The Ostrich

Biology, Production and Health

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The Ostrich
Biology, Production and Health

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Preface

In the National Gallery of Scotland in Edinburgh hangs a painting by the British artist Thomas Gainsborough (1727–1788) entitled *The Hon. Mrs Graham.* Ostrich plumes decorate the lady's hat and she is holding a wing plume. Several other pictures by Gainsborough and by Sir Joshua Reynolds (1723–1792) feature ostrich feathers as items of fashion, yet it is curious that these feathers were being worn by people who had probably never seen an ostrich. These images reflect the fact that ostriches had long fascinated and inspired humans well before these pictures were painted, and this continues up to the present.

My own fascination with ostriches came through working on problems of commercial incubation of their eggs. During a 3-year period working on a commercial ostrich farm in Britain, I was able to carry out research into problems of incubation and chick rearing, and together with a variety of colleagues and students, our knowledge of the behaviour of ostriches in a farming situation greatly increased. In 1996, I helped to organize a major scientific conference, 'Improving our Understanding of Ratites in a Farming Environment', which brought together many of the world's experts in Manchester, England. The Proceedings (which I edited) proved very successful and I felt that a book reviewing our knowledge about the ostrich would be equally popular. When, in 1997, I was made aware that CAB *International* were planning a book on ostrich farming I was keen to be involved, as this would fulfil an ambition of mine to bring together our current scientific knowledge in one volume and provide a medium to suggest areas for further research. I was very pleased that I was able to both edit and contribute to this book.

This volume brings together some of the world's experts in their respective fields of ostrich biology, production or health, and I believe that we have produced an exciting book which will prove to be the reference text on ostriches for

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many years to come. The contents, whilst revealing what we currently know, have particularly highlighted what is absent from our scientific understanding of the ostrich, and there is so much more scope for further research.

I would like to take this opportunity to thank all of the contributors for their hard work and for putting up with my constant badgering to produce their valuable contributions. It would not have been possible without them and it has been worth all of the effort. Particular thanks go to co-authors on my own contributions.

Finally, I must thank my wife Roslyn and my daughter Katherine, for putting up with me when I seemed to spend hours in front of my PC working on this book.

D.C. Deeming
Wallingford, January 1999

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1 Introduction

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Recent interest in ostrich farming has led to an increasing demand for information about this bird and how to manage it in a commercial environment. In this volume an attempt is made to bring together this information, and so subsequent chapters feature its anatomy, physiology and behaviour. Other chapters deal with more practical aspects of farming: reproduction, incubation, rearing and genetics. Later chapters deal with ostrich products, welfare and veterinary problems, and management of farmed ostriches. Each chapter provides a comprehensive review of these topics but there are instances where interesting aspects of ostrich biology do not fit within these categories. Therefore, Chapter 1 provides a short introduction to the ostrich, giving details about why this bird is unique. There is a description of geographical distribution and phylogenetic relationships followed by a short review of human relationships with ostriches. The chapter concludes with a brief history of ostrich farming to date.

GENERAL DESCRIPTION

The ostrich is the largest living bird, measuring up to 2.75 m in height and up to 150 kg in mass. The adult male bird is mainly black with white wing primaries and tail feathers, and a grey coloured neck. The female is a dull brown-grey all over with light grey to white wing primaries and tail feathers. Juvenile birds resemble the females, whereas young chicks are mottled brown, yellow, orange and cream with black quills on the back. Ostrich feathers are fluffy and symmetrical (Cramp *et al.*, 1977; Brown *et al.*, 1982).

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The combination of long legs and neck elevates the head some 1.8–2.75 m above the ground, where the exceptionally large eyes (50 mm diameter), the largest of any vertebrate (Brown *et al.*, 1982), are widely separated on the head and positioned to produce an image from in front of and below the eye. The large blind spot behind and above the head is considered to shade the eye (Martin and Katzir, 1995). The ear flaps face to the rear of the bird.

Unable to fly, the ostrich spends its time walking around its environment, only running if threatened. Nevertheless, these birds can achieve around 60–70 km h^{-1} (Cramp *et al.*, 1977; Alexander et al., 1979) and a large proportion of the energy required for running is probably saved by elastic storage in tendons (Alexander *et al.*, 1979). Leg anatomy reflects the walking lifestyle of the ostrich (see Bezuidenhout, Chapter 2). In common with other birds the ostrich is digitigrade, but uniquely, it has only two toes.

The wings of the ostrich are poorly developed and there are no substantial pectoral muscles. A keel is absent from the sternum, which is large and bowl shaped. Although unable to fly, the structure of the wing bones and the presence of air sacs, some pneumatized bones and the presence of the pygostyle strongly suggest that the ostrich evolved from a flying ancestor (Cramp *et al.*, 1977; Bruning, 1991).

TAXONOMY AND GEOGRAPHIC RANGE

Palaeontology

Space precludes an extensive description of the palaeontology of ostriches, but leg bones and fragments of eggshell are common in the fossil record (Mourer-Chauviré *et al.*, 1996a). Fossil evidence suggests that ostrich-like birds were once well distributed over Africa and Eurasia, extending from the Mediterranean across to India and China (Swinton, 1975), although their exact origins are not clear. The lineage may be very old (from the Eocene 65–38 million years ago) although there is stronger evidence that ostriches evolved during the Miocene period (26–7 mya) (Mourer-Chauviré *et al.*, 1996a, b).

One source of debate is about whether ostriches evolved in Africa and spread to Eurasia or vice versa. Cracraft (1973) suggested that all ratite birds shared a common origin in Gondwanaland, but most evidence backed the assertion that ostriches were derived from Eurasia and moved to Africa (Olsen, 1985; Mikhailov, 1986). Recent discoveries in Namibia of leg bones dated at *c.* 20 mya (Mourer-Chauviré *et al.*, 1996a, b) have led to the suggestion that ostriches did evolve in Africa and moved to Eurasia only around 10–5 mya.

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Extant ostriches

The ostrich, or the 'camel bird' because of its similarities with dromedaries, was named in 1758 by Linnaeus as *Struthio camelus*, based on the Greek and Latin name *Struthocamelus* (Bertram, 1992). There are four extant subspecies, all confined to Africa and occupying largely exclusive geographical areas (Table 1.1). The subspecies *S. c. syriacus* Rothschild was formerly found in the Syrian desert and north Arabia but was hunted to extinction by 1941 (Cramp *et al*., 1977). The North African subspecies *S. c. camelus* was heavily persecuted during the 20th century and is considered to be threatened (Cramp *et al*., 1977; Brown *et al*., 1982). *S. c. molybdophanes* is the most distinct race, although under artificial conditions it has produced fertile hybrids with *S. c. massaicus* (Brown *et al*., 1982; Bertram, 1992).

Swart (1988) described *S. c.* var. *domesticus* as reflecting the hybrid nature of farmed ostriches in South Africa. This bird, developed from breeding programmes started around the start of the 20th century, is characterized by small stature, well developed feather structure and a docile nature. This domesticated bird is often referred to as the 'black'. 'Red-neck' birds are mainly derived from wild populations of *S. c. massaicus*, although some zoological collections may have specimens of *S. c. camelus* which have been sold to farmers. Similarly, 'blue-necks' are mainly derived from wild populations of *S. c. australis* although some birds may be derived from populations of *S. c. molybdophanes*.

Freitag and Robinson (1993) investigated the phylogeographic patterns in the various wild subspecies by assaying restriction-site differences in mitochondrial DNA. This analysis aligned with the currently accepted designations of subspecies. Little genetic diversity was observed in the various locations inhabited by *S. c. australis*, suggesting considerable historical contact between different localized populations. By contrast, there were deep divisions between representatives of the East African subspecies (*S. c. molybdophanes* and *S. c. massaicus*) and those of the North African subspecies (*S. c. camelus*). The Ethiopian rift valley appears to have been an effective barrier between populations of *S. c. camelus* and *S. c. molybdophanes*. In Kenya, no physical barrier exists between *S. c. molybdophanes* and *S. c. massaicus* but it is likely that ecological or behavioural differences have limited interbreeding. Despite physical separation by a belt of *Brachystegia* woodlands in Tanzania and Zambia, there does appear to have been periodic contact in the recent evolutionary past between populations of *S. c. massaicus* and *S. c. australis*.

Habitats

The preferred habitat is open, short-grass plains and semi-desert, although ostriches are found in the hot, fringing desert steppes of the western Sahara and the true deserts of Namibia. They avoid areas of tall grass and dense woodland but will occupy (or cross) more open woodland. The birds tend to keep to

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Table 1.1. General description of the range and typical characteristics of the four subspecies of the ostrich (species *Struthio camelus*, family *Struthionidae*, suborder *Struthiones*, Order *Struthioniformes*). Based on data of Cramp *et al.* (1977), Brown *et al.* (1982) and Bertram (1992).

Subspecies	Range	Male skin colour	White neck collar	Bald crown	Tail feathers	Iris colour
S. c. camelus Linnaeus	Southern Morocco and Mauritania east to south-western Ethiopia and northern Uganda	Pinkish	Yes	Yes	White	Brown
S. c. molybdophanes Reichenow	North-eastern Ethiopia and Somalia extending into northern Kenya	Blue-grey	Broad	Yes	White	Blue
S. c. massaicus Neumann	Eastern Kenya and northern Tanzania	Pinkish-grey	Narrow	Less pronounced or absent	White	Brown
S. c. australis Gurney	Northern Namibia and Zimbabwe south to Cape Peninsula	Grey	Absent	Absent	Brown	Brown

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lowland areas (Cramp *et al.*, 1977; Brown *et al.*, 1982). In southern Africa ostriches can be found in desert grassland, semi-arid savanna, Karoo shrubland and coastal fynbos (Dean *et al.*, 1994). 'Coastal fynbos' is unique to South Africa and is characterized by a preponderance of small shrub bushes of the *Protea* and *Erica* families (Chambers and Odendaal, 1996). Bird densities are around one per 5–20 km^2 except where protected, when they can reach 0.8 birds km^{-2} (Brown *et al.*, 1982).

ASSOCIATIONS WITH HUMANS

Images of ostriches are seen in paintings and carvings in the Sahara dating between 5000 and 10,000 years BC (Bertram, 1992; Kreibich and Sommer, 1995). In Africa the birds have been hunted for their meat for centuries by bushmen who often adorned themselves in the feathered skin of the bird (Holtzhausen and Kotzé, 1990; Bertram, 1992; Drenowatz *et al.*, 1995). Empty whole eggshells have long been used as storage and drinking vessels in Africa and Arabia. Eggshell fragments have been fashioned into jewellery used by bushmen, and this continues to the present day (Holtzhausen and Kotzé, 1990; Bertram, 1992).

Laufer (1926) reported that empty eggshells have been commonly used as cups, with the first recorded instance around 3000 years BC. Assyrian kings are featured strangling and slaughtering ostriches on regal seals dated from the 8th century BC (Laufer, 1926), and the Assyrians considered the bird to be holy (Smit, 1963). Both ostrich eggs and feathers feature in Egyptian hieroglyphs (Laufer, 1926; Holtzhausen and Kotzé, 1990). Adult ostriches are featured as being presented to the pharaoh on a frieze displayed in the British Museum, London. A statue of Queen Arsinoë features her riding an ostrich, and a preserved ostrich was found in a tomb of the 18th Dynasty (Smit, 1963). Tutankhamun had a long-handled golden fan which held ostrich feathers and is decorated with an image of the Pharaoh hunting ostriches (Piper, 1994).

The ostrich is referred to in the Bible on several occasions (Laufer, 1926; Smit, 1963; Bertram, 1992; Kreibich and Sommer, 1995). In common with the Ancient Egyptians, Solomon saw the symmetrical ostrich feather as a sign of justice. Eggshells are also used as ornaments in Coptic and Greek Orthodox churches, and in West Africa they are used to protect Muslim houses from lightning (Brown *et al.*, 1982; Holtzhausen and Kotzé, 1990).

Greek and Roman generals decorated their helmets with feathers (Holtzhausen and Kotzé, 1990; Kreibich and Sommer, 1995), and bearskin hats worn by some regiments in the British Army are made out of black ostrich feathers. Ostriches were encountered by the Chinese during military missions and their images feature in sculptures on the sides of tombs of emperors (Laufer, 1926). Crusading knights returning from the Middle East introduced the ostrich feather into Western Europe where it became fashionable with the monarchy (Smit, 1963). The coat of arms of the British Prince of Wales has three ostrich

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feathers, an emblem established in the 14th century (Smit, 1963; Drenowatz *et al.*, 1995).

The skin of the ostrich has been used in protective jackets in the Arab world (Bertram, 1992). Other than aboriginal hunting, ostrich meat has been largely ignored, although in the 2nd century AD the Roman Emperor Heliogabalus had 600 ostrich brains served at a banquet (Bertram, 1992). In the Old Testament, ostrich meat is deemed as 'unclean' (Bertram, 1992; Kreibich and Sommer, 1995).

Ostriches are a common image in modern advertising, being used to sell items as varied as cars, malt stout and insurance. Ostriches and their eggs have also featured on stamps produced in south-west Africa (Swart *et al.*, 1987; Holtzhausen and Kotzé, 1990). Ostriches are often a source of humour (e.g. Larson, 1989), and in alphabet books for children they are often used to illustrate the letter 'o'. In English, 'ostrich' symbolizes a person who refuses to recognize reality.

HISTORY OF OSTRICH FARMING

South Africa

For centuries the demand for feathers was met by killing ostriches, with no attempt to develop a non-lethal method of harvesting. The first successful artificial hatching took place in 1857 in Algeria (Smit, 1963). Around the early 1860s, in the Karoo and Eastern Cape Province of South Africa, the ostrich was taken into captivity for production of feathers for fashion items (Smit, 1963; Jensen *et al.*, 1992). The invention of the artificial incubator for ostrich eggs by Arthur Douglass in 1869 provided a major stimulus for ostrich farming (Smit, 1963). The income from feathers stimulated massive development of ostrich farming in South Africa, particularly around Oudtshoorn in the Little Karoo, and despite two slumps in the market (1883–1890 and 1894–1899), the first few years of the 20th century saw a massive expansion of ostrich farming (Fig. 1.1; Smit, 1963). There was a parallel increase in income from the feathers (Fig. 1.1), and by 1913 feathers were the fourth highest export commodity in South Africa (Smit, 1963). In Oudtshoorn, farmers used their massive incomes to build ornate 'feather palaces', many of which still remain to the present day (Holtzhausen and Kotzé, 1990).

The market for feathers collapsed at the onset of World War I and the number of birds in captivity dropped rapidly (Fig. 1.1; Smit, 1963). Ostrich farming barely survived in South Africa; a cooperative society was established in 1925 in order to stabilize prices but failed to halt the decline (Smit, 1963). Following World War II there was a revival in use for dusters and fashion feathers, and there was increased production of biltong (salted dried meat). In 1945 a second co-operative, the Klein Karoo Landboukoöperasie (KKLK), was established in the

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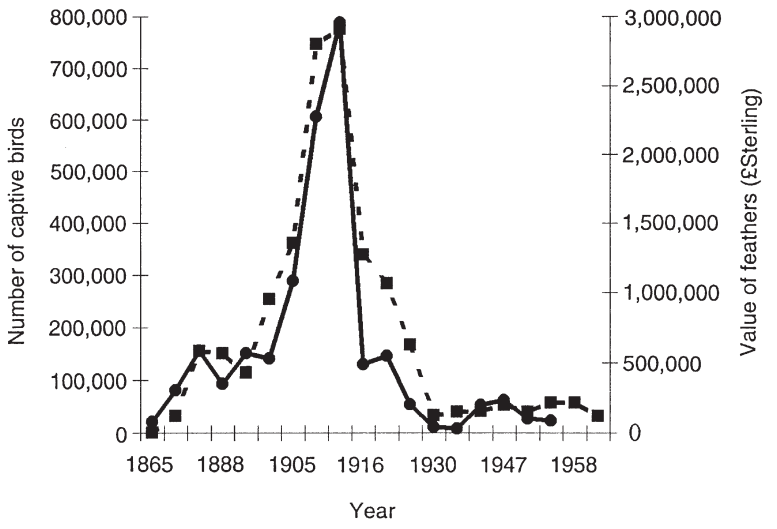

Fig. 1.1. The rise and fall in the number of captive ostriches, and the value of the feathers they produced, in the Cape Colony of South Africa during the first century of farming (data from Smit, 1963). ■, Captive population; ●, value of feathers.

Little Karoo to regulate feather sales (Drenowatz *et al.*, 1995), and during the early 1950s a leather market was developed. The KKLK gained control over all ostrich produce in 1959 (Smit, 1963) and is largely responsible for development of ostrich leather as a luxury fashion product. Feathers remained a secondary product, and meat produced from a KKLK abattoir opened in 1963 was used primarily for biltong production (Smit, 1963; Drenowatz *et al.*, 1995). A leather tannery, opened in Oudtshoorn in 1969, was expanded in 1974 and a new abattoir opened in 1981 (Drenowatz *et al.*, 1995).

Over the past 10–15 years, ostrich meat has become an increasingly important product and ostrich farming has increased in popularity in South Africa, with at least 150,000 birds being slaughtered each year (Smith *et al.*, 1995). Leather has remained the primary product, but meat sales have gained in prominence during the 1990s (Fig. 1.2; Drenowatz *et al.*, 1995). The KKLK has had tight control on marketing of ostrich products, but deregulation of the slaughter market in 1993 (Drenowatz *et al.*, 1995) has meant that the number of birds killed each year has steadily risen and at present may be around 300,000.

Rest of the world

Such was the interest in ostrich feather farming at its boom that there was considerable export of birds to the USA, Europe, North Africa, South America and Australia (Bertram, 1992; Jensen *et al.*, 1992). To protect this market an export ban on live ostriches and eggs was imposed by the South African government in

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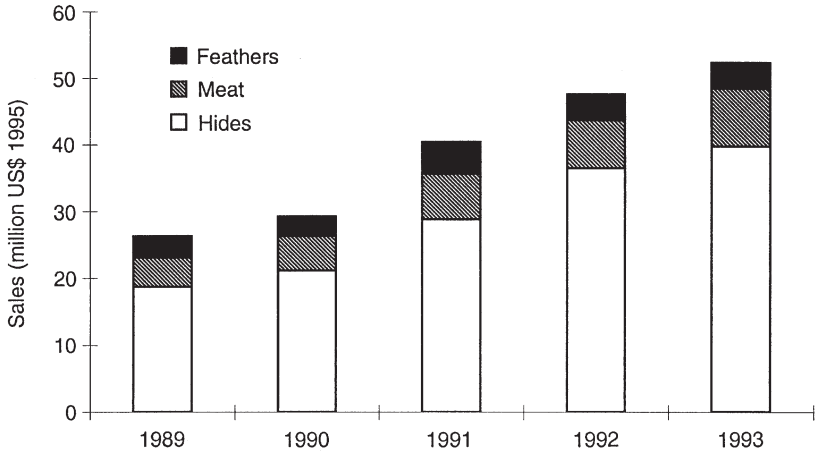

Fig. 1.2. Sales of the Klein Karoo Landboukoöperasie in South Africa for the three main products from ostriches (data from Drenowatz et al., 1995)

1906 (Smit, 1963). At the collapse of the market, most birds were slaughtered although some birds remained in captivity in the USA. In 1921 only 231 ostriches remained in the USA (Drenowatz *et al.*, 1995). Farmed ostriches in Australia were simply released and formed a semi-feral population (Simpson and Day, 1989).

Since the mid-1980s ostrich farming elsewhere in the world has been undergoing a renaissance, although generally the farms are on a small scale (Deeming and Angel, 1996). Outside South Africa, only a few larger-scale operations exist in the USA, Australia and Europe. Starting in the early 1980s Israel has developed a significant farming operation and their slaughter operations are second only in scale to those found in South Africa.

Interest in ostriches in the USA and Canada was supported by imports of birds and eggs (Drenowatz *et al.*, 1995). The market is now for slaughter birds (Deeming and Angel, 1996). Australians have also developed an ostrich industry although, until recently, they were working with a limited gene pool based on semi-feral birds. Again there has been a move towards a slaughter market (Deeming and Angel, 1996). Most European countries have been developing ostrich farms since around 1990 based on stock imported from Africa and Israel and have reached the slaughter market (Deeming and Angel, 1996).

Other African countries have developed ostrich farming systems in recent years (Deeming and Angel, 1996). Namibian farms, based largely on Oudtshoorn strain birds, are geared up to a slaughter market. Zimbabwe based its ostrich farming operation on the local indigenous ostrich sub-species and in 1995 was approaching a slaughter market (Foggin, 1995). Currently, other countries such as those in the Far East, South America and New Zealand have been exploring the feasibility of ostrich farming.

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In 1997 the ban on export of living ostrich material from South Africa was lifted, allowing farmers to export both birds and eggs. This may provide a boost for local farmers who will be able to supply new markets which may arise after confidence in ostrich farming has been revived.

The future of ostrich farming

Deeming and Angel (1996) suggest that productivity (egg fertility and hatchability, and chick survival) have to be significantly increased in order to maximize profitability. They pose two key questions: what is the elasticity of demand for ostrich hides? and what will happen to the price of ostrich hide as supplies increase? These questions may have been prophetic, because currently there is a worldwide slump in ostrich products and a decrease in confidence in farming. Over-production in South Africa since 1993 has almost certainly contributed to this, although additional suppliers have exacerbated the situation.

Deeming and Angel (1996) suggest that the challenge is in the marketing of ostrich products so as to expand meat markets as well as to explore new markets for the hides. This challenge could not be more relevant at this time. Maintaining the high quality image of ostrich products may command high prices, but turnover of product is small. Lowering prices may stimulate profits by increasing the turnover of products consumed in a larger marketplace. Current difficulties in ostrich farming may lead to a considerable reduction in the number of farmers worldwide, but I am certain that years from now there will still be a considerable ostrich industry in South Africa.

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2

Anatomy

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The anatomy of the ostrich has been studied for many years. The main focus of the earlier studies was to determine the phylogenetic relationships and affinities of the ostrich and its allies. Based on the structure of the sternum, Merrem (1813) was the first to separate birds into ratites (walking birds) and carinates (flying birds). Huxley (1867) described the palaeognathous (primitive) bony palate, and comparisons between the palates of different birds led to their division into paleognathic (primitive) and neognathic (modern) birds. The ostrich is a ratite, paleognathic bird.

