parliamentary time.

While good animal welfare law encompasses a broad range of issues, in regard to roaming cat populations some key areas need to be considered. Robust animal cruelty laws are needed to punish both individual acts of abuse and cruel animal control practices such as poisoning or inhumane trapping. It is not uncommon for roaming cats to be the victims of such abuse and cruelty. Legislation needs to promote the concept of responsible ownership and make owners accountable for their cats under a 'duty of care'. However, the term 'ownership' is hard to define from a legal standpoint, especially when we consider roaming cats and their community carers. Legislation needs to acknowledge the difference between owned pet cats and semi-owned roaming cats but should recognise an obligation for both to be protected and responsibility for their welfare should reside with the most appropriate person. It is also important that legislation openly allows humane cat population management programmes to be implemented. In some instances overly prescriptive laws have seen TNR deemed illegal because no differentiation has been made between inhumane trapping and removal and trapping for TNR purposes.

It is worth noting, however, that any legislation, however good, will be ineffective if it is not properly enforced. The infrastructure and resources need to be available to ensure that violations of laws can be properly addressed.

## Registration and identification

The registration of owned cats is rarely a legal requirement. It should, however, be encouraged as it establishes a clear connection between cat and owner and engenders a sense of responsibility. Registration, whether formally or informally administered, should reward and not discourage responsible ownership. Heavy fines and penalties for failure to register an animal, if suddenly imposed, can lead to a surge in abandonment. Conversely, differential registration fees that reward vaccination and sterilisation with lower-cost or free registration can encourage responsible ownership behaviour.

Registration and identification when used together are a useful tool for the enforcement of animal welfare legislation, for example, in cases of intentional abandonment. Additionally, it allows owners and cats to be reunited more easily if their cats roam or are brought into shelters.

One of the primary difficulties in being able to identify individual cats (for whatever purpose) is that it is often hard to distinguish one from another. One black cat can look very much like another black cat, especially from a distance. As noted previously, ear tipping is the preferred current method used for identifying sterilised unowned and semi-owned roaming cats. Other identification methods for owned cats (whether sterilised or not) are microchipping, tattooing or simply attaching a collar and tag carrying the owner's contact details.

In November 2011, the Government of Western Australia introduced the 'Cat Act'. The purpose of this Bill was to provide for the control and management of cats and to promote and encourage responsible ownership. The Act (which has a two-year lead-in period to allow for stakeholder compliance) requires the compulsory identification of cats through microchipping, compulsory registration and compulsory sterilisation. While the government understood that such legislation would not resolve all problems associated with cats, it would provide a mechanism to encourage responsible ownership, reduce the number of unwanted cats being bred, allow for cats found on public or private property to be seized and then reunited with their owners.

## Shelters for rehoming

Shelters are discussed in Chapter 10. The role of a shelter is very much dependent on the local situation, the public's attitude towards cats and whether rehoming is possible. The mere presence of a shelter can have consequences that, in themselves, affect the dynamics of a cat population. Shelters can inadvertently encourage 'responsible abandonment' where owners who no longer want their cats presume that a shelter is simply there to take on the burden. A misguided assumption is often that shelters are somehow a panacea for cat population problems despite the fact that shelters rarely address the root cause of the problem.

Shelters can clearly have a role in education, raising awareness about roaming cat population issues and promoting responsible ownership, but what is often seen as their primary role – that of taking in unwanted or abandoned cats and finding them new homes – may not be consistent with local attitudes. Without a culture of animal adoption, any cats taken in by a shelter are likely to remain there for some time, if not indefinitely (see Chapter 10). This can lead to severe overcrowding and poor welfare as shelters are compelled to keep accepting more animals. If, however, the adoption of animals is an accepted practice then shelters can indeed play a role in rehoming kittens and sociable adults from roaming cat colonies as part of a population management programme. At the University of Florida, their population management programme incorporated the rehoming of cats and kittens as well as TNR. In total, 47% of the cats on campus were successfully rehomed (Levy *et al*., 2003).