In this chapter most anatomical structures are described, although in some instances limitations on space have meant that some descriptions are rather brief and so, whenever possible, references are given to more detailed studies. Descriptions of the male and female reproductive systems are not included in this chapter, but are given by Soley and Groenewald (Chapter 6). The cloaca is illustrated in Figs 3.2, 3.3 and 6.4, and described by Soley and Groenewald (Chapter 6).

In order to standardize avian anatomical nomenclature, an International Committee on Avian Anatomical Nomenclature was established. The work of this committee culminated in the publication of a handbook of avian anatomical nomenclature, *Nomina Anatomica Avium* (Baumel *et al.*, 1993). This convention is employed here but for convenience, anatomical terms are anglicized in this chapter.

The standard anatomical position is defined as one in which the bird stands erect with knees and hocks slightly flexed, with wings outstretched laterally and with the neck completely extended. In this position, dorsal refers to the top of the head, the back of the neck, trunk and tail, while ventral refers to the opposite surfaces. In addition, the upper surface of the wing is dorsal and its lower surface

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ventral. Caudal denotes closer to the tail and cranial closer to the head. On the head itself, rostral denotes closer to the tip of the beak. In the pelvic limb, caudal and cranial apply proximal to the tibiotarso-metatarsal joint (hock), and dorsal and plantar are used distal to the hock joint. Unless stated otherwise dimensions of organs refer to adult birds.

INTEGUMENT

The skin consists of an outer epidermis and an underlying, thicker dermis. Contrary to the irregular arrangement of collagen fibres in the dermis of most birds, Lange (1929a, b) found that in the ostrich these fibres are arranged definitely, running at right angles in three dimensions, over the thighs and, to a lesser extent, all over the body. Dermal papillae, which usually are considered absent in the bird skin except in the foot and beak, are also found throughout the skin in the ostrich (Lange, 1929a, b). The epidermis and dermis give rise to many structures, e.g. feathers, claws, nails, scales and beak.

The beak (bill or rostrum) includes the bony upper and lower jaws and their keratinized covering (rhamphotheca). In the ostrich it is fairly flat and triangular in outline, with a broad base and a narrow apex. The mandibular rhamphotheca closely follows the profile of the mandible. Caudally, the two limbs of the mandibular rhamphotheca are separated by a broad, roughly triangular interramal space. The maxillary rhamphotheca carries the paired nostrils and its rostral apex bends ventrally, forming a short, blunt hook.

A horny nail encloses the terminal phalanx of the third digit of the pelvic limb. It is slightly curved and rounded at the apex. A small nail may be present on the distal part of the fourth digit. All the digits of other ratites carry nails (Cho *et al.,* 1984). Curved claws occur on all three digits on the wing in the ostrich, on the major digit in cassowaries, emu and kiwis, and on the alular digit and sometimes also on the other two digits in rheas (Fisher, 1934; Streseman, 1934; King and McLelland, 1984).

The ostrich has footpads, callosities and scales which are localized areas of thickened skin (mainly modified epidermis). Callosities are present over the cranio-ventral aspect of the sternum and the ventral surface of the pubis (MacAlister, 1864). Additional callosities are present on the plantar aspect of the hock. Single, large footpads consisting of thickened skin with long papillae cover the plantar surfaces of the third and fourth digits. The dorsal aspects of the tarsometatarsus and both digits are covered by smooth scales. All these structures are present at the time of hatching. Further details of these structures can be obtained from Lowe (1926).

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Feathers

Feathers (Fig. 10.2) are arranged in tracts (pterylae) with intervening featherless areas (apteria). The follicles of feather tracts form distinct patterns on the surface of the skin. The general consensus is that there are no true apteria in the ostrich (Lowe, 1928; Lucas and Stettenheim, 1972; Baumel *et al.,* 1993).

Lowe (1928) found that the feathers of paleognathic birds are primitive, i.e. there is no pennaceous structure in any of the feathers. Although barbules are present, they do not form an interlocking mechanism. The barbule of both the chick and adult is a narrow, flattened, ribbon-like structure which has undergone a considerable amount of keratinization. The barbules, whether they are from the proximal or distal row, are of equal length, springing from the barb at exactly the same angle and level.

Bristles are feathers generally characterized by a stiff, tapered rachis and the absence of barbs, except at the proximal end. Definitive down feathers (adult downs or plumes) are sparsely distributed or are entirely absent (Lucas and Stettenheim, 1972). Ratites lack a uropygial (preen or oil) gland (King and McLelland, 1984).

SKELETON

The skeleton is illustrated in Fig. 2.1 and the various bones are described below. Some of the skeletal bones are invaded by diverticula of the air sacs. One notable case is the large femoral diverticulum which invades the femur to replace the marrow in the entire shaft.

Skull

Detailed descriptions and discussion of the osteology of the ostrich skull are provided by D'Alton (1827), Brock (1937), Webb (1957) and Bock (1963). The skull of the ostrich is typically avian and although it is paleognathic, there are many cranial features that are neotenic in relation to other paleognathic and neognathic birds (Webb, 1957). Contrary to other birds, the sutures of the skull remain open for a considerable time after hatching (Webb, 1957; King and McLelland, 1984).

The skull consists of the cranium and the face. In lateral and dorsal views the skull is triangular in outline with the apex at the tip of the beak and the base at the occiput. The large eyeballs compress the bone in the depth of the bony orbit to a thin midline plate, the interorbital septum (mesethmoid), through the caudal edge of which various nerves emerge. Caudally, the cranial cavity bears the large foramen magnum for the passage of the spinal cord. Ventrally to the foramen lies the single occipital condyle for articulation with the first cervical vertebra. The dorsal surface of the condyle bears a groove that divides its upper part into two.

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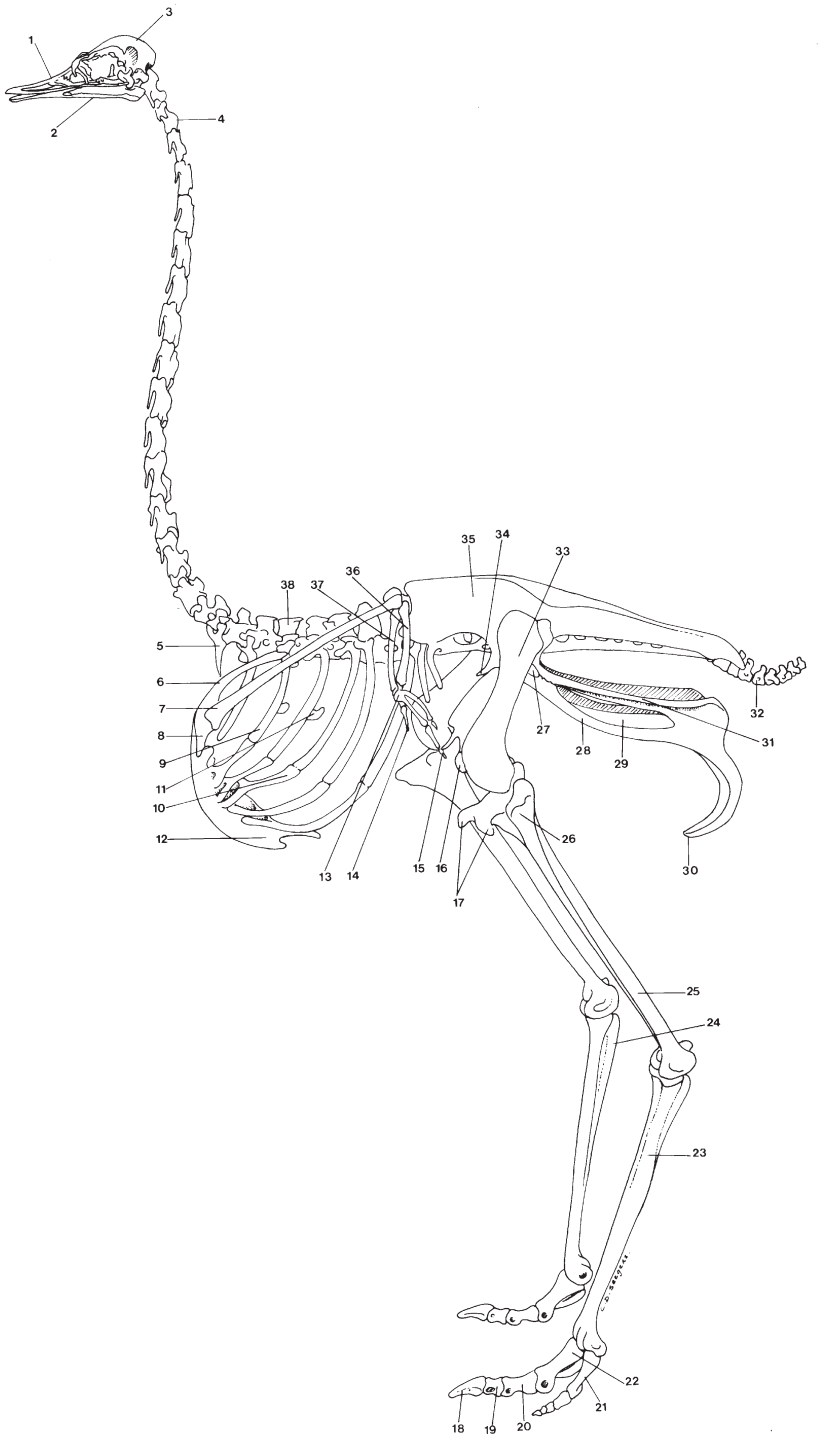

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Laterally to the condyle are two paracondylar processes for the attachment of muscles. The external auditory meatus lies rostrally to the paracondylar processes.

The hyobranchial apparatus consists of three central and four caudo-lateral sections. From rostral to caudal the central segments are the entoglossum, basibranchiale rostrale and basibranchiale caudale. The entoglossum and basibranchiale rostrale support the tongue, while the basibranchiale caudale is attached to the larynx. Two caudolateral projections, consisting of two segments each, suspend the apparatus from the ventral surface of the cranium. The first segment, the ceratobranchial, is attached to the rostral and caudal basibranchials, the second segment is cartilagenous and attached to the skull.

Vertebral column

The number of vertebrae in each section of the vertebral column is difficult to determine due to fusion with each other and with the pelvis. According to Mivart (1874) there are 56 (range of 54–57) vertebrae in the ostrich. This compares with 55 in the emu, 59 in the cassowary and 51 in the rhea (Lowe, 1928). Mivart (1874) divided the vertebrae into 17 cervical (without any articulating ribs), three cervicodorsal (carrying ribs that do not reach the sternum), five thoracic (carrying ribs that reach the sternum), two to three dorso-lumbar (carrying ribs that do not reach the sternum), eight lumbar vertebrae which are fused together, three sacral, eight sacro-caudal and eight to ten caudal vertebrae. Baumel *et al.* (1993) recognize only three vertebral sections: cervical ($n=19$), thoracic (29) and caudal (8).

Each vertebra consists of a body with cranial and caudal articular surfaces, an arch with cranial and caudal articular processes, and transverse processes. The development of the various parts differ between the vertebrae.

The cervical vertebrae increase in size from cranial to caudal. The first 17 cervical vertebrae have large transverse foramina at the bases of the transverse processes. The foramina of the atlas may be open ventrally. The first five thoracic vertebrae are separate and carry vertebral ribs. The rest of the thoracic vertebrae fuse extensively with each other as well as with the pelvis, forming a large synsacrum. The caudal vertebrae remain separate and lack a pygostylus (Friant, 1959). For additional comparative and descriptive detail of the vertebral column, see Mivart (1874, 1877), Virchow (1915) and Baumel *et al.* (1993).

Fig. 2.1 (opposite). The skeleton of the ostrich. 1, Face; 2, mandible; 3, cranium; 4, cervical vertebra; 5, asternal vertebral rib; 6, scapula; 7, humerus; 8, coracoid; 9, sternal vertebral rib; 10, sternal rib; 11, uncinate process; 12, sternum; 13, carpometacarpus; 14, alular digit; 15, main digit; 16, patella; 17, lateral and medial cnemial crests; 18, phalanx IV, digit III; 19, phalanx III, digit III; 20, phalanx II, digit III; 21, phalanx I, digit IV; 22, phalanx I, digit III; 23, tarsometatarsus; 24, hypotarsus; 25, tibiotarsus; 26, fibula; 27, obturator foramen; 28, pubis; 29, ischiopubic window; 30, pubic symphysis; 31, ischium; 32, caudal vertebra; 33, femur; 34, preacetabular tubercle; 35, ilium; 36, radius; 37, ulna; 38, thoracic vertebra.

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Ribs and sternum

The ribs (described in detail by Mivart, 1874) consist of two series, vertebral and sternal. Vertebral ribs are better developed both in number and size, being present on the last two or three cervical vertebrae and the first seven or eight thoracic vertebrae. Proximally each rib has a head which articulates with the vertebral body, and a tuberculum which articulates with the transverse process of the vertebra. The distal ends of the first five thoracic ribs articulate with the free ends of the corresponding sternal ribs (Fig. 2.1). These ribs are of approximately equal length. Thoracic ribs 2–4 carry uncinate processes along their caudal borders.

Sternal ribs are similar to the vertebral ribs, but are generally shorter and articulate with the sternum (Fig. 2.1). They increase in length from cranial to caudal in the series, the last one being as long as its vertebral counterpart.

In ratites the sternum is flat and lacks a keel (King and McLelland, 1984). The ostrich sternum (Mivart, 1874; Lowe, 1928) is slightly oval and dish-shaped lying almost perpendicular to the long axis of the body, with its concave surface facing caudally (Bezuidenhout, 1986). Nopcsa (1918) found that the sternum of female birds was longer, but narrower, than that of males.

The cranial margin of the sternum carries a groove for articulation with the coracoid. Immediately lateral to the articulation is a short craniolateral process. Caudally to the process, along the lateral border, lie the articular surfaces for the sternal ribs. Caudally it carries a fairly long lateral trabeculum.

Thoracic girdle

The thoracic girdle consists of scapulae and coracoid bones (Fig. 2.1). Ratites generally lack clavicles and triosseus canals, except in the emu where vestigeal clavicles are present. When clavicles are present, they remain separate from each other and are sometimes fused to the scapula or coracoid (King and McLelland, 1984). The ontogeny of the thoracic girdle is discussed in detail by Broom (1906), Lowe (1928); Friant (1959) and von Blotzheim (1958). The ossification of the thoracic girdle can be used to distinguish between carcasses from ostriches between 10 and 12 months of age, but it is not an accurate method for estimating the exact age at slaughter (Sales and Mellett, 1995).

The scapula is a slender, flat bone. Its cranial end is expanded to fuse with the coracoid and it bears a deep glenoid cavity along its caudal border, just proximal to coracoid. A large tuberosity is present on its cranial surface, medially to the glenoid cavity.

The coracoid is a thick, triangular bone, with the apex proximally and the base distally. The base of the coracoid articulates with the sternum. It lies transversely and fuses proximally and medially with the scapula, leaving a large foramen in the middle.

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Thoracic limb

The skeleton of the wing consists of a humerus, radius and ulna, carpus, metacarpus and digits (Figs 2.1 and 2.4). The wing is relatively long in the ostrich compared with other ratites.

The humerus is long (400–430 mm), thin and slightly curved. Its proximal end bears an elongated, low head for articulation with the glenoid cavity of the scapula, and a large ventral tuberculum for the attachment of muscles. The shaft is rounded and bears a low, sharp ridge along the greater part of its dorsal border. Distally the shaft expands to form a single condyle with a low supracondylar tubercle on the dorsal epicondyle. There is no pneumatic foramen.

The ulna is approximately one-third the length of the humerus and is slightly bowed. Its proximal and distal ends are enlarged to articulate with the condyles of the humerus and carpal bones, respectively. The radius is almost as long as, but slightly slimmer than, the ulna. Proximally it bears a rounded articular facet for articulation with the condyle of the humerus, and distally an articular facet for articulation with the carpal bones.

Two carpal bones are present. The radial carpal bone is the larger of the two and consists of the fused radial, central and intermediate carpal bones (Friant, 1959). By contrast, Broom (1906) states that the radial carpal bone contains elements of the first, second and third carpal bones. This bone articulates proximally with the radius and ulna and distally with the carpo-metacarpus. The smaller ulnar carpal bone articulates proximally with the ulna and distally with the carpo-metacarpus. All the other carpal elements fuse to the proximal ends of the metacarpal bones.

During early embryonic development four metacarpal bones are present (Broom, 1906), but only three are seen in the adult. Their proximal ends fuse with the distal row of carpal bones and with each other to form the carpo-metacarpus. The first metacarpal is short and fuses over its entire length with the second metacarpal bone. Distally it articulates with the first phalanx of the alular digit. The second metacarpal is straight and the thickest of the three. Distally it articulates with the first phalanx of the second digit. The third metacarpal is strongly bowed. It is fused to the proximal and distal ends of the second metacarpal and articulates distally with the proximal phalanx of the third digit. The first (alular) digit has two phalanges, the second (major) digit has two phalanges and the third (minor) digit has one phalanx (Friant, 1959).

Pelvic girdle

The elongated pelvic girdle consists of the paired ilium, ischium and pubis. The bones fuse to each other to form a very strong attachment for the pelvic limb and its associated muscles. Broom (1906), Friant (1959) and von Blotzheim (1960) give more details on the comparative ontogeny of the pelvic girdle.

The ilium is broad, flat and oriented perpendicularly, and is approximately

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600 mm long. The left and right ilia fuse to each other along the dorso-cranial midline to form a boat-like structure which accommodates and fuses to the synsacrum. The acetabulum, for articulation with the head of the femur, lies at the junction of the cranial and middle thirds of the ilium and is open medially. Caudodorsally to the acetabulum is a large articular surface, the antetrochanter, for articulation with the major trochanter of the femur. The ilium fuses cranioventrally with the pubis and caudoventrally with the ischium.

The pubis is long, slender and S-shaped and is approximately 640 mm long. Cranially it fuses with the ilium to contribute to the formation of the acetabulum. Caudally the pubis bends ventromedially to fuse with the pubis of the opposite side, to form a pubic symphysis which is thought to relieve abdominal pressure when the bird is recumbent (King and McLelland, 1984). The cranioventral end of the pubis forms a variably developed preacetabular tubercle (pectineal process). A small plate of bone is attached to the ventral surface towards the middle of the pubis (Fig. 2.7).

The ischium is a long, slender bone that lies dorsomedially to the pubis. It measures approximately 380 mm in length. Cranially it fuses to the ilium to contribute to the formation of the acetabulum. It also fuses to the pubis in two areas, one cranially and one caudally, creating two openings between the two bones. The cranial opening (obturator foramen) lies caudoventrally to the acetabulum, the larger, caudally situated opening is the ischiopubic window (fenestra ischiopubica).

Pelvic limb

The pelvic limb consists of the femur, patella, tibiotarsus and fibula, tarsometatarsus and digits (Fig. 2.2). The femur is a relatively short, but thick bone, measuring about 300 mm in length. Proximally it bears a head and neck, and a large trochanter. The head of the femur is rounded for articulation with the acetabulum and bears a deep depression for the attachment of the capital ligament. The femoral trochanter lies on the same level as the head and bears an elongated articular surface along its dorsomedial border for articulation with the antetrochanter of the ilium. This articulation is thought to reinforce the weak adductor muscles (King and McLelland, 1984). A large pneumatic foramen is present on the caudal surface of the femur, medioventrally to the trochanter.

The shaft of the femur is oval in outline and bears a number of ridges and tubercles for the attachment of muscles. Distally the shaft widens to form two epicondyles for muscle and ligament attachments, and two condyles for articulation with the tibia. Cranially the condyles are separated by a wide intercondylar groove for articulation with the patella. The distal surface of the lateral epicondyle bears an articular surface for the head of the fibula. The medial epicondyle is small. The patella is large and flattish with medial and lateral articular surfaces (MacAlister, 1864). A 'second patella' is present distal to the patella (see Arthrology, femoral-tibial joint, below).

The tibiotarsus is formed by the fusion of the tibia and proximal row of tarsal

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bones. At 550 mm it is almost twice as long as the femur. Its proximal end is wide and flat, bearing lateral and medial condyles for articulation with the condyles of the femur. The two articular surfaces are separated by an interarticular area for the attachment of ligaments. The cranial part of the proximal end is greatly expanded, forming a large ridge, the proximal end of which divides to form lateral and medial cnemial crests. The caudal surface of the tibiotarsal shaft is flattened, the cranial surface is rounded. The distal end is expanded to form lateral and medial condyles for articulation with the tarsometatarsus. The lateral and medial condyles are separated by a wide articular groove (sulcus cartilaginous tibialis). Relatively small lateral and medial epicondyles for the attachment of ligaments are present proximally to the corresponding condyles.

The fibula is shorter than the tibia, measuring about 400 mm in length . The proximal, expanded head of the fibula is attached to the lateral condyle of the tibiotarsus and bears two articular surfaces for articulation with the lateral condyle and epicondyle of the femur. The shaft of the fibula tapers to a point and is attached to the proximal end of the tibiotarsus.

The tarsometatarsus is formed by the fusion of the distal row of tarsal bones and the second, third and fourth metatarsal bones. In the early embryo all five metatarsals are present (Broom, 1906). The proximal end bears lateral and medial articular condyles. A single ridge, the hypotarsus, is present on its caudal surface. Medially to the hypotarsus is a single hypotarsal groove for the passage of tendons. Cranially the proximal end has a shallow groove for the passage of tendons. Just distal to the condyles, on the dorsal surface of the tarsometatarsus, is a large and deep depression, the dorsal infracondylar fossa which contains two canals that open on the plantar surface of the bone.

The shaft of the tarsometatarsus is triangular in outline and flattened dorsally. The dorsal surface bears a wide, shallow groove, while the plantar surface bears a ridge which is the continuation of the hypotarsus. The distal end bears three trochlea, a rudimentary one medially, a large one centrally and a smaller one laterally (Friant, 1959) which articulates with the first phalanx.

Two visible digits are generally present, although there are reports of three-toed ostriches (Hewitt, 1913). Riley (1836) showed that the number of toes present in the ostrich is the same as in the rhea and cassowary (three toes), although in the ostrich the innermost toe is rudimentary and completely covered by the skin. Dissection of a large number of legs indicates that remnants of the innermost toe are present in most specimens. In some the phalanges are well developed, in others they are merely fibrous strands of tissue. The medial toe represents digit II, the main toe is digit III and the smaller, outer toe is digit IV. The remnant digit II can have three phalanges, digit III has four and digit IV has five (Nassonov, 1896; Allis, 1838; Friant, 1957). The distal phalanges of digits III and IV are claw-shaped.

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ARTHROLOGY

Several studies have investigated the anatomy of joints in the ostrich. These are summarized here, and further details can be obtained from Langer (1859), Wyman (1863), MacAlister (1864) and Firbas and Zweymüller (1971).

Head

At the mandibular joint the quadrate bone is interposed between the mandible, jugal and pterygoid on the one hand and the squamous and basisphenoid bones on the other. The articulation between the skull and jaws therefore consists of five separate synovial joints (quadratomandibular, quadratojugal, quadratopterygoid, pterygobasisphenoidal and quadratosquamosal). The joints of the upper jaw are represented by moveable, elastic areas in the bones of the face. A simple synovial joint lies between the occipital bone and the atlas.

Vertebral column and ribs

There are articulations between the caudal and cranial ends of successive vertebral bodies, and articulations between opposing articular processes of successive vertebrae. Both are generally synovial joints. In the caudal thoracic, lumbar and sacral series the joints ancylose. Some of the intercorporal joints contain an intervertebral meniscus. Jäger (1858) provides comparative detail of the joints of the vertebral column.

The joint between the head of the rib and the vertebral body is cartilaginous (synarthrosis), while the joint between the tubercle of the rib and the transverse process of the vertebra is a synovial joint (Baumel *et al.*, 1993). The vertebral and sternal ribs are joined by a fibrous joint. Each sternal rib articulates with the sternum by means of two separate synovial joints.

Thoracic limb

The sterno-coracoid articulation is a synovial joint. The coraco-humeral connection is a condylar synovial joint. Distally the humerus articulates with the ulna and radius and one compound synovial joint is formed by the three bones (they share a common synovial capsule). Both proximal and distal ends of the radius and ulna are connected by fibrous joints. The wrist is a compound synovial joint formed by the ulna, radius, radial and ulnar carpal bones and the proximal end of the carpometacarpus (Streseman, 1934). The proximal ends of the carpometacarpal bones ancylose with each other. Distally, a synovial articulation is formed between the carpometacarpal bones and the first phalanges of each digit. Interphalangeal synovial joints are present between all the phalanges of the digits.

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Pelvic girdle and limb

The ilium, ischium and pubis ancylose to form the bony pelvis. Caudoventrally the left and right pubic bones are attached to each other by fibrous connective tissue to form a pubic symphysis. In older birds the connective tissue ossifies. Extensive ancyloses are also formed between the ilium and the vertebral column of the region.

The hip joint is surrounded by an extensive synovial capsule. A strong band passes from the ischium to the upper, caudal edge of the acetabulum. The ligament of the femoral head passes from the lower border of the acetabulum to the femoral head (Figs 2.7 and 2.8). A cartilaginous acetabular ridge is present on the dorsal and cranial edges of the acetabulum and serves to enlarge the articular surface. The articular cavity is separated from the deeper-lying air sacs by a strong membrane.

The stifle (knee) is formed by the condyles of the femur, patella, tibiotarsus and fibula. Two menisci are present on the articular surface of the tibiotarsus, with the medial meniscus being smaller than the lateral one. The menisci are attached to the tibiotarsus and fibula by cranial and caudal meniscotibial ligaments. A transverse ligament attaches the cranial horns of the two menisci to each other. Lateral and medial collateral ligaments extend from the epicondyles of the femur to the tibiotarsus and fibula.

Two cruciate ligaments are present in the stifle. The cranial cruciate ligament arises on the caudal aspect of the medial condyle and inserts on to the cranial edge of the medial meniscus and cranial border of the medial condyle of the tibiotarsus. The caudal cruciate ligament passes from the caudal and dorsal part of the intercondylar groove of the femur and inserts on the hypotarsus.

The patella is attached proximally to muscle whereas distally it is attached to the tibiotarsus by means of a wide tendon. A long, bony column ('second patella') extends from the medial, lower edge of the patella to the cranial bony ridge of the tibiotarsus. The bony column is proximally attached to the tibia by short ligaments and distally it articulates with the tibiotarsal ridge by means of a small synovial joint and to the ridge by short ligaments.

The intertarsal articulation is a simple, synovial hinge joint. A single meniscus is attached to the tarsometatarsus by one dorsal and one plantar ligament. All the metatarsophalangeal and interphalangeal synovial joints of the toes are held together by lateral and medial collateral ligaments.

MYOLOGY

Most of the literature on the muscular system of the ostrich dates from the 19th century (MacAlister, 1864; Garrod and Darwin, 1872; Gadow, 1880). There have been repeated but largely unsuccessful attempts to establish homology between muscles in birds and their counterpart in mammals. It is suggested that those interested in the myology of the ostrich should refer to Baumel *et al.* (1993).

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Head

The muscles of the eye and eyelid were described by MacAlister (1864). The M. levator palpebrae dorsalis is the elevator of upper eyelid and arises from the dorso-caudal aspect of the bony orbit and inserts into the tarsal border of the eyelid. The M. orbicularis palpebrarum consists of transverse fibres in the lower lid of the eye. The M. quadratus membranae nictitantis and M. pyramidalis membranae nictitantis move the nictitating membrane.

The muscles of the eyeball arise around the optic foramen and attach to the sclera of the eyeball behind the scleral ossicles. These muscles (M. rectus dorsalis, M. rectus ventralis, M. rectus lateralis, M. rectus medialis, M. obliquus dorsalis and M. obliquus ventralis) collectively rotate the eye in all directions.

MacAlister (1864) identified two elevator muscles of the lower jaw: the M. pseudotemporalis superficialis and M. pseudotemporalis profundus. The superficial muscle arises from the caudal part of the temporal fossa, almost as far back as the occipital bone, and inserts rostrally to the coronoid process on the ramus of the mandible. The deep muscle arises more rostrally in the temporal fossa and inserts on the small coronoid process of the mandible. In addition to these muscles, Garrod and Darwin (1872) also identified the M. pterygoideus, M. quadrato-mandibulae and M. quadrato-cranialis.

The following hyobranchial muscles are present (terminology of MacAlister, 1864 in brackets): the M. intermandibularis ventralis (mylo-hyoid) arises from the rostral four-fifths of the mandible and inserts on a median raphe and the hyoid bone. The M. branchiomandibularis (maxillo-keratic) arises just rostral to the condyle of the mandible and inserts on the ceratobranchial element of the hyoid. The M. interceratobranchialis is a small muscular slip that passes from one ceratobranchial element to the other. The M. genioglossus (genio-hyoid) originates from the symphyseal part of the mandible and inserts on the ceratobranchial element of the hyoid. The M. hypoglossus ventralis (hyoglossus) arises from the entoglossal element of the hyoid and passes rostrally into the tip of the tongue.

The following muscles were identified and described by MacAlister (1864) and his terminology is given in parentheses. The M. cricohyoideus (hyolaryngeus and thyrohyoid) consists of three parts which pass from the cricoid cartilage of the larynx to the rostral and caudal basibranchial elements of the hyoid. The M. constrictor glottiditis (proper arytenoid) and M. dilator glottidits (posterior dilator), as well as a crico-arytenoid muscle, are mentioned.

Neck

An extensive cutaneous muscle, M. cucullaris (platysma of MacAlister, 1864) extends from the coracoid along the ventral and lateral aspects of the neck as far as the head. It attaches to the skin of the neck. Additional cutaneous muscles extend dorsally from the sternum to the caudal cervical region. The M. sternotrachealis arises from the craniodorsal aspect of the sternum. It passes cranially

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along the lateral surface of the trachea, to which it is attached, and inserts on the cricoid cartilage and ceratobranchial bone (MacAlister, 1864).

A series of short muscles attach the head and neck (rectus capitis muscles). The musculature of the cervical vertebrae is complex, consisting of a large number of muscular fascicles that extend from one vertebra to the next. Of these, the intertransverse muscles, connecting transverse processes to the vertebral arch, form the principal lateral musculature of the neck. The M. longus colli ventralis forms the principal ventral musculature and the M. longus colli dorsalis the principal dorsal musculature of the neck.

Trunk

Some of the muscles of the cervical vertebrae are continued into the thoracic region. In addition, there are also the muscles that attach the wing to the trunk.

The external intercostal muscles lie superficially in the proximal intercostal spaces as far distally as the uncinate processes of the ribs. The internal intercostal muscles lie deep to the external muscles, but extend for some distance beyond the uncinate process. Two additional series of muscles are present: the first extend from uncinate processes of the ribs to the distal ends of the vertebral ribs, the other from the vertebrae to the proximal ends of the ribs (levatores costales and levatores costales posteriores of MacAlister, 1864). Costoseptal muscles (diaphragm of MacAlister) extend from the ribs to the horizontal septum. During embryonic development the post-pulmonary septum is split into two by the developing airsacs. The dorsal part of the split septum is the horizontal septum, the ventral part forms the oblique septum. The horizontal septum subsequently fuses to the ventral surface of the lungs.

There are four muscles that form the abdominal wall. These are the external oblique, internal oblique and transverse abdominal muscles, and a small rectus abdominis muscle. All the muscles have extensive aponeuroses that insert on the linea alba, pubis and sternum.

Muscles associated with the ilium and vertebral column are, from lateral to medial, the M. iliocostalis et longissimus dorsi and M. longus colli pars thoracica (semispinalis dorsi, longissimus dorsi and spinalis dorsi of MacAlister, 1964). A small, triangular scalenus muscle extends from the last cervical vertebra to the proximal end of the first rib (MacAlister, 1864). MacAlister (1864) described three muscles associated with the tail: the M. levator caudae (levator coccygis), M. depressor caudae (depressor coccygis) and the M. bulbi rectricium (coccygeus).

Pectoral girdle and limb

Most of the muscles found in the pectoral girdle and wing of birds are also present in the ostrich but they are poorly developed. MacAlister (1864) described the following muscles in some detail (his terms in parentheses): M. latissimus dorsi,

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M. rhomboideus superficialis and profundus (rhomboideus major and minor), M. serratus, M. pectoralis (great pectoral), M. supracoracoideus (second pectoral), M. coracobrachialis, M. subscapularis, M. biceps brachii (biceps), M. deltoideus major (deltoid), M. deltoideus minor (teres minor), M. triceps brachii, consisting of two parts, the scapulotriceps and humerotriceps (extensor cubiti), and M. brachialis (brachialis anticus).

Pelvic girdle and limb

The muscles of the pelvic limb are well developed and form an important part of the dressed commercial carcass. These muscles were described by MacAlister (1864), with additions by Garrod and Darwin (1872). Haughton (1865) discussed the anatomy and muscular mechanics of the ostrich, while Gadow (1880) reported on the comparative anatomy of the pelvic limb of ratites. More recently, Mellett (1994) illustrated the muscles of the proximal limb and updated the nomenclature to comply with Baumel *et al.* (1993). Mellett (1994) also determined the mean mass of the proximal thigh muscles in slaughter ostriches (see Sales, Chapter 10).

The muscles of the hip and stifle joints are illustrated in Fig. 2.2 and are as follows. The M. iliotibialis cranialis extends from the cranial aspect of the ilium to the medial surface of the stifle. It is the most cranial muscle of the hip and thigh region. The M. ambiens originates from the lateral surface of the ilium, deep to the iliotrochantericus cranialis, and inserts on the tendon of the superficial flexor muscles (see below). Contrary to the position in other birds, the pectineal muscle (M. pectineus) originates on the pectineal protruberance and inserts on the medial aspect of the proximal tibia.

The M. iliofemoralis externus is a short muscle taking its origin from the ilium, caudal to the iliotibialis cranialis, and inserts on the femoral trochanter. The internal iliofemoral muscle (M. iliofemoralis internus) lies deep to the external iliofemoral muscle. It extends from the ilium to the medial aspect of the

Fig. 2.2 (opposite). Musculature of the proximal pelvic limb (after Mellett, 1994). (a) Muscles of the superficial layer of the right pelvic limb, lateral view; (b) muscles of the second layer of the right pelvic limb, lateral view; (c) muscles of the third and fourth layers of the right pelvic limb, lateral view; (d) medial muscles of the pelvic limb, cranial view of the right leg. 1, M. Iliotibialis cranialis; 2, M. ambiens; 3, M. iliofemoralis externus; 4, M. iliotibialis lateralis; 5, M. iliofibularis; 6, M. flexor cruris lateralis; 7, M. opturatorius medialis; 8, M. femorotibialis medius; 9, M. fibularis longus; 10, M. gastrocnemius; 11, M. flexor cruris lateralis; 12, M. iliotrochantericus; 13, M. iliofemoralis internus; 14, M. iliotrochantericus caudalis; 15, M. femorotibialis accessorius; 16, M. femorotibialis externus; 17, M. ischiofemoralis; 18, M. iliofemoralis; 19, M. pubo-ischio-femoralis; 20, M. flexor cruris medialis; 21, M. femorotibialis internus; 22, M. pectineus; A, acetabulum; F, femur; IL, ilium; PS, pubic symphysis; T, tibiotarsus.

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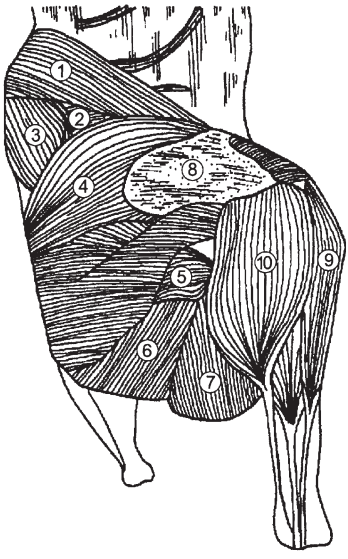

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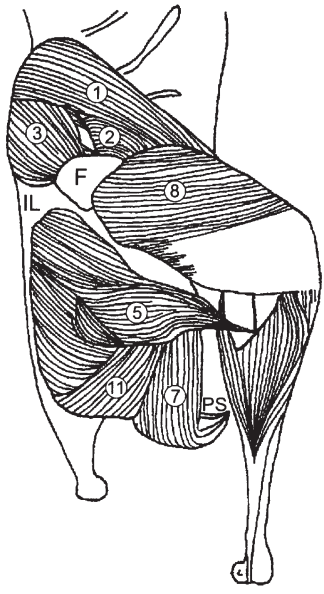

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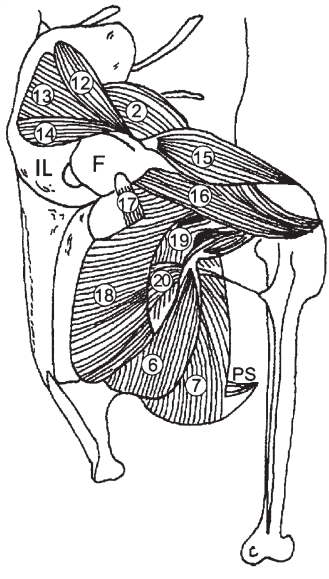

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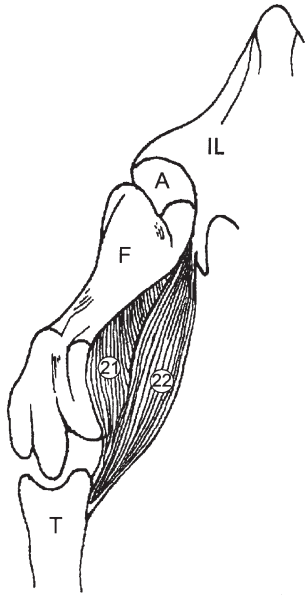

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femoral trochanter. The M. iliotrochantericus caudalis lies immediately caudal to the iliofemoralis internus and extends from the ilium to the femoral trochanter. By contrast, the M. iliotrochantericus cranialis lies cranially to the iliofemoralis internus and extends from the ilium to the femoral trochanter, immediately distal to the caudal iliotrochanteric muscle. The lateral iliotibial muscle (M. iliotibialis lateralis) is broad and flat. It takes its origin from the ilium, caudally to the external iliofemoral muscle. The cranial part of the muscle passes over the lateral aspect of the hip joint and inserts on the lateral region of the stifle. The M. iliofibularis takes its origin from the lateral aspect of the ilium, deep to the lateral iliotibial muscle and inserts laterally on the proximal fibula and lateral head of the gastrocnemius muscle. The M. iliofemoralis also takes its origin from the lateral aspect of the ilium but inserts on the proximal, medial aspect of the femur.

The M. flexor cruris lateralis is the most caudal of the thigh muscles, taking origin from the caudal point of the ilium and surrounding fascia, and inserts distally on the medial aspect of the femur. By contrast, the M. flexor cruris medialis extends from the caudal part of the ilium, deep to the iliofemoral muscle, to the medial aspect of the stifle. The M. pubo-ischio-femoralis takes its origin from the ischium and pubis, deep to the flexor cruris medialis, and inserts on the medial aspect of the distal femur. The M. ischiofemoralis is a deep, short muscle extending from the ischium to the proximal, caudomedial aspect of the femur. The medial obturator muscle (M. obturator medialis) takes its origin from the ischium and pubis, filling the ischiopubic window, and inserts on the proximal, medial part of the femur.

The M. femorotibialis medius lies laterally on the femur, covered by the lateral iliotibial muscle. It takes its origin from the shaft of the femur, distal to the femoral trochanter and inserts laterally on the patella. The M. femorotibialis accessorius lies cranially on the femur and inserts on the patella. The M. femorotibialis externus takes its origin from the caudal part of the proximal femur, just distal to the femoral trochanter and inserts by means of a flat tendon on the proximal tibia. By contrast, the M. femorotibialis internus lies medially along the shaft of the femur and inserts on the medial aspect of the patella.

MacAlister (1864) described seven muscles that act on the metatarso-phalangeal and interphalangeal joints. More recently, Pavaux and Lignereux (1995) described 16 muscles in the shank and foot, while Liswaniso (1996) studied the morphology and diagnostic imaging of the distal pelvic limb of the ostrich.

The M. gastrocnemius is the powerful extensor of the hock joint. Its four heads take origin from the distal end of the femur, the patella, collateral ligaments and the tibiotarsus (MacAlister, 1864). The heads unite to form a broad (40–50 mm wide) tendon that passes over the plantar surface of the hock, inserting on the plantar surface of the tarsometatarsus as far distally as the distal third. The M. tibialis cranialis is the flexor of the hock. It has two heads which take origin from the lateral condyle of the femur and medial aspect of the tibiotarsus. Distally, the tendon is held in position on the dorsal aspect of the tibiotarsus by an annular ligament. The tendon divides into two and inserts on the distal, dorsal aspect of the tarsometatarsus. The M. fibularis longus is well developed,

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taking its origin from the proximal end of the fibula and inserting on the tarsometatarsus, whilst the M. fibularis brevis is represented only by the tendon of insertion.

The M. extensor digitorum longus takes its origin from the proximal tibia, its tendon is held in position on the dorsal aspect of the hock by an annular ligament and it inserts on the first phalanges of digits III and IV. The M. extensor propius digiti III is a delicate muscle, unique to ratites and tinamous, which extends from the lower part of the tibiotarsus to phalanx IV of digit III. Both M. extensor brevis digiti IV and M. extensor brevis digiti III are small and insignificant. The lumbricalis muscle (M. lumbricalis) lies between the superficial and deep flexor muscles. It originates from the tendon of the deep flexor and inserts on the superficial tendons to digits III and IV.

The flexors of the toes can be grouped into superficial, intermediate and deep muscles. The superficial muscles include the M. flexor perforatus digiti III which arises by means of two heads, one from the femur and the other from the lateral collateral ligament of the stifle. Its tendon divides into three and inserts on phalanx I of digit III, phalanx II of digit IV and phalanx III of digit III. The M. flexor perforatus digiti III has two heads which originate from the distal femur, lateral collateral ligament and fibula. It also receives the tendon of the M. ambiens. The united tendon is perforated by the M. flexor perforatus digiti III and inserts on the base of phalanx II, digit III. The M. flexor perforans et perforatus digiti III is intermediate and has two heads that originate from the proximal tibia and lateral collateral ligament. Its tendon perforates the tendon of the superficial flexor and is in turn perforated by the tendon of the deep flexor before its insertion on the flexor surface of phalanx III, digit III. The M. flexor digitorum longus is deep and arises by means of two heads from the femur and proximal tibia. The tendons unite near the metacarpo-phalangeal joint and then divide to insert on phalanx IV of digit III and phalanx V of digit IV. The M. abductor digiti IV arises from the tibia and inserts on the base of phalanx I, digit IV.

CARDIOVASCULAR SYSTEM

Heart

The heart, contained in the pericardium, lies vertically in the cranioventral part of the thorax and is surrounded by the sternum, the first three sternal ribs and the two lobes of the liver. The medial compartment of the clavicular air sac separates the base of the heart from the oesophagus and trachea, and the intrathoracic diverticulum separates the heart from the sternum. The heart of the ostrich differs from the heart of mammals in that it receives both a right and a left cranial vena cava (Fig. 2.3), and that the right atrio-ventricular valve is a muscular flap (Bezuidenhout, 1981). The coronary circulation has been described by Bezuidenhout (1984). The heart rate of ostriches 2–3 months old is approximately 80 beats min^{-1}, while that of the adult is 30–60 beats min^{-1}.

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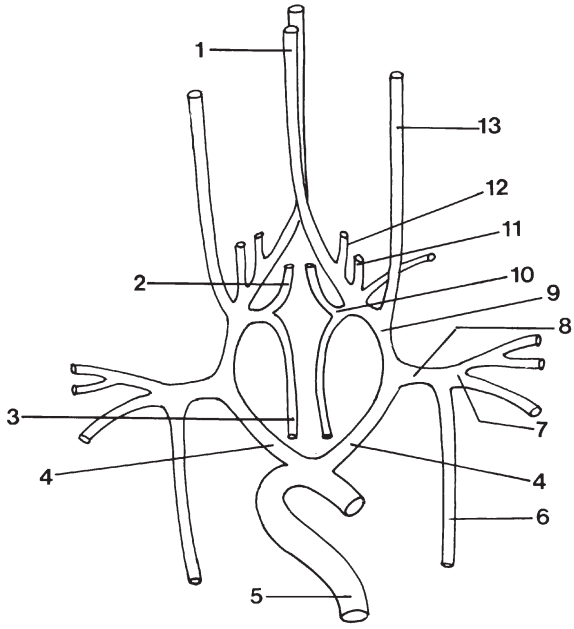

Fig. 2.3. Arteries at the base of the heart, schematic, dorsal view. 1, Internal carotid artery; 2, ascending vertebral artery; 3, descending vertebral artery; 4, brachiocephalic trunk; 5, aorta; 6, internal thoracic artery; 7, axillary artery; 8, subclavian artery; 9, common carotid artery; 10, vertebral trunk; 11, oesophagotracheal artery; 12, ascending oesophageal artery; 13, cervical artery.