### Euthanasia

The concept of cat population management as described in this section has been approached from the perspective of promoting good animal welfare and ensuring any management programme is implemented in a humane and sustainable manner. The decision to euthanise an animal, made on an individual basis and upon the best interest of that animal, is an extremely important part of any programme that values animal welfare. Clear criteria for euthanasia should be established in advance of any population management programme. For example, if a cat is suffering from an injury or illness which would prevent it from either being returned to its colony or rehomed, or when a threat to the cat's welfare is significant if it remains at its current location (a likelihood of poisoning or the location is to be demolished) and it is not possible for the cat to be relocated or rehomed. As well as criteria for when euthanasia should be considered it is also essential to have strict euthanasia protocols. Establishing, for example, who is responsible for the decision to euthanise, who will carry out the procedure and which method of euthanasia will be used.

However, the term 'euthanasia' has sometimes been used euphemistically when culling, the killing of a targeted population of animals, would have been a more accurate description. Historically, culling or physically removing cats to another location may have been attempted but, with the exception of certain specific island locations where this has led to the complete elimination of a population, it is unlikely to be successful. External factors such as migration, breeding and abandonment will ensure that these methods only provide a temporary reduction in the cat population. Even in locations where it has been successful, the idea of killing cats is often met with resistance from the general public. While the cats may be seen as a nuisance, the suggestion of killing them is not a popular proposal and is generally considered morally and ethically unjustifiable. On Marion Island, in the Southern Indian Ocean, cats (originally introduced in 1949 to control the mouse population) were detrimentally affecting the bird population. In 1977 (after four years of assessment) a multi-phased eradication programme was embarked upon. It took 15 years to completely eradicate cats from the island (from an estimated 1975 population of $>$ 2000 cats). Several factors, peculiar to Marion Island, led to the success of the eradication programme and therefore, if replicated elsewhere, would not guarantee success (see also Chapter 5). However, even on Marion Island it is clear that intensive and prolonged efforts were required eventually to eradicate the cats (Bester *et al.*, 2002).

## Conclusion

Managing a population of cats may be needed to reduce the problems these present to society or to improve the welfare of the cats themselves. The methods used must always respect the sentience of cats and hence be humane in their approach. It should be assumed that a range of elements will be needed to create an effective programme and selecting the right elements will require thoughtful prior assessment of the

characteristics and dynamics of the local cat population. Subsequently, efforts should be made to monitor the programme and refine its approach when needed. In the long term it will be the behaviour of local people, and in particular cat owners, that will dictate the success of any programme and whether beneficial impacts are sustained, hence the use of education and legislation to encourage appropriate human behaviours alongside cat-focused interventions such as sterilisation, vaccination, parasite control and rehoming.

# 16 Postscript: questions and some answers

Patrick Bateson and Dennis C. Turner

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## Introduction

When a cat behaves socially towards a human, the person has been treated as though he or she were a cat, although very possibly a particular *type* of cat. Anybody who loves cats is irresistibly drawn to treat them as though they had some of the characteristics of humans. Cat owners project themselves into the heads of cats and, in so doing, empathise with them. Whether or not they are right to do so raises a big and largely unanswered question. In any event, owners will have seen their cats behave in ways that are often puzzling and enigmatic. Why are they sometimes so friendly and at other times so distant? Those who study the behaviour of cats scientifically are often asked to provide the *real* answers to such questions. Unfortunately, many aspects of cat behaviour that most interest the lay public have not been the subject of extensive investigation. In part this is because the implied question is: 'Why does the animal *need* to behave in this way?' This is a question about the current utility to the animal of behaving in a particular fashion and is not an easy one to answer. The question also raises questions about the evolution of the domestic cat.

To understand the biological value to the animal of behaving in a particular fashion, scientists ask how the behaviour of a cat, freely living in a natural environment, helps it to survive and breed now. To understand the evolution of the behaviour, they must speculate about the natural environment of the modern cats' wild ancestors. If some patterns of behaviour have worked to the individual's advantage better than others in the past and they were inherited, they would eventually tend to be shared by most members of the cat population. The presumption is that by the process of Darwinian evolution, cats behave in a way that is well-adapted to the type of social and physical environment in which their ancestors lived.

Understandably, much of what is commonly known about cats is based on what people see them do in their own homes. Furthermore, when scientific studies are carried out, such work is usually done in the artificial environment of a laboratory. Studies of free-living cats in natural conditions are still relatively few in number. This means that when asked, say, why cats rub against us, in all honesty scientists usually have to reply that they don't really know. However, some speculative answers to functional and evolutionary questions will be given here, as most non-scientists like to be offered an informed guess and the scientists may want to be guided to the new areas of research.