Arteries

The pulmonary trunk leaves the right ventricle and passes dorsally, caudally and to the left (Fig. 2.7). This trunk lies cranially to the aorta and, after a short course, divides into left and right pulmonary arteries. The vessels enter the hilus of the lung dorsally to the bronchus and are distributed with the bronchial tree. According to MacAlister (1864) the left artery is larger than the right.

The aorta leaves the left ventricle and immediately gives off the left and right coronary arteries. As the aorta arches cranially (ascending aorta) it gives off the brachiocephalic trunks (Figs 2.3 and 2.8), turns dorsally (aortic arch) and then caudally (descending aorta). Glenny (1965) provides further details of the brachiocephalic trunks.

The vertebral arteries pass cranially through the transverse foramina of the cervical vertebrae, supplying the surrounding structures along their course. The left and right internal carotid arteries converge and ascend along the ventromedian aspect of the cervical vertebrae, covered by the ventral neck muscles. The vessels are fixed in this position, making them accessible for the collection of arterial blood. As the arteries approach the head at the level of the second

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cervical vertebra, they diverge and come to lie superficially. Elias *et al.* (1996) describe their division and distribution. The major arteries of the wing are shown in Fig. 2.4 (Bezuidenhout and Coetzer, 1986).

The descending aorta passes between the lungs, and at the level of the last thoracic rib it penetrates the horizontal septum. As the aorta continues caudally it gives off a variety of vessels. The coeliaca artery divides to supply the spleen, terminal oesophagus and proventriculus, gizzard and first part of the duodenum, and the liver. The cranial mesenteric artery goes to the pancreas, small intestine, caeca and part of the large intestine. The cranial renal arteries go to the kidneys. The testicular arteries come off the renal arteries or directly from the aorta, caudal to the cranial renal arteries. In the female the large left ovarian artery is generally a branch of the left cranial renal artery. Additional testicular/ovarian arteries can arise directly from the aorta. The external iliac artery gives off a branch to the oviduct before it supplies the femoral artery to the cranial femoral region. The ischiadic artery accompanies the ischiadic nerve along the caudomedial aspect of the limb to supply vessels to the kidneys, oviduct, caudal part of the thigh and the distal part of the limb (the middle renal arteries come off the ischiadic artery or directly off the aorta). In the distal limb the main artery lies dorsally on the tarso-metatarsus (dorsal metatarsal artery) and is well protected, lying laterally to the extensor tendons and covered by a thick layer of fascia. This vessel divides distally to supply both toes. The caudal mesenteric artery supplies to the large intestine and the internal iliac artery goes to the cloaca and associated structures.

Veins

The left and right pulmonary veins drain the lungs, lie ventrally to the bronchi and enter the left atrium independently (Bezuidenhout, 1981) or may unite just before they enter the left atrium. The veins draining the head follow the pattern of the arterial supply (Elias, 1996) with most of the veins eventually opening into the external jugular veins. The left external jugular vein is small, whereas the right external jugular vein is very large. The latter receives most of the blood from the left side of the head and forms a large arch ventrally to the second cervical vertebra, but superficial to the internal carotid arteries. The position of this arch is important during slaughter and subsequent bleeding of the carcass. The right jugular vein descends in the neck, caudally and laterally to the oesophagus, where it is accessible for venipuncture.

The veins that drain the wing (Fig. 2.5) join to form the axillary vein (Bezuidenhout, 1986). This enters the thorax where it is joined by veins draining part of the thoracic wall and neck to form the subclavian vein. The subclavian and external jugular veins join at the thoracic inlet, laterally and caudally to the sternotracheal muscle, to form the cranial caval vein. The right cranial caval vein is substantially bigger than the left, although both cranial caval veins receive azygous veins. The left azygous vein begins at the level of the ovary/testis and drains

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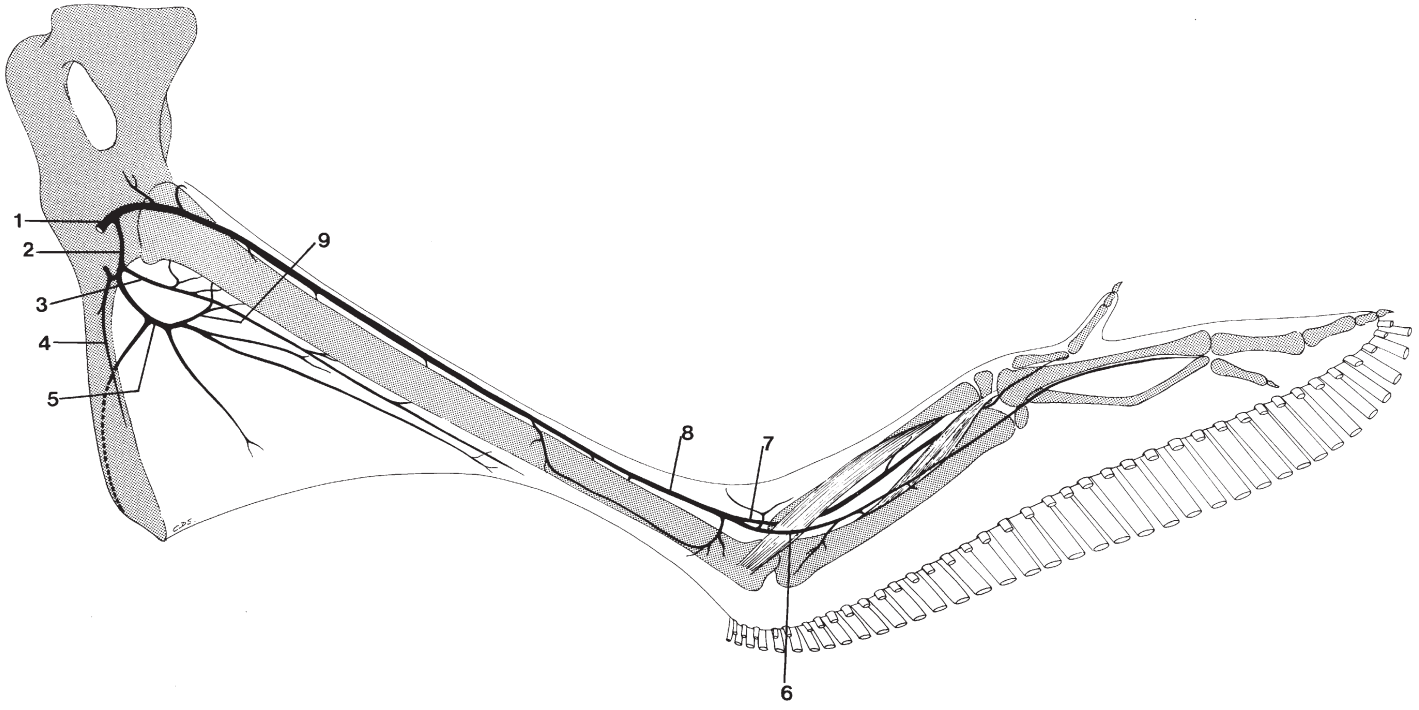

Fig. 2.4. Main arteries of the wing. 1, Axillary artery; 2, deep brachial artery; 3, collateral ulnar artery; 4, subscapular artery; 5, collateral radial artery; 6, ulnar artery; 7, radial artery; 8, brachial artery; 9, dorsal circumflex humeral artery.

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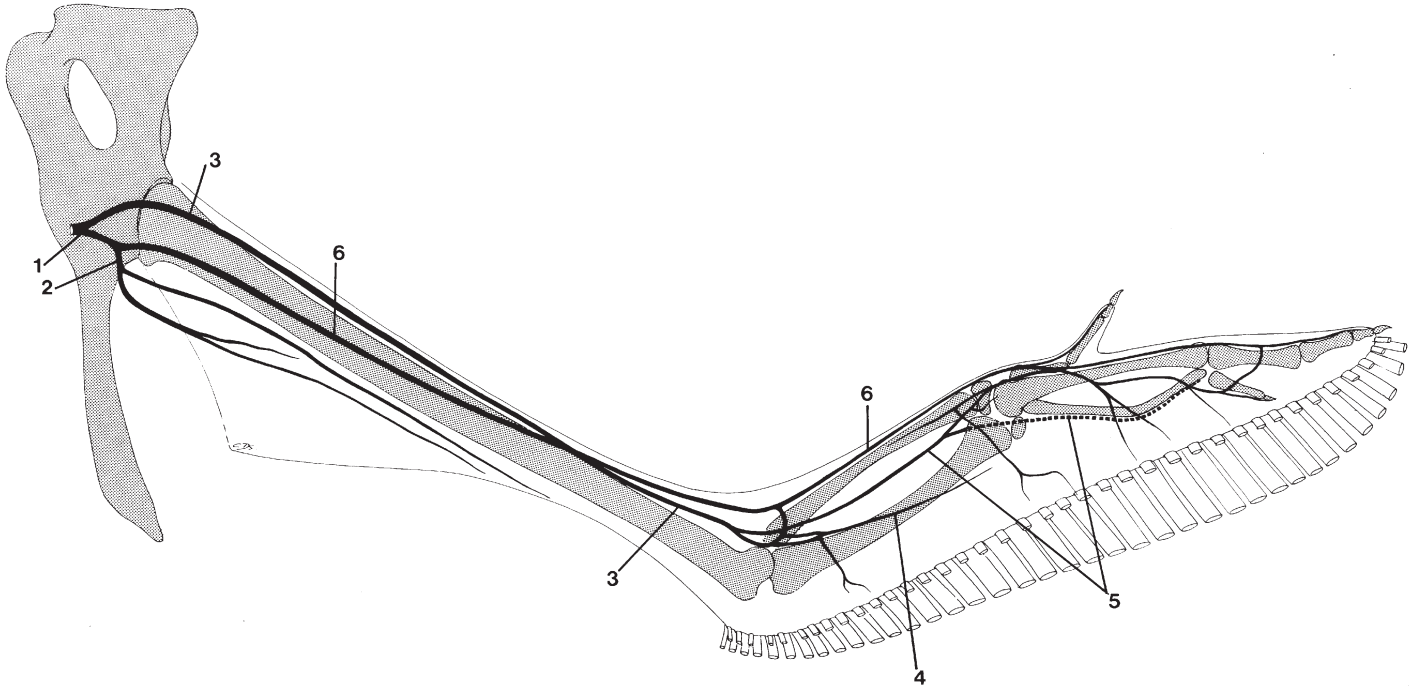

Fig. 2.5. Main veins of the wing. 1, Axillary vein; 2, deep brachial vein; 3, brachial vein; 4, ulnar vein; 5, radial vein; 6, basilic vein.

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the left body wall. The right azygous vein is very small (MacAlister, 1864). The caudal vena cava drains the entire caudal part of the body and is formed by the confluence of the common iliac veins. All caval veins enter the right atrium.

The superficial metatarsal vein drains the distal part of the pelvic limb. It lies on the medio-plantar aspect of the tarso-metatarsus, passing in the groove between the tarso-metatarsus and the flexor tendons. In this location the course of the vessel is superficial and visible, making it accessible for venipuncture (compare the position of the artery and vein in the metatarsal region). Proximally the metatarsal vein joins the popliteal vein which in turn drains into the ischiadic vein, which receives the blood from the distal limb and the caudal part of the proximal limb, whereas the femoral vein drains the cranial part of the proximal limb only.

Birds have a renal portal system (Fig. 2.6), i.e. blood from the pelvic limbs and pelvis pass through the kidneys and the flow is regulated by valves (described by Oelofsen, 1977). The veins draining the pelvic wall and viscera join to form the internal iliac vein which drains into the caudal renal portal vein. More cranially the caudal renal portal vein receives the ischiadic and external iliac veins from the pelvic limb. Beyond the junction with the external iliac vein, the caudal renal portal vein continues as the common iliac vein, which anastomoses with the caudal renal vein, and then joins the common iliac vein from the opposite side at the cranial pole of the kidney to form the caudal vena cava. The anastomosis with the caudal renal vein is guarded by three valves. As the caudal vena cava passes cranially and ventrally it receives veins from the gonads, adrenals and surrounding tissues. It passes through a groove on the dorsal surface of the liver where it receives the hepatic veins and then opens into the right ventricle.

The portal vein drains the gastro-intestinal tract. The veins of the gastro-intestinal tract are satellites of the arteries, but join to form a portal hepatic vein that enters the hilus of the liver. MacAlister (1864) described two veins: a larger right portal vein that drains into the right lobe of the liver, and a smaller, lesser portal vein that drains into the left lobe of the liver.

LYMPHATIC SYSTEM

Budras and Berens von Rautenfeld (1984) describe the topographic and functional anatomy of the lymph vessels and lymph hearts in ratites. The latter are situated ventral to the first coccygeal vertebra. For additional details of the afferent

Fig. 2.6 (opposite). Renal portal veins in relation to position of kidneys, ventral view. 1, Adrenal gland; 2, cranial lobe of the kidney; 3, external iliac vein; 4, middle lobe of the kidney; 5, ischiadic vein; 6, caudal lobe of the kidney; 7, caudal mesenteric vein; 8, caudal renal vein; 9, caudal renal portal vein; 10, renal portal valve; 11, common iliac vein; 12, caudal vena cava.

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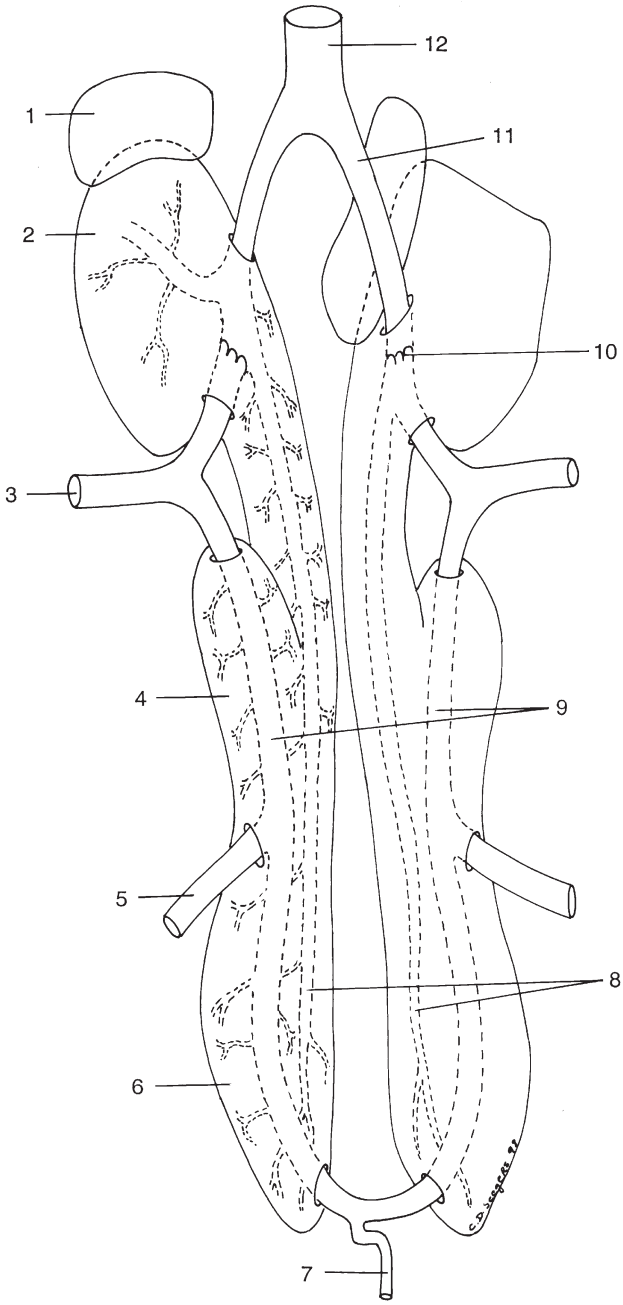

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and efferent vessels of the lymph hearts, see Budras and Berens von Rautenfeld (1984) and King and McLelland (1984).

Lymphoid tissues are found in the walls of most organs, notably in the gastro-intestinal tract, as local aggregations or accumulations. The thymus lies at the base of the neck, cranially to the first ribs (Fig. 2.7) and consists of two to four oval, lobulated bodies along the ventro-lateral borders of the neck. The right lobes lie lateral to the oesophagus, trachea and external jugular vein. The thymic lobes are largest in young animals and undergo a certain amount of involution as the birds mature. The lymphoid tissue of the cloacal bursa (Bursa Fabricii) of the ostrich lies in the dorsal wall of the proctodeum (Fig. 3.2), i.e. there is no true bursa (Berens von Rautenfeld and Budras, 1982). The spleen lies cranially to the right kidney between the sixth and eighth vertebral ribs, wedged in between the caudal vena cava on the right, the right kidney caudally and the visceral surface of the proventriculus on the left. It is sausage-shaped and enclosed in a dense layer of connective tissue and peritoneum. The spleen of an adult ostrich is approximately 80 mm long, 25 mm wide and dark reddish-brown in colour. The roof and dorsolateral walls of the oropharynx contain two large, oval and flat tonsils. They lie dorsally to the larynx and meet in the midline (Cho *et al.*, 1984). The presence or absence of lymph nodes is controversial. The only reference to lymph node-like structures in the ostrich is made by MacAlister (1864), who described them as being associated with the septa of the thoracic air sacs.

RESPIRATORY SYSTEM

Nostrils to lungs

The nostrils are oval, longitudinally arranged and face dorsolaterally (Fig. 3.4). The nasal cavity extends from the nostrils to the choanae with the left and right halves being separated by the nasal septum. The nasal cavity is divided into rostrodorsal, rostroventral and caudal compartments by nasal turbinate bones and a dorsally incomplete, transverse shelf of bone. The caudal compartment is complex, containing openings of both the lacrimal duct and the duct of the nasal gland (Fig. 3.4), and it communicates with the oral cavity and infraorbital sinus. The latter extends caudally around the dorsal, rostral and ventral parts of the eye. Its dorsocaudal limit lies just behind the medial canthus of the eye and its caudoventral limit lies caudally to the lateral canthus of the eye. The caudal compartment of each nasal cavity communicates with the oral cavity through a choana. The choanae are two oblique slits in the palate separated from each other by a low ridge of mucous membrane. Together the two choanae form a triangular opening in the palate with the apex directed rostrally.

The laryngeal skeleton consists of two cricoid and two arytenoid cartilages. The cricoid cartilages lie ventrally, and together form a ring. The mucous

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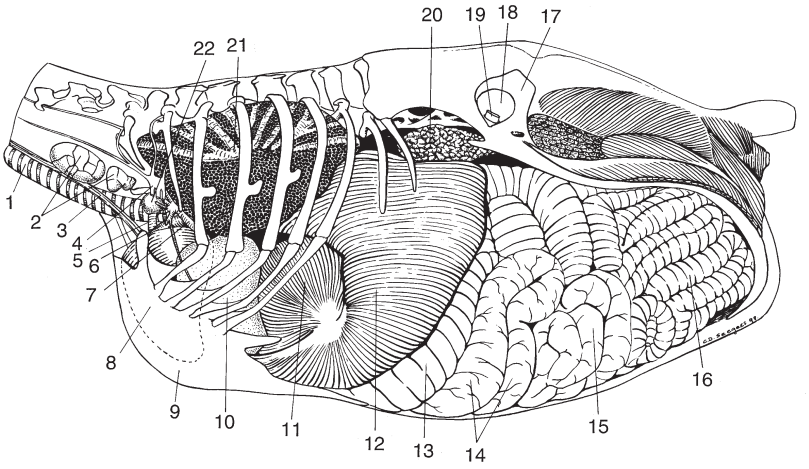

Fig. 2.7. Thoraco-abdominal viscera, left view. 1, Trachea; 2, thymus; 3, sternotracheal muscle; 4, brachial plexus; 5, left subclavian artery; 6, pulmonary trunk; 7, left cranial vena cava; 8, heart; 9, sternum; 10, left lobe of the liver; 11, gizzard; 12, proventriculus; 13, left caecum; 14, duodenum; 15, ilium; 16, rectum; 17, antetrochanter; 18, acetabulum; 19, capital ligament of the femur; 20, cranial lobe of the left kidney; 21, left lung; 22, thyroid gland.

membrane surrounding the larynx and laryngeal opening (glottis) lack papillae. The arytenoid cartilages lie dorsally, their lateral borders are serrated and the medial borders are smooth. The mucous membranes that overlie the medial borders are thickened, forming two longitudinal ridges which, when opposed by muscle action, close off the laryngeal cavity. The laryngeal opening lies caudally to the choanae and the respiratory pathway cannot be excluded from the buccal cavity. The tip of the tongue lies rostrally to the choanae and can therefore exclude off the nasal respiratory pathway from the buccal cavity.

The trachea extends from the larynx to the syrinx, is oval in transverse section and formed by approximately 200 complete, cartilaginous (MacAlister, 1864) or bony (Duerden, 1912a) rings. It lies ventrally to the cervical vertebrae. In the cranial cervical region the oesophagus lies dorsally to the trachea but when more caudally, to its right. The trachea enters the thorax and divides into the two primary bronchi.

The syrinx of the ostrich is simple and consists of the last tracheal rings and the proximal rings of the primary bronchi. Vibrating membranes are present in the walls of the bronchi (Duerden, 1912a). Forbes (1881) compared the syrinx of the various ratites. The bony rings of the bronchi are incomplete and extend into the lungs for a short distance only (Duerden, 1912a). King and McLelland (1984) give more details of the bronchi and their divisions.

The lungs lie in the dorsal third of the thorax, between the second and seventh vertebral ribs (Figs 2.7 and 2.8). They are closely bounded dorsally by the

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thoracic vertebrae and the heads of the ribs, such that the dorsal and dorsolateral surfaces of the lungs are deeply grooved. Laterally they are limited by the vertebral ribs as far ventrally as the uncinate processes and ventrally by the horizontal septum. The primary bronchus, pulmonary artery and pulmonary veins enter and leave the ventromedial (septal) surface of the lung. A series of openings along the ventral surface of the lung open into the air sacs. There is no pleural cavity. The ostrich lung is typically avian in structure. Additional details of the lung and its bronchial tree can be obtained from Schultze (1908), Duerden (1912a) and King and McLelland (1984).