## What is the environment to which cats are adapted?

What *is* the natural world of a cat? Have some populations of cats been in contact with humans long enough for the artificially created environment of humans to have become the one to which cats are now best adapted? Has the cat itself been subject to artificial selection by humans so that characteristics have been picked out that would have never been maintained under harsh, competitive conditions. Some of the characters which humans have selected would surely be disastrous for a cat in an unsupported environment. Take, for example, the long coat of the Persian breeds, the virtually non-existent

coat of the Rex breeds or the limp response of the Ragdoll when handled. Cats that maintain kittenish behaviour are especially attractive to people. As a consequence, some of the things that cats do as adults, such as kneading and mouthing soft tissues as if they were suckling like a kitten, may also have been the unwitting consequence of artificial selection for other aspects of the behaviour of young cats.

How domesticated is the cat? The best answer would come from comparing the domestic cat with what is thought to be its wild ancestor, the African wild cat (*Felis silvestris libyca*). Unfortunately, little is as yet known about the behaviour of the African wild cat under either free-living or captive conditions. Domestic cats resemble other domesticated mammals in that they probably produce more variable offspring than non-domesticated forms, other things being equal. Studies of the frequency with which chromosomes cross over suggest that domestic cats (like dogs, sheep and goats) have higher rates than would be expected for a wild-living animal which reaches sexual maturity at the same age (Burt & Bell, 1987). The genomic changes involved in domestication are increasingly well-understood in both animals and plants (e.g. Glémin & Bataillon, 2009). The evidence suggests that the cats commonly found in homes and laboratories have probably been under intense artificial selection for producing novelties among their offspring or have been released from the pressure to keep variability in check. However, many feral cats live under conditions that are quite as harsh and as competitive as any endured by non-domesticated species. In the case of the feral cat, then, products of artificial selection are likely to be stripped away very quickly. Furthermore, many other members of the cat family behave in ways that are almost identical to the domestic cat. Biologists recognise that some useless characters are maintained in the repertoire of an animal because they are by-products linked to the expression of other beneficial traits, because they do no harm, or because insufficient time has elapsed for them to have been purged after a change in the environment to which they had been adapted. The line taken here is that if behaviour patterns are found in breeding populations of feral cats and better still in other members of the cat family, scientists are probably *not* wasting their time in supposing that the behaviour patterns represent adaptations to a natural environment.

One distinctive feature of the domestic cat is the raising of the tail to a vertical position. It is given in social situations and is prominent when cats respond in a friendly way to humans (see Chapter 4). This pattern of behaviour has not been recorded in African wild cats uncontaminated by breeding with domestic cats. A great many photographs of the African wild cat have been taken and can be seen on Google Image. None of them shows a cat with a vertical tail. We offer one conjecture for why the domestic cat should differ from its wild ancestor. In Ancient Egypt cats were reared in enormous number so that they could be offered to celebrants at temples with their necks broken. The dead cats were put into vast graves which were so extensive that they were mined for fertiliser in the nineteenth century. If the Ancient Egyptians had cat farms in which the animals were kept in dense groups, the tail-up signal may have evolved rapidly to inhibit the aggression that would have been commonplace in such colonies. Unfortunately, ways of testing this idea are not obvious. It might be disproved,

however, if further studies of the African wild cat, either in the wild or in hand-reared animals, showed that the tail-up signal does occur in the domestic cat's wild ancestor.

## Why do cats specialise in taking particular prey?

Catching live prey can be risky. A bite from a rodent could become infected. A peck in the eye by a bird could lead to the loss of sight in that eye. It is not so surprising, therefore, that cats become specialists in hunting for particular types of prey. That much is clear to many pet owners and from some laboratory studies (see Chapter 2). However, a host of questions remain to be answered. Is it the case that a cat specialising on birds will turn its attention to voles if there should be a vole plague? Will an individual employ different hunting strategies such as roaming and stalking as well as sitting and waiting? If so, under what conditions do they change from one to the other? At present little is known about the conditions in which a cat will switch the mode of hunting which it normally uses. The change ought to be easy for such clever animals, but perhaps the change in habits is more difficult and costly in time than might be supposed.