Air sacs

There are ten air sacs in the ostrich (Fig. 2.9; Roche, 1880; Schultze, 1908; Bezuidenhout *et al.*, 1998). Soley *et al.* (1998) describe the ultrastructural features of the epithelial linings of the air sacs which resemble those observed in other birds, although in the ostrich ciliated and non-ciliated cuboidal elements, together with globlet cells, make up a large component of the luminal epithelium. This is in contrast with the squamous cells observed in other birds.

The cervical air sacs communicate freely with each other, forming an unpaired structure which extends up the neck as far as the head, and is closely related to the cervical and thoracic vertebrae and the vertebral canal. This air sac is vulnerable to injury at the base of the neck.

The paired lateral clavicular air sacs lie ventrolaterally in the cranial thoracic region, with sternal and axillary diverticula. The axillary diverticulum does not enter the humerus. The left and right medial clavicular air sacs fuse with each other, forming a centrally situated air sac. It has diverticula between the large blood vessels above and cranially to the heart, as well as diverticula that extend caudally along the dorsal and ventral surfaces of the oesophagus. The diverticulum along the ventral surface of the oesophagus communicates with a large gastric diverticulum. The latter extends along the caudal surface of the proventriculus, curves ventrally around its distal border and into the gizzard.

The paired cranial thoracic air sacs are small and lie ventrally to the lungs, against the ribs between the horizontal and oblique septa. They are separated from the clavicular and caudal thoracic air sacs by transverse septa. The paired caudal thoracic air sacs are larger than the cranial air sacs and occupy a similar region, but more caudally.

The right abdominal air sac is relatively small and lies to the right of the mesentery, dorsally to the liver. The left abdominal air sac is large and lies to the left of the mesentery. Both abdominal air sacs have femoral and perirenal diverticula. The femoral diverticulum enters the proximal end of the femur, invades the hip joint and forms an extensive intramuscular diverticulum. The latter diverticulum extends distally along the medial aspect of the limb to the level of the stifle (Fig. 2.9). The perirenal diverticulum extends over and around the kidneys and extends almost to the caudal limit of the abdomen.

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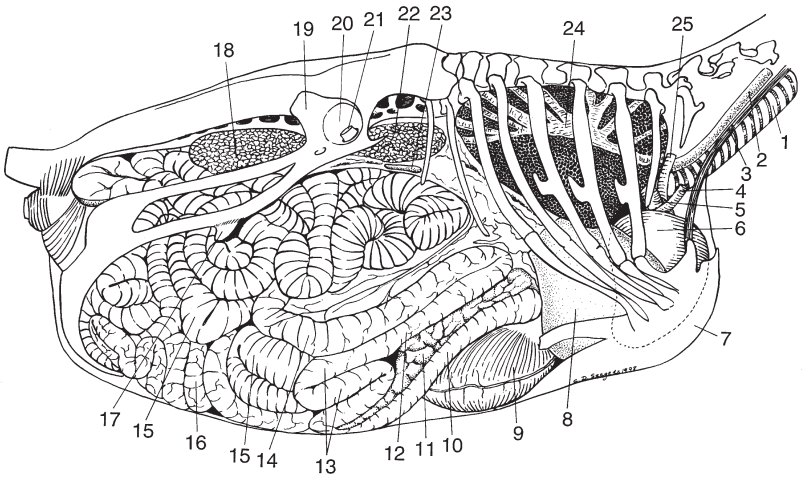

Fig. 2.8. Thoraco-abdominal viscera, right view. 1, Trachea; 2, oesophagus; 3, sternotracheal muscle; 4, right cranial vena cava; 5, aorta; 6, heart; 7, sternum; 8, right lobe of the liver; 9, gizzard; 10, descending limb of the duodenum; 11, pancreas; 12, ascending limb of the duodenum; 13, secondary loop of the duodenum; 14, jejunum; 15, rectum; 16, ileum; 17, 'marsupial bone'; 18, caudal lobe of the right kidney; 19, antetrochanter; 20, acetabulum; 21, capital ligament of the femur; 22, cranial lobe of the right kidney; 23, right testis; 24, right lung; 25, right subclavian artery.

DIGESTIVE SYSTEM

The digestive system of ratites is extensively reviewed by Gadow (1879). Here the basic anatomy of the gastro-intestinal tract is summarized, and illustrated in Figs 2.7 and 2.8.

Foregut

The oral cavity is bounded ventrally by the ramphotheca of the mandible and mucous membrane, and dorsally by the ramphotheca of the upper jaw and the palate. The tongue lies in the floor of the cavity and is small, smooth and triangular or U-shaped (Gadow, 1879; Cho *et al*., 1984). The palate of the ostrich has both hard (bony) and soft (connective tissue and mucous membrane) parts. Two openings are present in the palate, rostrally the choanae and caudally the openings of the Eustachian tubes.

The oesophagus begins dorsally to the larynx and its initial portion is very wide. The cervical oesophagus lies to the right, dorsally to the trachea and large external jugular vein. In the cranial thoracic region the oesophagus passes dorsally to the bronchi and then lies between the heart and lungs (Figs 2.7 and 2.8).

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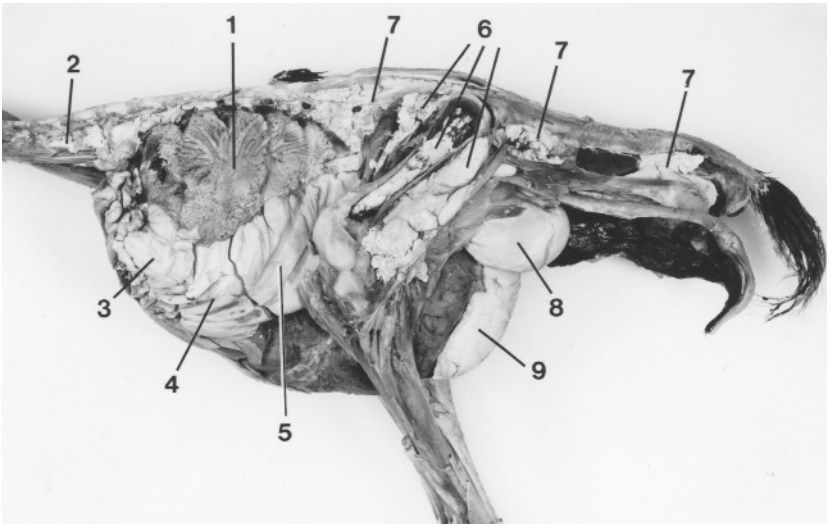

Fig. 2.9. Left lateral view of the air sacs (filled with latex) of a 3-month-old ostrich after removal of the pectoral limb, lateral body wall and laterally positioned thigh muscles. The femur has also been opened longitudinally to expose the air sac housed within the bone. 1, Lung; 2, cervical air sac; 3, lateral component of clavicular air sac; 4, cranial thoracic air sac; 5, caudal thoracic air sac; 6, femoral diverticulum of abdominal air sac; 7, peri-renal diverticulum of abdominal air sac; 8, abdominal air sac; 9, gastric diverticulum of clavicular air sac. A.J. Bezuidenhout, H.B. Groenewald and J.T. Soley, personal observations, 1998.

It is ventrally separated from the heart by the clavicular air sac. Caudally to the heart it lies between the thoracic air sacs. At the level of the sixth cervical rib the oesophagus dilates and opens into the proventriculus, although there is no sharp demarcation between these two organs (MacAlister, 1864; Bezuidenhout, 1986).

The sac-like proventriculus (Fig. 2.7) occupies the cranial part of the abdomen on the left. Its dorsal margin extends from the sixth intercostal space to as far caudally as the level of the acetabulum, depending on the amount of food in it. The caudal margin is almost vertical. It is adjacent to the left abdominal wall, and on the right of the gizzard, small intestine, caeca and colon. Distally the proventriculus turns cranially along the floor of the abdomen to open into the gizzard. The proventricular glands are restricted to an elongated area on its dorsal and caudal interior walls (MacAlister, 1864; Gadow, 1890). The glandular area is about 300 mm long, containing approximately 300 raised openings of the glands.

The biconvex gizzard lies in the cranioventral part of the abdomen (Fig. 2.7), between the liver cranially and the proventriculus caudally. Its cranial half rests on the sternum, the caudal half on the abdominal floor. The left and right tendinous centres face ventrolaterally and dorsolaterally, respectively. The duodenum leaves the gizzard on the right just above the right tendinous centre (MacAlister, 1864; Bezuidenhout, 1986).

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Small intestine

The duodenum is approximately 800 mm long and forms a narrow, extended loop with ascending and descending limbs (MacAlister, 1864; Bezuidenhout, 1986). It receives the hepato-enteric duct (bile duct) from the liver approximately 70 mm from the gizzard and the pancreatic duct at the distal end of its ascending limb. The ascending limb has a smaller, secondary loop. At the level of the seventh vertebral rib the ascending limb turns to the right to continue as the jejunum.

The jejunum is approximately 1.6 m long. It is suspended by the mesentery and forms extensive coils which occupy the cranioventral part of the abdomen, dorsal to the duodenum. In some birds it can also occupy the dorsal part of the abdomen between the right kidney and gizzard. The transition from jejunum to ileum is indicated by the vitelline (Meckel's) diverticulum on the antemesenterial side of the gut.

The ileum is the longest part of the small intestine, extending to the caeca; it measures up to 4 m in length. Suspended by the mesentery, it forms extensive coils that occupy the caudoventral part of the abdomen and pelvis.

Large intestine

The two caeca begin from a common opening at the ileo-rectal junction. They are approximately 900 mm long and extend caudally on either side of the ileum (MacAlister, 1864; Bezuidenhout, 1986). The caeca have a sacculated appearance due to the presence of an internal spiral fold which enlarges its surface area (Bezuidenhout, 1993).

The rectum (or colon) extends from the ileo-rectal junction to the cloaca. It is approximately 16 m long and occupies the dorsal part of the abdomen (Bezuidenhout, 1986). Three fairly distinct regions can be identified. The terminal part of the rectum dilates to form a sac-like structure which is often mistaken for part of the cloaca (Figs 3.2 and 3.3). In the newly hatched ostrich chick, the ratio of small intestine to rectum is 1:1, at 3 months it is 1:1.5 and at 6 months it reaches the adult ratio of 1:2.

Other organs

The liver lies within the hepato-peritoneal cavities in the caudoventral part of the thorax (Figs 2.7 and 2.8). It is bounded cranially by the heart, caudally by the gizzard, ventrally by the sternum and dorsally by the caudal vena cava, oesophagus and proventriculus. The left lobe is divided into a small caudodorsal lobe, a large caudoventral lobe and a small left intermediate lobe. The right lobe is larger than the left, but undivided. There is no gall bladder and the bile duct leaves the porta of the liver just to the left of the hepatic artery and portal vein (MacAlister, 1864; Duerden 1912a, b; Bezuidenhout, 1986).

The pancreas lies in the mesoduodenum between the two limbs of the

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duodenum. It extends from the gizzard to the end of the loop and is approximately 200 mm long. A small part can also project into the secondary loop. The pancreatic duct opens into the distal part of the duodenum (MacAlister, 1864; Duerden, 1912a, b; Bezuidenhout, 1986).

UROGENITAL SYSTEM

The kidneys (Figs 2.6–2.8) lie in the depression along the ventral surface of the synsacrum, covered by peritoneum and a variable layer of fat. They are red-brown with a granular appearance and are 300 mm long and 70 mm wide. Each kidney is divided into cranial, middle and caudal divisions by large veins. The oval cranial divisions lie between the last vertebral rib and the pelvis. The narrow middle divisions lie along the midline of the synsacrum between the two acetabula. The caudal divisions are the largest and extend from the acetabula to the middle of the pelvis. Medially they reach the midline. The pair of ureters leave the ventral, caudomedial surfaces of the kidneys, passing caudally, close to the midline and opening into the urodeum of the cloaca on small papilla (Fig. 6.4).

NERVOUS SYSTEM

Meninges

The dura mater is the outer, tough covering of the central nervous system. In the cervical and thoracic regions it is separated from the periostial lining of the vertebral canal, forming an epidural space. In the cranium, and towards the end of the thoracic region, it fuses with the periosteum of the surrounding bone. The arachnoid is a delicate membrane in contact with but not attached to the dura. On its inner surface it is attached to the pia by long threads, resulting in a substantial subarachnoid space. The pia mater is closely attached to the surface of the brain, spinal cord and associated nerves within the cranium or vertebral canal. It forms the choroid plexuses in the lateral, third and fourth ventricles (Coupin, 1924).

Central nervous system

The spinal cord is as long as the vertebral canal and lacks a cauda equina. Two distinct enlargements of the spinal cord, a small cervical and large lumbosacral, are associated with the brachial and lumbosacral plexi, respectively (Streeter, 1904). In the dorsal midline of the lumbosacral enlargement is a long, rhomboid sinus which contains a gelatinous body. The dorsal and ventral roots of the spinal nerves penetrate the dura separately and unite in the intervertebral foramen.

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The medulla oblongata of the hindbrain (rhombencephalon) is the continuation of the spinal cord into the cranium. Its dorsal surface contains a large rhomboid fossa which forms the floor of the fourth ventricle. Ventrally the medulla has a groove which contains the basilar artery. The medulla gives rise to cranial nerves V to XII. The pons can be seen as a broad, flat bundle of transverse fibres at the rostral end of the medulla.

The cerebellum lies dorsally to the medulla and is attached to the underlying medulla, pons and mesencephalon by caudal, middle and cranial peduncles, respectively. It consists of a central vermis and two small, laterally situated hemispheres. The entire surface of the cerebellum is grooved by transverse sulci, transforming the surface into leaves or folia.

The aqueduct of the midbrain (mesencephalon) divides it into a dorsally situated tectum and ventrally situated tegmentum. The tectum is connected to the optic nerves and forms two distinct, rounded bodies commonly called optic lobes, which lie caudally to the cerebral hemispheres and laterally to the cranial end of the cerebellum. A large ventricle is present in the tectum. The tegmentum gives rise to cranial nerves III and IV.

The forebrain (prosencephalon) consists of a centrally positioned diencephalon and two cerebral hemispheres (telencephalon). The diencephalon contains the third ventricle and is divided into the thalamus and epithalamus (pineal) dorsally, and the hypothalamus ventrally. The hypothalamus gives rise to cranial nerve II. Caudally to the optic nerve the hypophysis is attached by the infundibulum. The surfaces of the two cerebral hemispheres are smooth (they lack sulci and gyri). An oblique dorsal depression, the vallecula telencephali, divides each hemisphere into rostromedial and caudolateral parts. The rostral point of each hemisphere contains a small olfactory bulb which gives rise to the first cranial nerves. Each hemisphere contains a large lateral ventricle.

Peripheral nervous system

The cranial and spinal nerves are described in detail by King and McLelland (1984) and some are illustrated in Fig. 3.4. A short summary is provided here. There are 12 cranial nerves (numbered CN I–XII). The olfactory nerve (I) passes through the olfactory foramen to the mucous membrane of the nasal cavity. The optic nerve (II) passes through the optic foramen to the retina of the eye. The left and right nerves decussate to form the optic chiasma. The oculomotor nerve (III) supplies some of the muscles of the eye. The trochlear nerve (IV) innervates the dorsal oblique muscle of the eye. The trigeminal nerve (V) supplies sensory innervation to the head and motor innervation to the muscles of mastication. The abducent nerve (VI) innervates the lateral straight muscle of the eye and the striated muscles of the third eyelid. The facial nerve (VII) is complex and innervates some of the muscles of the head and carries autonomic and taste fibres. The vestibulocochlear nerve (VIII) supplies the inner ear. The glossopharyngeal nerve (IX) forms extensive anastomoses with the vagus nerve and innervates the epithelium of the entire tongue, mucous membrane and muscles of the pharynx

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and larynx, and carries autonomic fibres. Due to its anastomoses with the vagus nerve its exact distribution is not known. The vagus nerve (X) innervates the pharynx and larynx, and accompanies the jugular vein to the thorax where it innervates the viscera of the thorax and abdomen. The accessory nerve (XI) is enclosed in a common sheath with the vagus nerve and its distribution is difficult to determine. The hypoglossal nerve (XII) innervates the muscles of the tongue, trachea and syrinx.

Spinal nerves come off the spinal cord and are segmentally arranged (Gadow, 1880). In the caudal cervical region the ventral roots of the nerves unite to form the brachial plexus. The ten nerves that originate from the plexus supply the wing. In the lumbosacral region the ventral branches of the spinal nerves unite to form the lumbosacral plexus. The plexus lies dorsally to the kidneys (the roots often pass through the kidneys) and gives rise to the nerves of the pelvic limb. Two main trunks are formed, one cranially to the acetabulum, the other caudally to it. The femoral nerve comes from the cranial trunk and emerges cranially to the acetabulum where it supplies the cranial thigh muscles. The ischiadic nerve arises from the caudal trunk and emerges caudally to the acetabulum. This nerve and its branches pass distally between the caudal thigh muscles and are accompanied by the ischiadic blood vessels as well as a diverticulum of the abdominal air sac.

ENDOCRINE SYSTEM

Cephalic tissues

The hypophysis is attached to the diencephalon at the base of the brain stem by a stalk or infundibulum (Elias, 1996). It lies in the sella tursica of the basisphenoid bone (the bone completely surrounds the hypophysis, making it difficult to remove) and is surrounded by blood vessels and venous sinuses. The hypophysis receives blood from infundibular and caudal hypophyseal arteries, as well as from the hypophyseal portal vessels. The pineal is attached to the roof of the third ventricle and lies between the cerebrum and cerebellum. It is an elongated organ, firmly attached to the meninges.

Visceral glands

The two thyroids are round, dark brown bodies situated on the cranial borders of the subclavian arteries (Fig. 2.7). They lie dorsally to the common carotid arteries and are partly surrounded by the clavicular air sac. The parathyroids are generally embedded in the medial aspect of the thyroid glands.

Both adrenal glands lie opposite the last thoracic vertebral ribs (Fig. 2.6). The left adrenal is crescent-shaped, approximately 60 mm long by 10 mm wide, lying between the cranioventral pole of the kidney and the cranial pole of the left

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testicle of the male (closely associated with the appendix of the epididymis) or the ovary of the female. The right adrenal is more triangular in shape, is approximately 30 mm long and lies dorso-lateral to the caudal vena cava, between the cranio-ventral pole of the right kidney and the spleen.

SENSORY ORGANS

Eye

The eye of the ostrich is the largest amongst contemporary terrestrial vertebrates, measuring about 50 mm in diameter, and is of the flat type (King and McLelland, 1984). The wall of the eyeball consists of fibrous, vascular and nervous layers. The fibrous layer consists of an anterior, transparent cornea and a large posterior section, the sclera. The sclera and cornea meet at the limbus of the eye. Immediately posterior to the limbus a series of bony plates, the scleral ossicles, are found. These form a bony ring, 6–9 mm wide, which strengthens the wall and provides attachment for the ciliary muscles. The optic nerve enters the eye through the ventromedial aspect of the sclera. At this point the dura mater surrounding the optic nerve attaches to the sclera.

The vascular layer consists of the choroid, the ciliary body and the iris. The choroid is a thick, highly vascular and darkly pigmented layer between the sclera and retina. It is continued anteriorly with the ciliary body, a thickened ring that suspends the lens by zonular fibres. The iris is dark in colour and has a round pupil. The lens is round and flattened anterior–posteriorly and is firmly attached to the ciliary body.

The retina forms the innermost layer of the eye, covering the choroid, ciliary body and the posterior surface of the iris. A specialized part of the retina, the pecten, lies on the optic disc. It is a vaned, oval cone, approximately 12 mm long, 5 mm wide and 15 mm high, and plays a role in the nutrition of the retina.

The cavity of the eyeball is divided into three parts. The part behind the lens and ciliary body contains the vitreous body, the part between the lens and iris is the posterior chamber; and the part between the iris and cornea is the anterior chamber. The posterior and anterior chambers are continued through the pupil and both are filled with aqueous humour.

The cornea is protected by upper and lower eyelids and a nictitating membrane. The lower eyelid is thinner and more extensive than the upper eyelid and is mainly responsible for closing of the eye. The free margins of both lids carry rows of long, overlapping bristle feathers which resemble eyelashes.

Martin and Katzir (1996) examined the visual fields of the ostrich and found that, in comparison to other birds, their binocular fields of vision are surprisingly narrow. Furthermore, they also employ a 'sunshade' to prevent imaging of the upper sky and the sun, which results in a large blind area above and to the rear of the head.

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A small lachrymal gland lies ventrally to the lateral canthus of the eye (Fig. 3.4). Its ducts open on the inside of the lower eyelid. Excess tears drain via the nasolachrymal duct to the nasal cavity. MacAlister (1864) described a large, oval Harderian gland between the medial and ventral rectus muscles.

Ear

The entrance to the external ear is formed by two thickened folds of skin. The folds form a vertical, oval opening that is guarded by a large number of bristle feathers. From the opening the cavity narrows cranially to form a short external acoustic meatus. The tympanic membrane is round and lies obliquely, its dorsal margin being lateral and caudal to the ventral margin. It bulges outwards and faces towards the rear aspect.

The middle ear cavity lies between the tympanic membrane and inner ear. It contains the columella (Frank and Smit, 1976) and communicates with the oral cavity via the Eustachian tube. Extensions from the middle ear cavity aerate the bones of the skull. The inner ear consists of bony and membraneous labyrinths (Gray, 1906).

CONCLUSION

The anatomy of ratites in general corresponds to that of other birds. There are, however, notable differences and areas that need further investigation. In particular, the respiratory system needs investigation to try and find some answers to the problem of air sacculitis.

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3

Physiology

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Physiology refers to the normal functioning of the organism, particularly the regulatory systems that maintain normal body mass, temperature, composition of the milieu interieur, growth and reproduction. This chapter reviews current knowledge about osmoregulation, thermoregulation, respiration, metabolism and the endocrine system of the ostrich.

OSMOREGULATION

Osmoregulation is the turnover and homeostasis of water and the major electrolytes of plasma and extracellular fluids (Skadhauge, 1981). These are sodium and chlorine ions, which together with potassium and ammonium ions, constitute the major fraction of osmolality of ureteral urine. The organism can be described as a flow system in which the major components with respect to water and salts are: intake of water and salts; production of metabolic water and loss of water by evaporation; and excretion of salts and water through the kidney, gut, and (when present and functional) the nasal gland. In its native Africa the ostrich cannot readily escape either the dry heat of deserts or solar radiation, and this species requires special adaptation for osmoregulation and thermoregulation (i.e. evaporative cooling).

Water intake and turnover

Although the ostrich has a 'frugal water economy' (Williams *et al*., 1993), this species will drink free water, if available and needed (Sauer, 1971). Drinking can

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be unnecessary, at least in adult birds, if the diet consists of fairly succulent food, and the birds are not excessively heat-stressed. Under these conditions the water in food is supplemented by production of metabolic water which is sufficient to counterbalance the losses through urine, faeces and evaporation. This is the case even in xeric habitats, such as the Namib Desert (Williams *et al*., 1993) or around Nairobi, Kenya, in February (E. Skadhauge, personal observations, 1981). The parameters of water balance can be quantified by direct measurement of water intake and output in captive birds and by hydrogen isotope flux studies in both captive and free-living birds.

The total body water content (measured as the tritium space) is 68% of body mass in adult birds (Withers, 1983), and declines from 84% in 35-day-old chicks to 57% in 1-year-old birds (Degen *et al*., 1991). Degen *et al*. (1989) recorded a water content of 70% in 5- to 6-month-old growing chicks. These values are within the range encountered in other avian species (Skadhauge, 1981), and different values in the same age group most probably reflect the presence of different amounts of fat tissue.

Absence of drinking in free-living adult ostriches is possible since the water content of plants on which the birds feed can be high. In Kenya, birds shot by Skadhauge *et al*. (1984a) had been feeding exclusively on *Euphorbia heterochroma*, which contains 87% water and only has a small electrolyte content compared to the combustible energy (Skadhauge *et al*., 1991). Ostriches in the Namib Desert grazed on *Bohenia*, which contains 68% moisture (Louw, 1972). Milton *et al*. (1994) observed that ostriches avoided succulent foods with sodium concentrations above 9%, and selected plants with relatively low concentrations of calcium and oxalate. When the diet consisted mainly of low-sodium plants the birds would selectively forage for a salt-rich plant. Milton *et al*. (1994) estimated 'natural forage' to contain a total water content of 70%.

Williams *et al*. (1993) studied free-living ostriches in the Namib Desert, and calculated energy expenditure as well as the water turnover using the double isotope method. This permitted estimation of water in food, and metabolic water production. Intake of water was 2.5 l day^{-1} which was five times higher than the metabolic water production (Table 3.1). If less succulent food is offered to domesticated ostriches then their water intake is higher. In Israel, Degen *et al*. (1991) observed an intake in adult birds of 3.5 l day^{-1}, whereas in Oudtshoorn, South Africa, Withers (1983) recorded a value of 7.9 l day^{-1}. A relatively higher rate of drinking is observed in ostrich chicks. Levy *et al*. (1990) recorded 4.5 l day^{-1} in 12 kg chicks, whereas Degen *et al*. (1991) recorded 0.7 l day^{-1} in 4 kg chicks, and Williams *et al*. (1993) calculated 0.7 l day^{-1} in 'subadult' ostriches in the Namib Desert (Table 3.1). Again in Oudtshoorn, adult birds fed a 'dry' maize diet had a water intake of 18 l day^{-1} although this was at the height of summer (Skadhauge *et al*., 1995; unpublished observations, 1983). The drinking rate went up by approximately 50% when natural bore water containing a low concentration of salt was offered as the only drinking solution, whereas a hyper-osmotic saline solution reduced the intake to 50% of the fresh water value (Fig. 3.1). Urine osmolality suggested that hyper-osmotic salt-loading stimulated maximal water conservation.

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Table 3.1. The water balance of ostriches showing observations on water gain from drinking and ingestion in food and metabolic processes, and water loss by excretion in faeces and urine and by evaporation. (Data from Williams *et al.* (1993), and Degen *et al.* (1989, 1991). Withers (1983) worked with birds offered water *ad libitum* (hyd.) and after 4–7 days of water deprivation (dehyd.)

	Water gain (l day^{-1})				
Process	Williams *et al.* (1993)	Degen *et al.* (1989)	Degen *et al.* (1991)	Withers (1993) (hyd.)	Withers (1993) (dehyd.)
Drinking	0.1	*	3.5	7.9	0
Metabolic production	0.5	0.7		0.4	
			1.0†		0.5†
Preformed in food	2.5	0.3		0.2	
Total	3.1	10.1	4.5	8.5	0.5

	Water loss (l day^{-1})	
Process	Withers (1993) (hyd.)	Withers (1993) (dehyd.)
Faeces	2.9	0.3
Urine	2.5	0.5
Evaporation	3.1	1.5
Total	8.5	2.3

*Water intake not measured in this study; †Metabolic production and in food combined.

Total water balance has been examined in detail by Withers (1983) who measured intake and output under 'semi-natural' conditions. Observations were made in birds on free water intake and after 7 days of dehydration (Table 3.1). The hydrated birds were in water balance at a turnover of 8.5 l day^{-1} whereas the dehydrated birds lost water with a deficit of more than 1 litre day^{-1}. Metabolic water production, approximately 0.5 l day^{-1}, is only 25% of the minimum water requirement (*c.* 2 l day^{-1}; Table 3.1). Williams *et al.* (1993) showed the importance of water in food, and Withers (1983) recorded the fairly high rate of faecal and urinary water loss, making the ostrich dependent on free water when receiving the 'dry' food offered in captivity (Table 3.1).

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Kidney function

No studies have been published of flow rate and composition of ureteral urine in the ostrich. Knowledge of renal function is therefore based on samples of cloacal urine, and samples or quantitative collections of voided urine.

In two studies quantitative urine collection has been made, both on *ad libitum* water intake and during dehydration. Levy *et al.* (1990) studied young birds (12 kg average body mass), and Withers (1983) adult birds, and so values of the former study have been recalculated per 100 kg. During normal hydration Levy *et al.* (1990) measured the flow rate at 20 l day^{-1} compared with 2.5 l day^{-1} measured by Withers (1983). This difference is beyond the possible effect of age, probably due to the level of hydration being much higher in the former study. Levy *et al.* (1990) measured plasma osmolality at 284 mOsm and urine osmolality at 62 mOsm, whereas Withers (1983) obtained values of 330 and 163 mOsm, respectively. In both studies water deprivation resulted in a remarkable reduction in flow rate, to 0.3 and 0.5 l day^{-1}, respectively.

Levy *et al.* (1990) measured clearance of creatinine, a fairly reliable marker of glomerular filtration rate (GFR), at 92 ml min^{-1} during normal hydration, which was reduced to 25% after 48 h dehydration. The former value is lower per kg body mass than observed in other avian species (Skadhauge, 1981), but within their range when the decrease in rate of metabolism associated with higher body mass is taken into account (Kleiber, 1961). The reduction of GFR during dehydration is remarkably high. Based on these values, the fractional excretion of water (urine flow rate as a percentage of GFR) is 15% during normal hydration and 1% during dehydration, values identical to those observed in other birds (Skadhauge, 1981).

When water is freely available the ostrich may reduce its urine osmolality to 60–70 mOsm (Louw *et al.*, 1969; Levy *et al.*, 1990), thus not losing solutes when excess water is excreted. On the diets offered in captivity, ostriches will excrete a urine which is nearly isosmotic to plasma (Fig. 3.1; Gray *et al.*, 1988; Skadhauge *et al.*, 1995). In dehydrated (Louw *et al.*, 1969; Withers, 1983; Skadhauge *et al.*, 1984a) or salt-loaded (Gray *et al.*, 1988; Skadhauge *et al.*, 1995; Fig. 3.1) birds, a maximal urine osmolality of approximately 800 mOsm is reached. When plasma osmolality has been measured simultaneously (Table 3.2) the maximal osmotic urine/plasma ratio is 2.6:1, which is among the highest encountered in avian species (Skadhauge, 1981).

Cloacal urine is quite fluid in the ostrich but only when the flow rate is high. The tiny amount produced during water deprivation is thick and yellow. It contains mucus and upon standing forms a large precipitate of urates and uric acid. This colloid material does not contribute to the osmotic pressure. The osmolality of the supernatant is largely accounted for by sodium, potassium and chlorine ions (Table 3.2 and Fig. 3.1), but calcium, magnesium, ammonium, phosphate and sulphate ions may also be excreted (Fourcroy and Vauquelin, 1811; Schütte, 1973; Levy *et al.*, 1990). Taking the difference in renal concentrating ability into account, the concentrations of the measured ions in the liquid part of ostrich

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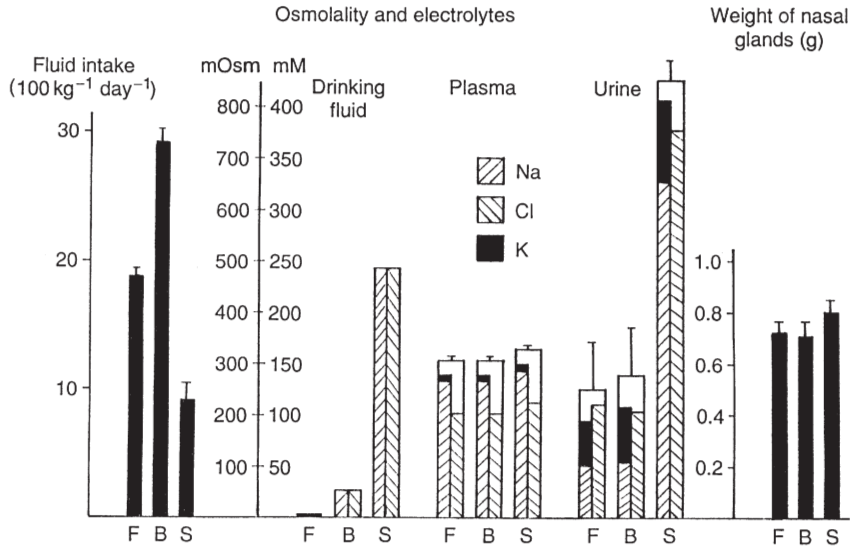

Fig. 3.1. Osmotic response to drinking fluids of different salinity. The figure indicates osmotic and ionic concentrations of the drinking fluids, and of plasma and urine, as well as the rate of fluid intake and the weight of the nasal glands. F, Fresh water; B, bore water; S, 1.5% NaCl. Mean ± SE. Data from Skadhauge *et al.* (1995; unpublished observations, 1983).

Table 3.2. Average plasma and urine osmolality and electrolyte concentrations in the dehydrated or salt-loaded ostrich. Data from a variety of studies as shown.

Study		Osmolality (mOsm)	Sodium (mM l^{-1})	Chlorine (mM l^{-1})	Potassium (mM l^{-1})
Skadhauge *et al.* (1984a)	Plasma	338	160	123	3.8
	Urine	838	92	134	154
Gray *et al.* (1988)	Plasma	323	172	125	4.1
	Urine	829	116	429	353
Skadhauge *et al.* (1995)	Plasma	328	151	111	4.5
	Urine	846	327	378	83

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urine do not differ from the values observed in other avian species (Skadhauge, 1981).

Uricotelism may be viewed as a pre-adaptation to desert life, as it allows urinary excretion of nitrogen with much less water than urea would require. Birds excrete about 80% of renal nitrogen as dihydrates of uric acid in super-saturated colloid suspension. The remaining nitrogen is predominantly excreted as either urea or ammonium, depending on the acid load (Skadhauge, 1981, 1983). The concentration of uric acid is high in ostrich urine particularly in the dehydrated state. Values of approximately 15% (Fourcroy and Vauquelin, 1811; Louw *et al.*, 1969), and up to 43% (Schütte, 1973) have been reported, whereas the undissolved uric acid in urine from normally hydrated birds is 0.8–1.2%. Quantitative measurements of renal clearance of urea and uric acid have been made by Levy *et al.* (1990), who observed after 48 h dehydration that in 'the fluid portion of the urine' 89% of the sum of uric acid and urea was excreted as uric acid. The urine-to-plasma concentration ratio was 177:1 for uric acid compared with 113:1 for the filtration marker creatinine, thus proving the process of renal secretion.

Role of the alimentary tract

Birds typically have a fairly short rectum directly connected with the coprodeum. Urine entering from the ureteral urificia is transported from the urodeum by retrograde peristalsis into the coprodeum and rectum, and during this storage is mixed with faeces. When defecation/voiding occurs, the most anal mixture is excreted. In species in which the paired caeca are large, a fraction of urine may be transported to the ileo-rectal junction (Skadhauge, 1981). The ostrich rectum is long, measuring between 8 and 11 m (Gadow, 1879; Fowler, 1991; Skadhauge *et al.*, 1984a, 1995; Bezuidenhout, Chapter 2). (The word rectum, meaning straight, is rather inappropriate in this species but is used here to follow the convention employed by Bezuidenhout, Chapter 2; colon better describes the morphology of this large intestine.) At the ileo-rectal junction are located two caeca approximately 0.8 m long. Furthermore, the special structure of the ostrich cloaca results in no mixture of urine and faeces leading to separate defecation and voiding of urine (Louw *et al.* 1969; Withers, 1983; Skadhauge *et al.*, 1984a; Levy *et al.*, 1990). Faeces uncontaminated by urine are stored in the terminal rectum, and urine without faeces in the coprodeum (in spite of its name).

The caeca and rectum form huge fermentation chambers in which production of short-chain fatty acids (SCFAs) takes place (Skadhauge *et al.*, 1984a; Swart *et al.*, 1993a; Cilliers and Angel, Chapter 5). This hindgut function resembles the digestive physiology of horses (Skadhauge *et al.*, 1996). Of osmoregulatory importance are the mechanisms and regulation of resorption of water from the distal end of the hindgut, and the resulting lower water content of the faeces.

The fermentation of plant material in the rectum leads to high concentrations of SCFAs, up to 200 mM in the supernatant of the chymus (Skadhauge *et al.*, 1984a; Swart *et al.*, 1993b). The absorption of solutes and water along the

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rectum is, however, so efficient that the water fraction in the chymus (g H_2O (g H_2O+g dry matter)$^{-1}$) in normally hydrated birds is only 67% in the 'terminal' rectum (Skadhauge *et al.*, 1984a) and 72% in the 'distal' rectum (Swart *et al.*, 1993b). The latter value is similar to the water content of 72% reported in faeces (Withers, 1983). Dehydration brings about a reduction in faecal water content by 18% (absolute values were not stated by Louw *et al.*, 1969), and a fall to 55% (Withers, 1983). The values observed during normal hydration, as well as those observed during dehydration, are at the lower end of the range measured for total droppings in other avian species (Skadhauge, 1981).

Faecal water loss amounts to 35% of total water loss in normally hydrated ostriches, being reduced to 13% or less in dehydrated birds since the latter calculation does not take panting into account (Withers, 1983). The mechanism behind the formation of drier faeces in the dehydrated state is not well understood. One possibility is a higher rate of rectal absorption of sodium (with accompanying water) as dehydration increases the plasma level of aldosterone (Levy *et al.*, 1990). Conversely, salt loading decreases rectal sodium ion and water absorption (Skadhauge *et al.*, 1995, 1996).

Classical accounts of avian splanchnology (Skadhauge, 1981; King and McLelland, 1984) do not provide detailed descriptions of the ostrich cloaca. Recent descriptions (Fowler, 1991; Duke *et al.*, 1995) are variable and incompatible with the well documented separate passing of urine and faeces. Inaccurate descriptions of the ostrich cloaca may be caused by the difficulty in getting the organ orientation right on 'flat' abattoir material. Only fixation *in situ* will preserve the *in vivo* organ configuration, particularly the presence of the rectal-coprodeal fold (Skadhauge *et al.*, 1995; Warüi and Skadhauge, 1998).

According to Warüi's dissection (Figs 3.2 and 3.3) a strong sphincter separates the terminal rectum and coprodeum. The coprodeum is located ventrally to both terminal rectum and urodeum (into which the ureters open). Faeces are stored in the terminal rectum and, since the rectal-coprodeal sphincter is closed, no reflux of urine takes place. Defecation (without urination) occurs by relaxation of the rectal-coprodeal sphincter and contraction of the thick-walled terminal rectum. This expels the faecal pellet via the dorsal part of coprodeum and the proctodeum, and urine remains in the ventral sack of the coprodeum. When ureteral urine enters the urodeum it passes by force of gravity, and possibly some retrograde peristalsis (as in other birds; Duke, 1989), into the ventrally located coprodeum. Urination occurs without defecation by contraction of the abdominal muscles which, with the rectal-coprodeal sphincter tightly closed, presses urine out via the copro-urodeal and uro-proctodeal apertures to the vent. This quick ejection of fluid urine is spectacular (Berens von Rautenfeld, 1977).

In the avian species studied so far, cloacal storage leads to significant change in the ureteral urine in the dehydrated state and on a low salt diet (Skadhauge, 1981). During hydration and with high salt intake the renal output of water and salt, respectively, is so large that the coprodeal (and rectal) transport capacity amounts to only a few percent of the renal excretion (Skadhauge, 1977). During water deprivation, absorption of salt (with solute-linked water flow) may,

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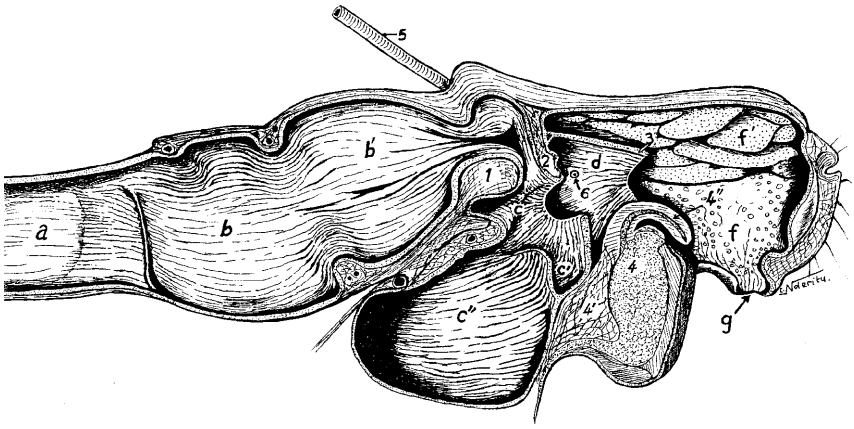

Fig. 3.2. Lateral view of a mid-sagittal section through the cloaca and the terminal rectum of a young male African Ostrich. a, caudal part of the rectum proper; b, proximal pouch of the terminal rectum; b′, distal pouch of the terminal rectum; c, c′, and c″, dorsal part, lower region of the dorsal part, and ventral sac of the coprodeum; d, the urodeum; f, ventral region of the proctodeum; f′, lymphoid folds of the cloacal bursa; g, vent; 1, thick apical part of the plica recto-coprodealis; 2, plica copro-urodealis; 3, plica uro-proctodealis; 4, 4′, 4″, parts of the phallus; 5, ureter; 6, opening of ureter. Illustration courtesy of Dr Charles N. Warüi, Department of Veterinary Anatomy, University of Nairobi.

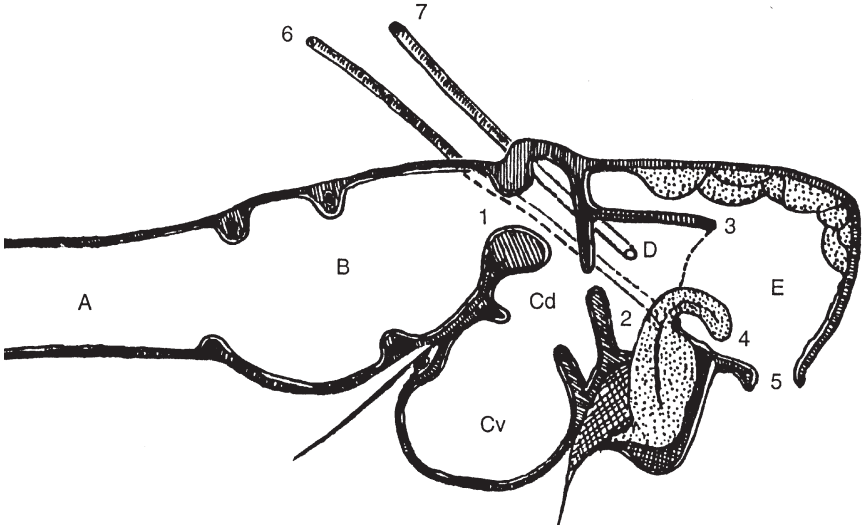

Fig. 3.3. Schematic drawing of a mid-sagittal section through the cloaca and the terminal rectum of a young male ostrich fixed *in situ*. A, rectum; B, terminal rectum; Cd, dorsal part of coprodeum; Cv, ventral part of coprodeum; D, urodeum; E, proctodeum; 1, plica recto-coprodealis; 2, plica recto-urodealis; 3, plica-uro-proctodealis; 4, phallus; 5, vent; 6, ductus deferens; 7, ureter. Illustration courtesy of Dr Charles N. Warüi, Department of Veterinary Anatomy, University of Nairobi.

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however, overcome the osmotic inflow of water from plasma across the coprodeal wall caused by the hypertonicity of ureteral urine, so the net result is a limited water conservation (Skadhauge, 1977). In species with functional nasal salt glands the combined effect of coprodeal-rectal salt and water absorption and nasal gland secretion of salt in a concentrated solution may lead to a significant net gain of water excreted by the kidney (Skadhauge *et al.*, 1984b).

Since the dehydrated ostrich can pass cloacal urine more than 500 mOsm hyperosmotic to plasma (Table 3.2), coprodeal 'dilution' by water dragged osmotically from plasma across the epithelium is obviously avoided. The most likely reason is that the coprodeal wall is protected by a thick layer of mucus. Louw *et al.* (1969) have observed a large amount of mucin-producing goblet cells in the ureteral epithelium. Even in a much smaller bird, the domestic fowl (*Gallus gallus*), unstirred layers adjacent to the coprodeal epithelium allow establishment of substantial osmotic (Bindslev and Skadhauge, 1971) and ionic (proton; Laverty *et al.*, 1994) gradients. Further clarification of post-renal modification of urine in the ostrich must await careful comparison of the osmolality of ureteral and voided urine, and measurements of the area of coprodeal epithelium and its transport properties.