As with the issues of prey preferences and hunting style, little is known about what influences a cat as to when it should start to hunt, where it should hunt, when it should change hunting places and when it should give up hunting. For instance, how do local differences in prey availability within the home range affect where cats hunt? What do cats do when faced with a conflict between hunting and performing other activities? What do mothers do, for example, when hunting means they must leave their offspring? Do mothers faced with the heavy load of providing milk for their offspring have different nutritional requirements from males and non-lactating females? Do they take different prey? Many of these questions could be answered in part by field experiments in which the diet of feral cats was supplemented at the home area.

## Why do cats scratch the floor near food?

Cats sometimes cover up leftovers or food items that they have rejected in the same way that they cover up urine and faeces. This looks especially bizarre on a hard floor on which they may sometimes scratch without effect for minutes on end. Sometimes, these actions may be purely for sanitary reasons, as they are typically performed besides food for which they do not have much liking. However, they could represent attempts by the cat to cache leftover food. Occasionally feral cats have been observed to retrieve uneaten food that has been cached in this way (Fitzgerald, pers. comm.). Whatever the explanation, the behaviour pattern is remarkably robust and resistant to repeated failure to achieve any positive outcome. Some cats continue throughout their lives to scratch the floor after taking their fill from an abundant plateful of food. Such robust and evolutionary ancient forms of behaviour are not subject to the usual rules of learning whereby unrewarded activities disappear from the animal's repertoire.

## Why do cats scratch with their fore-claws?

Domestic cats, kept as pets, often stretch themselves upwards, extend their forelegs and scratch furniture, sofa and curtains – much to the annoyance of their owners. Feral cats do the same on trees and other rough surfaces. Less frequently, scratching is done with the back legs accompanied by treading movements. As claw sheaths are sometimes found where cats have been scratching, people usually suppose that the cats are sharpening their claws. Indeed, this may have been its original function. However, dominant cats will sometimes ostentatiously scratch their claws in front of subordinate ones. In such cases it looks like a display of confidence. Claw-scratching may also occur in bouts of oestrous rolling. If during the rolling the cat's forepaws come into contact with a rough surface, she may briefly scratch. Similarly, claw-scratching sometimes occurs in bouts of play as do other displays, such as arching. Finally, claw-scratching might involve some scent-marking (see below) by smearing secretions of glands on the feet onto the scratching posts.

## Why do cats spray?

When cats spray urine, they behave differently from when they are simply emptying their bladders. When merely excreting, cats dig a hole, urinate in to it without tail movements, turn, sniff, and then cover the hole, often sniffing again and covering some more. Spraying is characterised by tail-quivering, and by the cat rarely sniffing the sprayed surface afterwards. Spraying is most commonly done onto a vertical surface (erect-spraying) but sometimes onto the ground (squat-spraying). In erect-spraying the tail is held at 45–90° and quivered during spraying. The cat's hind-quarters are held high, and one or both hind feet may leave the ground briefly during the spraying. In squat-spraying the cat makes several abrupt treading movements with its hind feet, lowers its hind-quarters and the tail quivers as it sprays. Here again it walks away without sniffing the marked surface. All reproductive adult males and most females will spray urine onto trees, fence poles, shrubs, walls and so forth. The male's sprayed urine has a particularly pungent and characteristic odour.

While the usual interpretation of spraying is that it scares away intruders, cats have rarely been observed to approach an object marked by another cat, sniff it *and withdraw*. Cats may mark the same object more than once. The scents left after spraying are likely to indicate that another animal of the same or a different sex has recently passed by. So it may act either as an advertisement, indicating that a female is in oestrus or an adult male is in the area, or serve a similar function as a visual threat, reducing the likelihood that the marker and the sniffer will come into physical contact. It is not yet known whether a cat that sprays or marks in other ways receives any benefit from doing so. But spraying, like front claw-scratching, is performed by confident cats and, as such, could play an important role in the assessments that cats, like other animals, continually make of each other. Turner (pers. comm.) has also suggested that depositing a spray mark might re-establish the cat's presence when entering an area not visited recently.