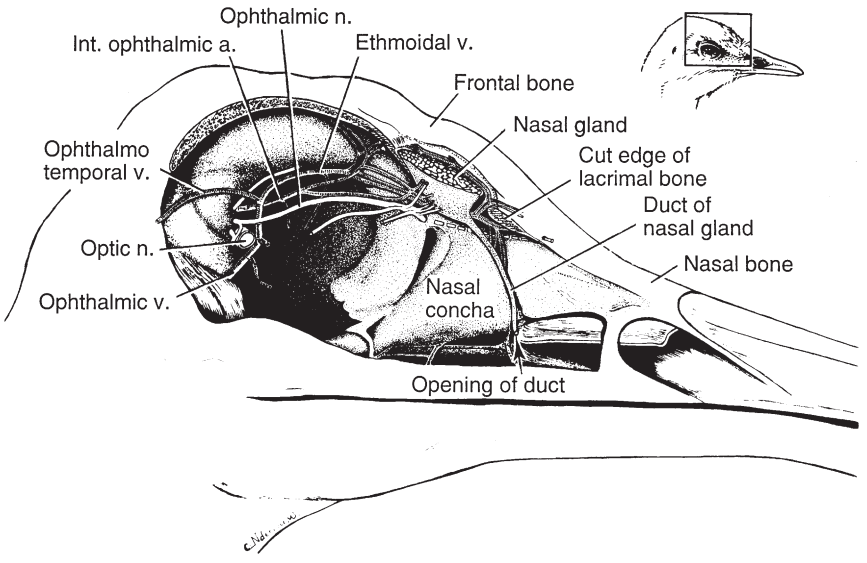

Fig. 3.4. The location of the nasal gland in the ostrich skull with its duct leading directly to the nasal cavity. a, Artery; n, nerve; v, vein. Illustration courtesy of Dr Charles N. Warüi, Department of Veterinary Anatomy, University of Nairobi.

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Function of the nasal glands

Like marine birds, the ostrich has paired nasal glands (Fig. 3.4; Technau, 1936). They are situated in grooves of the frontal/lacrimal bones with ducts leading directly into the nasal cavity (Skadhauge *et al.*, 1984a). The glands weigh 'approximately 0.3 g each' (Gray and Brown, 1995) in 2-year-old birds. Skadhauge *et al.* (1995; unpublished observations 1983) estimated the mass as 0.7–0.8 g each in adult birds on a low-salt diet, with an insignificant change on a high-salt intake (Fig. 3.1). The mass of each gland is thus less than 10^{-5} of the body mass. This is in sharp contrast with marine birds and domestic duck which can excrete about 50% of a salt load through the nasal glands (Skadhauge, 1981). In 3 kg salt-adapted ducks each gland weighed approximately 0.5 g (Skadhauge *et al.*, 1984b), having a relative mass 20-fold higher than in the ostrich.

The question of secretion from the nasal glands in the ostrich is not settled. Initial claims of nasal gland secretion have not been confirmed. Schmidt-Nielsen *et al.* (1963) noted high concentrations of potassium, sodium, calcium and chlorine ions in fluid collected from the nostrils of an ostrich exposed to high ambient temperature, but precise analytical values were not reported. Cloudsley-Thompson and Mohamed (1967) also observed nasal secretion but did not report the composition of the fluid. Skadhauge *et al.* (1984a) failed to observe any secretion from the nares after acute oral salt loading (10 mM kg^{-1} body mass). Skadhauge *et al.* (1995; unpublished observations 1983) exposed ostriches to a high salt level with 1.5% salt as drinking solution followed by an acute oral salt load, without observing any activation of nasal secretion. Gray and Brown (1995) were unable to stimulate the nasal glands to secretion by an increase in plasma osmolality (to an average of 329 mOsm) induced by a hyperosmotic saline infusion (1500 mOsm) in five birds subjected to a high-salt diet for 3 months. These authors did note in two birds a 'dampness' around the nares, but this lasted only for 5–10 min and produced no collectable fluid. Skadhauge *et al.* (1995; unpublished observations, 1983) noted that excited and heat-stressed birds panted, and this panting was accompanied by a rather copious mucus secretion from the mouth and throat. It is possible that this mucus may be mistaken for nasal gland secretion. In conclusion, it is not ruled out that the nasal glands may become functional in certain ostrich populations exposed to long-term salt loading or heat stress, but such secretion cannot play any quantitative role in osmoregulation.

THERMOREGULATION

Body temperature and heat dissipation

Thermoregulation involves the mechanisms by which warm-blooded animals maintain a near-constant body temperature. For desert-adapted birds such as the ostrich, the main problem is to avoid overheating. Excess heat can be discharged

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by three physical principles: radiation, convective (and conductive) cooling, and evaporation of water. The latter process interacts with osmoregulation. The heat exchanged by all three physical principles can be modified by behaviour (Louw, 1972) and physiological means such as seeking shade and panting.

At approximately 39°C, normal 'deep' (intramuscular or cloacal) body temperature is slightly lower in the ostrich than in other avian species (Bligh and Hartley, 1965; Crawford and Schmidt-Nielsen, 1967; Schmidt-Nielsen *et al.*, 1969; Louw *et al.*, 1969). The body temperature is kept within the range of 38–40°C unless the birds are exposed to heat stress and dehydration simultaneously. This leads to a rise in body temperature up to 4°C (Crawford and Schmidt-Nielsen, 1967) as panting is attenuated. Even day-old chicks are able to maintain near-adult body temperatures at ambient temperatures around 13°C (Brown and Prior, 1998).

Under desert conditions, heat loss by radiation and by convective cooling can be augmented by behavioural adjustments which are also affected by the wind speed (Louw *et al.*, 1969). At high ambient temperature and with a wind blowing, the birds react with feather erection; Crawford and Schmidt-Nielsen (1967) recorded an increase in the feather layer 'from about 3 to some 10 cm', and wing drooping thereby exposing bare skin on the thorax. The birds will also pant when there is no wind, with an abrupt change of respiration frequency from 4 to 40 breaths min^{-1}. During low ambient temperatures at night the feathers are flattened. Measurements of the temperature in the air space between the skin and the feather layer demonstrate a variation from 30 to 39°C.

Evaporative cooling, its physical basis, regulation, and quantitative role have been studied extensively in the ostrich. Crawford and Schmidt-Nielsen (1967) exposed an adult ostrich to an intermittent rise in ambient temperature up to 51°C during a water deprivation period of 7 days. The normal cloacal temperature was 39.3°C which remained unchanged even at 51°C. The typical respiratory rate of 5 breaths min^{-1} increased abruptly to 45 breaths min^{-1} at an ambient temperature of 25°C. When panting began, the heat dissipated by respiratory evaporation increased linearly with ambient temperature, matching the rate of heat production at 45°C. During the 7-day period of dehydration the respiratory rate at 45°C was halved (from about 50 to 25 breaths min^{-1}), resulting in a reduction in evaporation rate also to one half the value on the first day. This resulted in a rise in cloacal temperature of 1°C on the first day to an increase of 4°C on the seventh day during the daily period of heat exposure. The neurophysiological mechanism behind this adjustment remains unknown. Suppression of panting has also been observed in heat-stressed, water-deprived emus (Skadhauge, 1974).

Schmidt-Nielsen *et al.* (1969) studied the temperatures along the trachea and in the air sacs of a panting ostrich, confirming that the ostrich can maintain body temperature below 40°C during 8 h at an ambient temperature as high as 50°C. This is achieved by panting from the entire respiratory tract with all air sacs being highly ventilated both during rest and panting. The maximal evaporative water loss is about 750 ml h^{-1}. In the panting ostrich the water loss through the skin amounts to less than 2% of the water evaporated from the respiratory surfaces.

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Quantitative role of evaporative water loss

Dawson and Bartholomew (1968) observed that 'evaporative water losses are best considered in relation to metabolic rate'. The evaporative water loss of wild birds at moderate ambient temperature is in the range 0.9–3 g H_2O l^{-1} O_2 and these values may be lower during dehydration, the lowest observed in the zebra finch to 0.54 g H_2O l^{-1} O_2 (Skadhauge and Bradshaw, 1974). The hydrated ostrich has relatively low value of 0.9 g H_2O l^{-1} O_2 (Crawford and Schmidt-Nielsen, 1967).

Two physiological mechanisms are involved in keeping the evaporative water loss low in the ostrich. The first is the attenuation of panting during dehydration, which may result in a rise in body temperature up to 4°C. With a specific heat of 3.3 kJ kg^{-1} body mass this allows 1339 kJ in a 100 kg ostrich stored for later dissipation by radiation and convective cooling. This is equal to a saving of 550 ml of evaporated water (Schmidt-Nielsen *et al.*, 1969). In this context it should be noted that the overall thermal conductance (14 kJ m^{-2} h^{-1} $°C^{-1}$ at 30°C) in the ostrich lies in the range of the values observed in other birds (Dawson and Hudson, 1970). The ostrich is, however, able to regulate the body surface temperature better than the emu or cassowary (Phillips and Sanborn, 1994). The second mechanism is the expiration of unsaturated air (Withers *et al.*, 1981), due to a temperature gradient along the trachea (Schmidt-Nielsen *et al.*, 1969). The process of desaturating and cooling results in a recovery of nearly half the water added to the inspired air. Withers *et al.* (1981) calculated the saving by this process to be 200–500 ml day^{-1}. This is a significant amount compared with the minimum water turnover of 2 l day^{-1} (Table 3.1).

RESPIRATION

Lungs and air sacs

Birds (and reptiles) utilize a costal pump for ventilation rather than a diaphragmatic pump as seen in mammals. Birds have a series of air sacs connected to each lung (Bezuidenhout, Chapter 2). This forms the basis of three distinctive avian respiratory characteristics. Firstly, air flows continuously in one direction through the lung, making it more efficient than the mammalian lung. Secondly, it provides birds with a large residual volume, which allows birds to breathe much more slowly and more deeply than a mammal of the same body mass. Thirdly, it provides a large source of air that can be used not only for gaseous exchange, but also for the transfer of heat by evaporation.

A detailed description of the structure and function of the respiratory system in ostriches is provided by Schmidt-Nielsen *et al.* (1969), Brackenbury (1986) and Bezuidenhout (Chapter 2). Despite being flightless, ostriches still have a well developed system of air sacs. The total volume of the respiratory system, the lungs

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and the nine air sacs of a 100 kg ostrich is about 15 l. The trachea branches into two primary bronchi, each passing to one of the lungs. The lungs are relatively immobile structures situated in the dorsal thoracic cavity. The primary bronchi continue directly through the length of the lungs (where they are called mesobronchi) and connect to the posterior air sacs. Connections from the mesobronchi to the more anterior air sacs are through secondary branches. The ventral end of the mesobronchus branches into several ventrobronchi, and the caudal end of the mesobronchus branches into several dorsobronchi. The ventrobronchi and dorsobronchi are connected by intra-pulmonary airways, the parabronchi, which form an arcade structure within the lung called the paleopulmo (Duncker, 1972) and is the only structure found in primitive birds such as ratites. Other birds have an additional system – the neopulmo, with air capillaries arising from the parabronchi forming the gas-exchange sites.

Ventilation through the lung is unidirectional; air flow through the parabronchi of the paleopulmo is in the same direction during inspiration and expiration (Scheid and Piiper, 1986). Inspired air moves into the respiratory system as a result of the expansion of thoraco-abdominal cavity, which is executed by inspiratory muscles, and during expiration air is expelled by the action of expiratory muscles. In this respect, the situation is little different from that in mammals. However, unlike mammals, there is little change in the volume of the lung. During inspiration, air is drawn in through the trachea, bronchi and mesobronchi. Some of this fresh air is drawn into the four caudal air sacs and the rest passes into the ventrobronchi. At the same time stale air is drawn from the dorsobronchi into the five anterior air sacs. During expiration, relatively fresh air passes from the caudal air sacs into the ventrobronchi, and stale air passes from the anterior air sacs to the mesobronchi, bronchi and out through the trachea. So during both inspiration and expiration air is passing from the ventrobronchi, through the parabronchi of the paleopulmo, to the dorsobronchi. The characteristics of the intrapulmonary carbon dioxide receptors in birds with only a paleopulmo (e.g. the emu, *Dromaius novaehollandiae*) appear to be similar to those of birds with a neopulmo, although the location of these receptors may differ (Burger *et al*., 1976).

Respiration rates of ostriches fall within two ranges, either within a low range of 3–5 breaths min^{-1} or a high range of 40–60 breaths min^{-1} (Schmidt-Nielsen *et al*., 1969). Equivalent figures from another study (Louw *et al*., 1969) are a low range of 6–12 breaths min^{-1}, and a high range of 36–47 breaths min^{-1}. At the same time, the tidal volume doubles resulting in a 16-fold increase in ventilation (Jones, 1982). This respiration rate is the slowest of any bird (Calder, 1968). The increase in respiration rate from the low range to the high range is sudden and occurs in response to heat stress. Birds lack sweat glands, and under heat stress they rely upon increased evaporation from the respiratory system for heat transfer. The increase in respiration rate is not necessarily associated with an increase in the rate of oxygen consumption.

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Blood supply to the lungs

The major branches of the pulmonary arteries and veins of birds, unlike mammals, are not associated with the bronchi in the lungs. The large arterial branches divide repeatedly to end as vessels running in parallel to the parabronchi. Capillaries run from these vessels towards the centre of the parabronchi and rejoin veins which pass close to the centre of the parabronchi. These veins unite to form the pulmonary vein. Because air is pumped by the air sacs rather than the lung itself, the capillaries in the parabronchi need not be robust. As a result they have thinner walls, permitting more efficient gaseous exchange.

Louw *et al.* (1969) recorded resting heart rate in ostriches as between 28 and 36 beats min^{-1}. There was a diurnal rhythm, with the lowest heart rate at night when birds were lying down. However, heart rate was very sensitive to stress. Sudden noises caused an increase of 30–50%, and restraint caused an increase of up to 100%. Bezuidenhout (Chapter 2) reports that the heart rate of 2- to 3-month-old chicks is around 80 beats min^{-1} compared with 30–60 beats min^{-1} for adults.

METABOLISM

Birds generate their energetic requirements from the oxidation of absorbed nutrients. Energy expenditure is at its minimum in a bird that is unfed and inactive and when the ambient temperature is high (i.e. in the thermo-neutral zone). This level of expenditure is known as the basal metabolic rate (BMR) and can be calculated by measuring the amount of oxygen consumed. The BMR varies with the mass of a bird; large birds use more energy than small birds in absolute terms but less per unit mass. The BMR in ostriches has been calculated as 0.113 ml O_2 g^{-1} h^{-1} (Withers, 1983), which is particularly low, being only 58% of the predicted value for a 100 kg non-passerine bird (passerines have BMRs higher than other birds). The BMR of ratites is best described as: BMR (ml O_2 g^{-1} h^{-1}) = 389 $kg^{0.73}$ which describes a line which is parallel to, but with only about 60% of the intercept of, the relationship for other non-passerine birds. In addition to BMR, energy is required for a range of other activities. When ambient temperature is lower than the thermo-neutral temperature, heat must be produced to maintain body temperature. The metabolic rate of a resting unfed bird that is also producing heat is known as the standard metabolic rate (SMR). The SMR of an ostrich is 0.26 ml O_2 g^{-1} h^{-1}, which is 2.3 times the BMR (Withers, 1983). Energy is also required to power all of the animal's physical activities. The maximum metabolic scope of an ostrich is at least 28 times the BMR. The daily energy turnover rate for an ostrich with free access to water is 12,700 kJ day^{-1}, which is equivalent to 0.26 ml O_2 g^{-1} h^{-1} (Withers, 1983).

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ENDOCRINE SYSTEM

The broad pattern of the endocrine system is the same throughout the vertebrates. However, with the exception of reproductive endocrinology, which has been studied in ostriches and emus, and thyroid endocrinology, which has been studied in ostriches, the ratite endocrine system has received little attention. There is little reason to think that ratites differ in any significant way in this respect from other birds. The following brief description therefore represents a broad avian perspective, but refers to specific information on ostriches or other ratites where this exists. Harvey and Etches (1997) provide a more detailed description of avian endocrinology.

Endocrine control of metabolism

As with most other aspects of endocrinology, little is known relating specifically to ostriches: this description is based almost entirely on work done on the domestic fowl. A wide variety of hormones are involved in the control of carbohydrate and lipid metabolism. The adipose tissue of birds only has a limited capacity for *de novo* fatty acid synthesis, and most of the fatty acids that accumulate there are derived directly from the diet or are synthesized in the liver. Metabolism of fatty acids in the liver is controlled by insulin, glucagon, prolactin, growth hormone, thyroid hormones and corticosteroids. In mammals, insulin is a potent stimulator of hepatic lipogenesis, but birds appear to be much less responsive. On the other hand, glucagon is a potent inhibitor of lipogenesis in birds. Glucagon may be a much more significant partner in the insulin/glucagon relationship in birds than it is in mammals. Growth hormone inhibits lipogenesis and corticosteroids promote lipogenesis.

Homeostasis of carbohydrate metabolism is maintained by insulin and glucagon. Although birds are relatively insensitive to insulin, it has metabolic effects similar to those in mammals, promoting uptake of glucose from the circulation. Glucagon has the reverse role and stimulates glycogen breakdown from tissues to increase blood glucose. There are several other related polypeptide hormones which are important in avian metabolism. Pancreatic polypeptide, produced in the pancreas, is antilypolitic and suppresses glucose-induced insulin release. Similarly, polypeptide YY, which is mainly produced in the lower gut, also suppresses glucose-induced insulin release. A third member of the family, neuropeptide Y, is found mainly in the brain and may also regulate insulin secretion. It is involved in modifying behaviour to regulate food intake. Growth hormone is important in regulating carbohydrate metabolism in favour of growth. Corticosteroids and adrenaline have the opposite effect: they stimulate the mobilization of energy reserves so that an animal is better prepared to respond to stress.

A recently discovered hormone, leptin, is also involved in metabolism in mammals (O'Rahilly, 1998). Leptin is produced by adipocytes in adipose tissue. The more adipose tissue there is, the higher the levels of leptin, thereby

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providing a measure of fatness. Its role is to reduce appetite and so the fatter an animal is, the more its appetite is suppressed. Several laboratories have tried to clone the gene for leptin in birds, including emus, but as yet none has produced a convincing product. It remains possible that leptin does not occur in birds.

All of these metabolic effects act in harmony as a result of complex interrelated control mechanisms. Thyroid hormones have a direct effect on metabolic rate and increase oxygen consumption. The thyroid hormone active in increasing metabolic rate is tri-iodothyronine (T_3) which is produced by de-iodination of thyroxine, the main secretory product of the thyroid glands, and this occurs mainly in the liver. The amount of T_3 in the circulation depends on the amount of thyroxine released from the thyroid glands, the rate of conversion of thyroxine to T_3, and the rate of breakdown of T_3. The release of thyroxine from the pituitary glands is comparatively straightforward, being determined by the amount of the pituitary peptide hormone, thyrotrophin-releasing hormone (TSH). However, de-iodination to T_3 and the breakdown of T_3 is affected by corticosterone, adrenocorticotrophic hormone (ACTH), growth hormone and prolactin, all of which have their own independent effects on metabolism.

Hormones and osmoregulation

The antidiuretic hormone of birds is arginine vasotocin (AVT) (Skadhauge, 1981) which has been isolated from the ostrich neurohypophysis (Saayman *et al.*, 1986). Gray *et al.* (1988) developed an accurate radio-immunoassay for AVT and for angiotensin II (ANG II) and followed the plasma concentration of both hormones for 5 days of dehydration. Water deprivation elevated the average plasma AVT from 10.2 to 32.3 pg ml^{-1} on average, and ANG II from 44.3 to 143.1 pg ml^{-1}. These AVT data established the relationship between plasma osmolality and AVT concentrations, and indicated a sensitivity of 0.54 pg ml^{-1} $mOsm^{-1}$ with a threshold for release of 271 mOsm. Plasma concentrations of both AVT and ANG II are similar to the concentrations found in other birds. The ostrich did not show a greater sensitivity for AVT release, whereas the osmotic threshold was relatively low. In a subsequent study Gray and Brown (1995) exposed ostriches on a low and a high salt intake to a hyperosmotic intravenous salt load. This resulted in increased plasma concentrations of AVT and permitted calculation of the relationship between plasma osmolality and plasma AVT concentrations. The osmotic sensitivity for AVT release was 0.25 and 0.21 pg ml^{-1} $mOsm^{-1}$ in the low- and high-salt birds, respectively. Although lower than previously encountered in association with dehydration, these values are similar to those found in other avian species, confirming that enhanced sensitivity for AVT release is not a part of an ostrich's adaptation to osmotic stress.

The major part of plasma osmolality is due to, and therefore proportional to, the concentrations of sodium and chlorine (Table 3.2 and Fig. 3.1). Normal values in the ostrich of these and other plasma or serum chemistry parameters have been published by van Heerden *et al.* (1985); Levy *et al.* (1989); Palomeque *et al.*

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(1991) and Angel (1996). The sodium balance is expected to be influenced by aldosterone produced by the adrenals; the plasma concentration of this hormone was augmented after 2 days of dehydration (Levy *et al*., 1990), and it was higher in non-laying than in laying ostriches (Levy *et al*., 1996). Average values of plasma and electrolyte concentrations from normally fed and watered ostriches (i.e. not exposed to osmotic stress) are summarized in Table 3.3.

The hypothalamus and pituitary

Central control of the endocrine system resides within the hypothalamus, a region of the brain posterior to the optic chiasma (where the optic nerves cross). The hypothalamus is the focus for a wide variety of external environmental information (e.g. day length), stressors, behavioural cues and internal information (e.g. temperature, osmolality and nutritional status). In response to these cues, neurosecretory neurones within the hypothalamus synthesize a variety of releasing hormones (specific small peptide hormones). In mammals, these pass down nerve fibres directly to the anterior pituitary or the posterior pituitary gland, but in birds the situation is slightly different.

The posterior pituitary is connected to the hypothalamus, as in mammals, and it releases neurohormones such as mesotocin, vasotocin, oxytocin and vasopressin. These hormones have been identified in ostriches (Rouillé *et al*., 1986); they affect the contractility of smooth muscle and have roles in osmoregulation.