## Why do cats bury their faeces?

The belief that cats invariably bury their faeces is incorrect. In feral cats most scats are not buried and many are left elevated on grass tussocks (Corbett, 1979; Fitzgerald & Karl, 1986). Domestic cats close to home do tend to bury their scats, but when further afield often leave them exposed (Liberg, 1980). Panaman (1981) following female domestic cats, observed them defecate 58 times, but only on 2 occasions were brief attempts made to dig a hole before defecating. The substrate was scraped over more than half the holes, although most faeces were not completely covered. Significantly more scats were left exposed outside the home area. This picture was confirmed (Macdonald *et al*., 1987). The evidence suggests, then, that faeces are by no means always buried even by house cats. Near the main living area, burying is commonplace and may be done for hygienic reasons. It may also be the case that the habit has been encouraged by humans selecting those animals that were 'clean'. Further away from home, scats are much less likely to be buried and may be used as another form of marking in free-ranging cats.

## Why do cats rub?

Cats frequently rub parts of their body against objects, other animals and their owners. Robert Prescott, working at Cambridge in the early 1970s, was the first to suggest that such familiar patterns of behaviour involve scent-marking; work by others followed in due course (Verberne & Leyhausen, 1976; Macdonald *et al*., 1987). The patches between the eyes and the ears (which are only lightly covered with fur), the lips, the chin and the tail are all richly supplied with glands producing fatty secretions. The lips, chin and tail are primarily used in marking objects and the head patches and also the tail are used in marking other cats. Leyhausen (1979) noted that his cats rubbed people much more actively than they did each other. He suggested that the relaxed, uncompetitive relationship that people have with their pet cats allows the expression of behaviour that would normally only be seen in young cats with their mother. However, relaxed, uncompetitive relationships are not simply limited to humans. Studies of feral cats have shown that rubbing by one friendly adult against another is commonplace in well-established groups, but is particularly likely to be expressed by a subordinate individual towards a dominant one (see Chapter 6; Macdonald *et al*., 1987). A pet cat rubbing on its owner behaves as it would towards a dominant cat and might therefore be regarded in the same way as a pet dog fawning and tail wagging to a human.

The result of marking with the head patch may sometimes be seen if a friendly cat on the other side of a window can be persuaded to approach and rub. If the light is right, a broad smear, which quickly dries, may be seen where the cat has pushed its head against the glass. Given that other cats are marked with the patch and the rubbing is reciprocated, it would seem that all the cats in a social group end up smelling alike. If that is so then the common odour would be an olfactory badge which might denote common kinship (see Chapter 5). Head-rubbing is frequent in the early stages of

courtship and commonly the male comes from outside the female's own social group. However, study is needed of whether or not such rubbing involves assessment of how closely related the other animal might be. Verberne and de Boer (1976) found that a wooden peg which had been lip-rubbed by a female cat was sniffed significantly longer than an unmarked peg. The duration of sniffing by males probably varies with the state of oestrus of the female.

Rubbing with the tail by females occurs intensively in the early stages of oestrus. This could indicate to passing males that a female in heat is nearby. Tail-rubbing of objects (and humans) also occurs when cats are not sexually motivated. So does rubbing with the upper-lip and chin. Pet owners can readily see their cat rub its lip along the corners of a new cardboard box. Outside the house, cats also do it on head-height twigs on shrubs. As with claw-scratching and spraying, such rubbing is sometimes performed vigorously by a confident animal after aggressive encounters with other animals. When no other cats are present, rubbing with the tail, chin and upper lip may simply give notice to other cats that an individual has recently been in the area. If this interpretation is correct, the behaviour may be very similar in function to spraying. A question remains about why so many different forms of scent-marking are used. Is it possible that some more patterned form of information is provided by combinations of scents?

## Why do cats grimace after sniffing?

Apart from the tongue and the nose, the cat has a third organ for sensing chemical stimuli. This is the vomeronasal organ found throughout the cat family and some other mammalian groups such as the horses. The entrance to this organ is in the roof of the mouth. When cats use it, they first locate the source which is to be investigated, approach it closely and then hold their heads still with partially retracted lips. This grimace, known by the German word *flehmen*, may be held for a second or more and is often misinterpreted as a threat. After sampling in this fashion, the cat usually licks its nose. Cats use the vomeronasal organ when they are analysing urine sprayed by other cats, faeces, gland secretions and also many other non-biological odours.

## Why do cats purr?

Domestic cats resemble many other species of cat in their ability to purr, although it is often claimed that the large roaring cats (genus *Panthera*) do not do it. Purring can occur simultaneously with other vocalisation. The purr can be produced with the mouth closed and continued for long periods of time at a frequency of 26.3 Hz (Sissom *et al*., 1991). The frequency at mid-expiration exceeds that at mid-inspiration by 2.4 Hz. Purring frequency for individuals does not change with age. The primary mechanism for sound and vibration production is by laryngeal modulation of respiratory flow. The diaphragm and other muscles appear to be unnecessary for purring other than to drive respiration.

Purring is almost certainly a form of communication in as much as it indicates to other individuals that the purring animal is in a particular state (usually relaxed and contented). Kittens first purr while suckling when they are a few days old. Their purring might signal to the mother that all is well, acting like the smile of a baby. If so, the purr helps to establish and maintain a close relationship. Probably for similar reasons, the purr is used by adults in social and sexual contexts. For instance, an adult female will purr while suckling her kittens and when she courts a male. Again like the human smile, purring can be used in appeasement by a subordinate animal towards a dominant one. The implication is that purring reduces the likelihood of attack. Whether relationships are impaired when purring does not occur has never been investigated as far as we know. It would be possible as a first stab in such a study to exploit the considerable natural variation that is found in the amounts that cats purr. As things stand, the function of this most familiar and distinctive feature of the cat remains largely unexplored.

## What indicates that a cat is friendly?

Apart from purring and rubbing, which have already been discussed, one of the most characteristic signals of a cat entering or leaving a social group is the raising of its tail. It seems likely that the raised tail is a visual signal to the others (as it is to humans) that the individual is relaxed and friendly (see Chapter 4). Such signals may be performed regularly because, like a human hand-shake, the cat maintains stable social relationships in this way and reduces the chances that it will be disrupted in its daily round by the other individuals with which it lives. If so, do naturally tailless cats such as the Manx experience any difficulties in their social relationships with other cats because they are unable to give the tail-up signal? Answering this question would go some way towards answering our conjecture about the evolution of the tail-up signal.

Another friendly gesture is the blink. A prolonged stare is intimidating and may cause a subordinate cat to withdraw. Perhaps for this reason, non-aggressive cats when staring at other cats or at humans will blink, thereby signalling that the scrutiny is not hostile. In evolutionary terms, once again, cats that did this were more likely to maintain their social relationships and thereby derive the benefits that such relationships provide.

Although many of the friendly interactions between pet cats and their human owners can be related to identical interactions seen between one cat and another, the meaning may change as the kitten grows up within a human household. Such special significance attached to certain types of behaviour could develop because the human–cat relationship is generally relaxed and rarely competitive. Some of the friendly behaviour directed at a person may be strengthened by the human reciprocating particularly strongly when a cat behaves in a certain way, such as rubbing. So what starts as a perfectly natural piece of marking of a dominant group member may be reinforced by stroking. Eventually, the behaviour pattern is expressed by cats in search of human attention.

## Do cats cooperate?

The house cat's independence has encouraged a widespread view that it is unsocial and uncooperative. However, the studies of feral cats have revealed that, apart from an intense early family life, the females in particular may stay in groups as adults (see Chapters 5). While living together, cats may help each other in terms of mutual defence against intruders and caring for each other's offspring.

It is a myth that, because wild animals are the products of an intense struggle for existence, they always are in a state of social conflict. Two evolutionary explanations for cooperation are now widely accepted. The first is that, at least in the past, the aided individuals were relatives. Cooperation is like parental care and has evolved for similar reasons; by successfully helping close kin, the patterns of behaviour involved in such care become common in the population. The second evolutionary explanation is that cooperating individuals jointly benefited, even though they were not related; the cooperative behaviour has evolved because those that did it were more likely to survive and reproduce than those that did not. In keeping with these ideas, modern work strongly suggests that the cooperative behaviour of animals is exquisitely tuned to current conditions. The benefits to the individual of cooperation change as conditions change and, in really difficult circumstances, previously existing mutualistic arrangements may break down. Or if members of a group are not familiar with each other, no mutual aid may occur until they have been together for some time. As familiarity grows, individuals come to sense the reliability of each other. Furthermore, expectation of an indefinite number of future meetings means that deception or conflict are much less attractive options. Once evolutionary stability of cooperative behaviour under some conditions was reached in a social animal, features that maintained and enhanced the coherence of the behaviour would then have tended to evolve. Signals that predicted what one individual was about to do, and mechanisms for responding appropriately to them, would have become mutually beneficial. Furthermore, the maintenance of social systems that promoted quick interpretation of the actions of familiar individuals would have become important. Finally, when the quality or quantity of cooperation depended on social conditions, increasing sensitivity and self awareness would have become advantageous. All these evolutionary changes probably occurred in the cat.

## Why do cats switch from being friendly to being distant?

A highly affectionate cat that moves around the house with its human companion and readily sits on his or her lap may at other times appear to be totally uninterested in human company. In this respect cats differ markedly from dogs. The explanation for the disappointing change in the cat's mood may lie in the way it hunts. Unlike the domestic dog, which descends from the pack-hunting wolf, the cat hunts on its own. It may wait for hours for rodents to stir within pouncing range or it may rely on its stealth in creeping up on a bird feeding on the ground. Either way, hunting by the cat is not a group activity. If two or more cats were to hunt together, their chances of success

would be greatly reduced. This may explain, therefore, the seemingly enigmatic character of the cat's behaviour. Owners should understand why the evolutionary ancient patterns of predatory behaviour were necessary for the survival of their pet's ancestors.

## Concluding remarks

The cat that walks by itself is no less social because it has to hunt on its own. The strong use of the cat's sense of smell and the communication by means of olfactory cues provides for the cat a perceptual world that is unavailable to humans. Yet that world is accessible to scientific analysis. We do not think that cats become less interesting as some of their enigmatic qualities yield to research. As so often happens, new questions are posed by the answering of old ones. We hope, though, that interested cat owners and professional scientists alike will have gained pleasure from the increased understanding. The cat is much more social than popular myth would suggest. It is exquisitely sensitive to the behaviour of other individuals. A great deal of its own behaviour is devoted to maintaining its social relationships. That much is clear, but many of the influences on its behaviour remain uncertain. As yet the astonishing differences between individual cats are largely unexplained in terms of both how they are generated and why they might exist. We hope that this book will have served to stimulate the lay-reader and the professional scientist to view the cat with even greater sympathy and also to whet their appetites for what remains to be discovered.

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# Index

# Technical detail from Chapter 15 by Hiby, E., Eckman, H. & MacFarlaine, I. in *The Domestic Cat* (3rd edition)

## Cat population management

To estimate population growth rate the following formula is derived from the balanced equation that relates the number of kittens born in a population growing at a constant rate to the number of recruited females. The growth of the population over the interval between successive breeding times is calculated first. In populations with an annual breeding season that interval equals one year; however, in populations that are not limited to one annual breeding opportunity the interval is the reciprocal of the number of litters per year, $1/L$. The factor, $\lambda$, by which the population grows over such an interval can be calculated by iteratively solving the following equation:

$$\lambda = (S_b\lambda^{rL-1} + KS_j)^{1/rL}$$

where $S_b$ is adult survival over one interval. Annual growth is then calculated as $\lambda^L$. Using this equation example 1 has an estimated annual growth rate of 1.01 and example 2 has a rate of 2.11; the growth rate of example 2 is thus more than double that of example 1. Similarly, the percentages of females that would need to be sterilised per interval to stabilise such populations are very different. This percentage equals $100(1 - m)$ where $m$ can be calculated by iteratively solving the following equation:

$$m = \left(\frac{1}{KS_j\left(1/(1 - S_b m)\right)}\right)^{1/rL}$$

The formulae above are for a closed population; however, the value for adult survival can be reduced to allow for dispersal to surrounding areas in addition to mortality and for the number of females permanently adopted from the feral population and confined. Similarly, to allow for immigration from surrounding untrapped areas or from previously confined owned animals the average litter size can be increased by a factor reflecting the resulting increase in recruitment, for example by 1.2 if 20% of the recruits are immigrants.