The anterior pituitary of birds is not directly connected to the hypothalamus. Instead of passing directly to the anterior pituitary as in mammals, the releasing hormones are secreted from the ends of the neurosecretory neurones, at the median eminence (the base of the hypothalamus), and pass via a blood capillary

Table 3.3. Average values for plasma osmolality and selected electrolyte concentrations.

Study	Osmolality (mOsm)	Sodium (mM l^{-1})	Chlorine (mM l^{-1})	Potassium (mM l^{-1})
Skadhauge *et al.* (1984a)	300	143	106	3.5
van Heerden *et al.* (1985)	–	151	104	3.5
Gray *et al.* (1988)	293	148	99	4.3
Levy *et al.* (1989)	286	148	100	3.3
Gray and Brown (1995)	303	149	–	4.4
Skadhauge *et al.* (1995)	307	142	101	4.0

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portal system to the anterior pituitary gland. Within the anterior pituitary gland, each of these releasing hormones stimulates specific cells to synthesize and secrete much larger amounts of specific large peptide hormones which then pass into the general circulation. These 'trophic' hormones act in one of two ways. They may act directly on their target tissue(s), e.g. growth hormone stimulating the bones to grow; or they may stimulate a target endocrine gland to produce its particular hormone products, e.g. the thyroid gland to produce thyroid hormones, which are in turn released into the circulation and have their effects on their target tissues. In most cases hormone levels are in part controlled by negative feedback mechanisms, where one or more of the products of an endocrine gland inhibits release of its trophic hormone, e.g. thyroid hormones inhibit release of TSH from the pituitary.

Adrenal

The avian adrenal consists of the cortex and the medulla, which have different origins and functions. In response to a perceived stress, neurosecretory neurones within the hypothalamus synthesize and secrete the peptide corticotrophin-releasing hormone (CRH). In the pituitary, CRH stimulates cells to synthesize and secrete larger amounts of another peptide hormone, ACTH, and this passes in the circulation to the adrenals. ACTH stimulates cells within the adrenal cortex to synthesize corticosteroids. The major corticosteroid in birds, and presumably ostriches, is corticosterone. The corticosteroids are important in mobilization of energy reserves and in immune responses. Another product of the adrenal cortex is the steroid aldosterone which is important in osmoregulation.

Within the medulla of the adrenal glands are cells which, unlike the cortical cells, are not controlled by a pituitary trophic hormone. Instead, they are innervated directly. In response to a perceived stress, they secrete the catecholamine hormone, adrenaline which, like corticosterone, is important in preparing an animal for 'flight or fight'.

Reproductive endocrine system

The hypothalamic releasing hormone responsible for the control of reproduction is gonadotrophin-releasing hormone (GnRH), a decapeptide consisting of 10 amino-acid residues. In mammals there is only one GnRH; in birds there are two, designated GnRH-I and GnRH-II. Avian GnRH-I is identical to mammalian GnRH except that glutamine is substituted for arginine at position 8 (and so is designated as [Gln^8]–GnRH). Avian GnRH-II has three substitutions and is designated as [His^5, Trp^7, Tyr^8]–GnRH. Both avian GnRH-I and GnRH-II have been found in ostriches (Powell *et al.*, 1987). GnRH-I cell bodies are located in the septal and pre-optic regions of the hypothalamus, and project to the median eminence, whereas GnRH-II is more widely distributed. Only GnRH-I is secreted from the median eminence and is thought to play the major endocrine role in

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reproduction. GnRH-I secretion is stimulated by the catecholamines adrenaline and noradrenaline, and is inhibited by opioid peptides.

The release rate of GnRH-I presumably increases at the beginning of the breeding season, although this has not been measured directly. In response, the pituitary synthesizes and secretes larger amounts of the two gonadotrophic peptide hormones, luteinizing hormone (LH) and follicle-stimulating hormone (FSH). The complete amino-acid sequences for these two hormones in ostriches have been determined (Koide *et al.*, 1996). Both LH and FSH consist of two subunits, a common α subunit and a hormone-specific ß subunit. The α subunit comprises 96 amino-acid residues and has 70–80% sequence identity with the α subunit of most vertebrates. The ostrich FSH ß subunit consists of 106 amino-acid residues and shows 70–74% sequence identity with mammalian FSH ß subunit. The ostrich LH ß subunit consists of 128 amino-acid residues and shows 76–78% sequence identity with other avian LH ß subunits. Purified ostrich FSH is effective in a mammalian bioassay system, confirming its similarity to the mammalian hormone (Yu *et al.*, 1996).

Annual changes in circulating LH concentrations have been measured in ostriches (Degen *et al.*, 1994). In both males and females, LH reaches a peak which coincided with the beginning of egg-laying. However, the amplitude of the seasonal cycle is small compared with that of other birds. Similarly, in emus LH shows a subdued annual cycle (Malecki *et al.*, 1997). LH and FSH together stimulate growth and maturation of the gonads, the testes of the male and the left ovary of the female. FSH specifically stimulates maturation of the follicles in the ovary and the Sertoli cells in the testes. Feedback inhibition of FSH in females is mediated by inhibin, another peptide consisting of alpha and beta subunits, produced by the granulosa of the ovarian follicles. Inhibin may also have a direct role within the ovary.

LH stimulates the interstitial cells of the ovary and the Leydig cells of the testes to synthesize the gonadal steroid hormones, of which the most important is oestradiol in females and testosterone in males. These have a variety of effects, including sexual differentiation, development of secondary sexual characters, behaviour, metabolism, gamete production, moult and feedback inhibition of LH secretion. In addition, oestradiol stimulates the liver to synthesize vitellogenin, which passes in the blood to the ovary where it is taken up by ovarian follicles to form the yolk. The largest ovarian follicle, when nearing maturation, begins to secrete another steroid hormone, progesterone, which has a positive feedback effect on the pituitary causing it to secrete a surge of LH and resulting in ovulation. Levels of both oestradiol and testosterone have been measured in ostriches (Degen *et al.*, 1994). As with LH, peak levels coincide with egg laying, but the seasonal amplitude is small compared with other seasonally breeding birds.

Prolactin

Prolactin is a pituitary peptide hormone with a wide range of functions amongst vertebrates. In birds it induces broodiness and other parental behaviours, gonadal

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regression and moult. In pigeons it stimulates crop sac development, and the secretion of crop milk on which the young are fed. In mammals, release of prolactin from the pituitary occurs autonomously in the absence of hypothalamic control. Unlike most other hormones, whose secretion is stimulated by hormones from the hypothalamus, release of prolactin is inhibited by the hormone dopamine. By contrast, in birds synthesis and secretion of prolactin from the anterior pituitary is stimulated by a hypothalamic hormone, vasoactive intestinal polypeptide (VIP – a 28 amino-acid-residue peptide). Avian VIP differs from mammalian VIP by just one residue ([Glu^{16}]–VIP).

In most birds studied, there are marked seasonal changes in circulating concentrations of prolactin. Typically, prolactin levels increase during late spring and this is in response to increasing day length. Peak levels occur in late spring or summer, often coinciding with the end of the breeding season. This is associated with two of the functions of prolactin, namely inducing gonadal regression and incubation. Seasonal changes in prolactin have not been measured in ostriches, but they have been measured in emus (Malecki *et al.*, 1997). The emu is unusual in that it breeds during winter. Prolactin levels in non-breeding males increased from mid-winter until mid-spring and highest levels coincided with a rapid decrease in testosterone levels, marking the end of the breeding season. This may reflect the anti-gonadal role of prolactin. In many birds, breeding behaviour has an effect on prolactin which is superimposed on the seasonal cycle (Sharp *et al.*, 1997). The presence of a nest and eggs further stimulates prolactin secretion, possibly as a direct tactile response. In breeding male emus (as in ostriches, it is the males which incubate the eggs), prolactin levels in incubating birds were higher than in non-incubating birds at the same time (Malecki *et al.*, 1997). Testosterone levels in these incubating birds were much lower than in non-incubating birds, i.e. testosterone levels decreased in incubating birds in advance of the seasonal decrease in non-incubating birds. Again, this probably reflects the anti-gonadal role of prolactin. There have been a few measurements of prolactin in incubating ostriches, but levels in one incubating male were higher than in non-incubating birds (P.J. Sharp, personal communication, 1997).

Growth hormone

Growth hormone is related to prolactin and has a range of effects which result in somatic growth, maintenance of metabolic homeostasis and maintenance of the immune system. It may also have a role in the control of appetite. Its effects are diverse and include alteration of lipid, nitrogen and carbohydrate metabolism, activation of thyroid hormones and cellular differentiation. Growth hormone stimulates synthesis of insulin-like growth factor (IGF–1) which mediates many of the functions of growth hormone.

Growth hormone is synthesized and secreted by the anterior pituitary, but control of the rate of secretion is complex and not fully understood. Release is stimulated and inhibited by a variety of hypothalamic factors. Release may be stimulated by growth hormone-releasing hormone (GHRH), as it is in mammals,

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and inhibited by somatostatin. However, the major stimulus to release in birds appears to be thyrotrophin-releasing hormone (TRH). In adult birds, TRH is more important in stimulating the release of growth hormone than of thyroid-stimulating hormone.

Growth rates amongst young ostriches vary considerably more than between young of other avian species. To investigate whether this could be related to growth hormone, blood samples were taken from 23 5-month-old ostriches whose body mass varied from 11 to 52 kg (Dawson *et al.*, 1996). Plasma growth hormone concentrations ranged from 0.7 to 45.6 $\mu g\ l^{-1}$, but there was no correlation between growth hormone and body mass. However, this does not preclude an effect of growth hormone. Release of growth hormone from the pituitary occurs as a series of pulses rather than a steady release, and so concentrations in blood will vary with time, which could account for the variation between individuals. A detailed time-series analysis would probably be necessary to establish any association. However, it was clear from the data that slow growth in some birds was not simply due to an absence of growth hormone: the distribution of high and low growth hormone values was similar amongst small and large birds.

Pineal

The pineal gland produces the hormone melatonin but only during darkness; circulating levels are high at night and low during the day. Consequently, the daily pattern of melatonin changes seasonally as day length changes. In mammals, this photoperiodic signal is important in timing seasonal events such as breeding. In birds, it is not used to time seasonal events, but is important as a circadian clock to time daily activities. Whether melatonin is present in ostriches has yet to be investigated.

Thyroid

The avian thyroid comprises two dark red ovoid lobes located low in the neck, internal to the jugular vein and external to the carotid (at its junction with the subclavian artery). It is composed of roughly spherical follicles, each consisting of a colloid-containing lumen surrounded by a single layer of epithelial cells. These follicles contain thyroglobulin, a large molecular-weight protein. The major hormone secreted by the thyroid is thyroxine (tetra-iodothyronine), which is an iodinated derivative of the amino acid tyrosine with each molecule of thyroxine containing four iodine atoms. The thyroid gland extracts and accumulates iodide ions from the blood which are used to iodinate tyrosine residues within thyroglobulin, which is inactive but releases thyroxine when it undergoes proteolysis.

In mammals, the activity of the thyroid gland is controlled by TRH, which is a tripeptide (Glu–His–Pro) synthesized in the hypothalamus. TRH stimulates the pituitary to synthesize and release TSH. This mammalian mechanism is also true

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for embryonic birds, but in adult birds the pituitary appears to function more autonomously. TRH does not stimulate release of TSH but appears to be more important in stimulating the release of growth hormone from the pituitary. TSH is a large peptide consisting of an α and a ß subunit. The α subunit is the same as that of LH and FSH. TSH passes in the blood to the thyroid, where it stimulates release of thyroxine. Ostrich TSH is similar to that found in other vertebrates, and in a purified form it is able to stimulate thyroxine release in a variety of species (MacKenzie and Licht, 1984).

In mammals, most thyroxine in the circulation is bound to a specific binding protein, thyroid-binding globulin (TBG). Birds lack TBG and instead thyroxine is bound less specifically to albumins. The active thyroid hormone is not thyroxine itself, but tri-iodothyronine (T_3) produced by de-iodination of thyroxine, which occurs mainly in the liver. T_3 has a variety of effects, including increasing metabolic rate. A rather complex negative feedback system has evolved. TRH does not stimulate secretion of TSH in adult birds, but does stimulate growth hormone secretion. Growth hormone stimulates conversion of thyroxine to T_3, and T_3 inhibits secretion of TSH and growth hormone.

The thyroid of ostriches has received particular attention because of its possible importance during the evolution of ostriches and the other ratites (Dawson, 1996). The flightless condition of ostriches had led to them being regarded as primitive birds. However, de Beer (1956) argued that many of the apparently primitive characters were in fact juvenile rather than primitive, and that ratites were neotenous descendants of flying birds. Neoteny is the evolutionary process by which animals become sexually mature while still retaining juvenile features and so true adult features are eventually lost. Of particular importance in the case of ostriches is the arrangement of the palate, which is palaeognathous. This is in contrast to most birds where it is neognathous, but pass through a palaeognathous stage in their development. Other juvenile characters of ostriches include: very large eyes, comparatively long legs and downy feathers. In short, adult ostriches are simply overgrown chicks; although they grow to an enormous size, their morphology remains surprisingly unchanged.

Neoteny is a common strategy amongst living amphibians where it is related to thyroid function. Most amphibians have a well developed metamorphosis from an aquatic larval form (tadpoles) to an air-breathing adult form. This metamorphosis is thyroid-dependent; experimental removal of the thyroid glands results in tadpoles that continue to grow but never metamorphose. However, several species of amphibian are naturally neotenous. They become sexually mature as larvae and never metamorphose into an adult form. In some of these species, if they are treated experimentally with thyroxine, they do metamorphose into an adult, a form not known in nature.

There are two lines of evidence which suggest that thyroid function may have played a role in the evolution of ratites. Firstly, removal of the thyroid glands from nestling European starlings (*Sturnus vulgaris*) resulted in an apparently neotenous condition: birds remained looking like juveniles yet they became sexually mature (Dawson *et al.*, 1994). Several somatic and behavioural features of

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these neotenous thyroidectomized starlings resembled features found in ostriches: a chick-like head with large eyes, lack of fusion of skull sutures and a juvenile structure of the palate. The feathers also lacked cross-linking barbules and so were more 'downy' than usual. Furthermore, the distribution of feathers over the body resembled that of ostriches: feathers developed only along the central axes of the major feather tracts, leaving large areas of the body unfeathered. One obvious somatic difference, however, was that growth of thyroidectomized starlings ceased before adult size was attained, resulting in permanently small birds, whereas most ratites are huge. Thyroidectomized starlings were slow to learn which is presumably an effect of hypothyroidism on the development of the central nervous system. Such effects in humans (cretinism) have been known for centuries and have been widely documented in other mammals. Ostriches are anecdotally famous for their lack of intelligence. As young birds, many have difficulty learning to feed, and even older birds often ingest totally inappropriate items (Degen *et al.*, 1989; Deeming and Dick, 1995). The innate curiosity shown by young of other precocial species of bird appears to be retained by ostriches throughout life.

The second line of evidence is that there are several aspects of ostrich biology that suggest abnormal thyroid function. Some of these present serious commercial problems. As well as the behavioural problems already mentioned, farmed ostriches are particularly susceptible to a variety of diseases, they often have variable growth rates, problems with ossification, and difficulties with absorption of food from the gut (Deeming *et al.*, 1993; Deeming and Ayres, 1994; Kreibich and Sommer, 1995; Sales and Mellett, 1995). All of these could be symptoms of thyroid abnormality. Hypothyroidism in birds increases susceptibility to disease and decreases the mass of the avian lymphoid organ, the bursa of Fabricius. Conversely, treatment with thyroxine increases bursa mass and increases numbers of lymphocytes. Incidentally, the bursa of ostriches does not develop to the adult form seen in other birds (Berens von Rautenfeld and Budras, 1982), possibly another feature of their neoteny. Hypothyroidism reduces growth rates in birds, and TRH in birds is a potent inducer of growth hormone release. Thyroid hormones are involved in ossification and, finally, hypothyroidism can result in malabsorption syndrome.

None of the above is proof of thyroid dysfunction in ratites, but taken together they were compelling enough to warrant a study of thyroid function in ostriches. An initial experiment (Dawson *et al.*, 1996) showed that plasma thyroxine measured in a group of 23 5-month-old ostriches ranged from very low values of 0.2 to 6.5 nmol l^{-1}. Body mass of these birds ranged from 11 to 52 kg. There was a close correlation between body mass and plasma thyroxine, which suggested an association between slow growth rates and low thyroxine. However, it is possible that this correlation may have been, at least in part, an anomaly due to stress. The smaller birds had been restrained for longer, and stress causes a marked decrease in plasma thyroxine (Fig. 3.5).

A series of experiments compared thyroid function in ostriches with that in two non-ratite birds, European starlings and Japanese quail (*Coturnix coturnix*;

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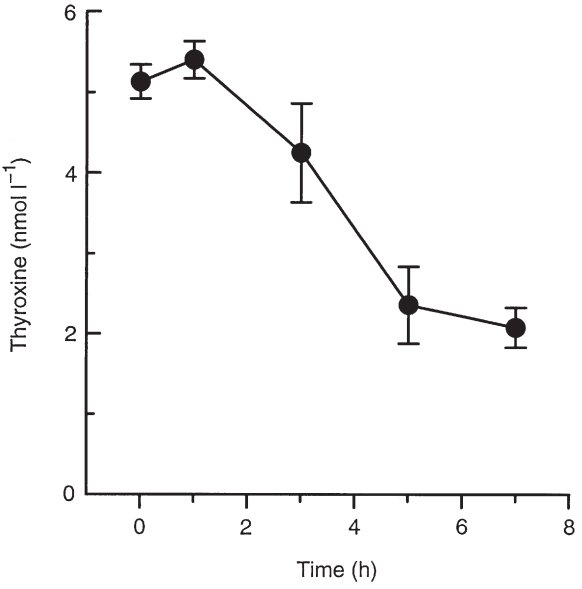

Fig. 3.5. The effect of stress on plasma thyroxine concentrations in ostriches. Plasma thyroxine decreased to 50% of initial values by 6 h after birds were initially sampled. Each point represents the mean of six birds. Data from Dawson and Deeming (1997).

Dawson and Deeming, 1997). In starlings and quail, a saline injection resulted in a slow decline in thyroxine (Fig. 3.6). In ostriches there was a more dramatic decrease. TSH resulted in a marked and sustained increase in thyroxine in starlings and quail. In ostriches, it merely compensated for the saline (stress?)-induced decrease. In all three species TRH caused a marginally greater rate of decrease in thyroxine than did saline. This is because TRH stimulates growth hormone secretion, which increases conversion of thyroxine to T_3, which in turn inhibits secretion of TSH.

It was apparent that restraining and repeatedly sampling ostriches resulted in a marked decrease in plasma thyroxine. This confounded attempts to compare thyroid function between the species. In a further experiment, an attempt was made to minimize this stress by collecting only one blood sample after treatment (Dawson and Deeming, 1997). This was done at 4 h, approximately corresponding to the time of the peak response to TSH. In addition, in this experiment the response to exogenous T_3 was examined, and the effects of treatments on plasma T_3 were assessed.

The general conclusion of this study was that there is no fundamental difference in thyroid function between a ratite and non-ratite species. Circulating levels of thyroxine and T_3 in non-stressed ostriches fell within the range of values from starlings and quail. The response to stress in ostriches was pronounced, making quantitative comparisons difficult. Nevertheless, it is clear that in all

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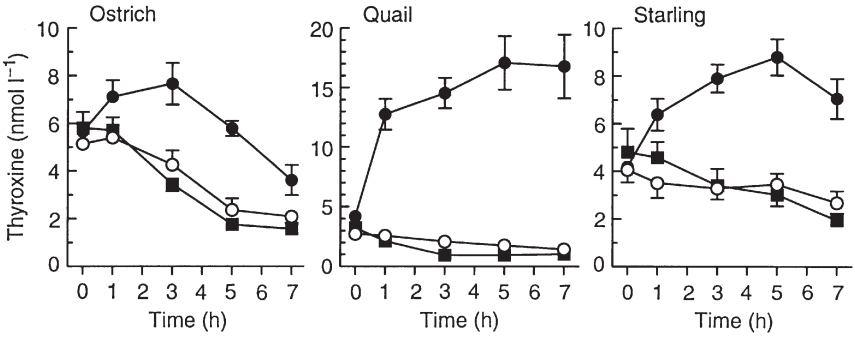

Fig. 3.6. Changes in plasma concentrations of thyroxine during the 7 h following an intramuscular injection of saline (❍), TRH (3 μg kg^{-1}; ■) or TSH (0.1 IU kg^{-1}; ●) in ostriches (n=6), quail (n=8) and starlings (n=8). Each point represents the mean ± SE. Data from Dawson and Deeming (1997).

three species stress tended to cause a decrease in thyroxine and an increase in T_3; treatment with TRH caused a decrease in thyroxine and an increase in T_3 above that due to stress; treatment with TSH resulted in an increase in both thyroxine and T_3; and finally, exogenous T_3 caused a decrease in thyroxine. The response of ostriches to TSH was poor; they would have failed a standard thyroid function test, suggesting ostensibly a lack of hypothalamic control. However, when the decrease in thyroxine following saline alone is taken into account, there clearly was a response to TSH.

Plasma thyroxine has also been measured in ostriches during the first few months after hatching (Dawson *et al.*, 1996). In this study, blood samples were collected from 18 birds from 4 days after hatching until they were 13 weeks old. Only 12 of the original 18 survived until 13 weeks. In these 12 birds, body mass increased steadily from a mean of 0.87 kg 4 days after hatching, to 7.7 kg by 13 weeks. For each individual, body mass increased at a fairly constant rate, but the rate varied widely between individuals so that by 13 weeks body masses ranged from 4.8 to 16.0 kg. At 4 days after hatching, mean thyroxine was 7.66 nmol l^{-1} and it decreased to 2.3 nmol l^{-1} by 10 days. Levels decreased further and then remained below 2 nmol l^{-1}. The high levels soon after hatching may have been a result of maternal thyroxine stored in the yolk. At all time points there was considerable variation in thyroxine values. However, although growth rates amongst the 12 birds which survived varied considerably, there was no apparent relationship between growth rate and thyroxine.

Of the six birds which did not survive, two were culled because they had tibiotarsal rotation and the other four died (*post-mortem* examination suggested *Escherichia coli* septicaemia). All four of these birds had thyroxine levels below the mean of the surviving birds. Furthermore, at 9 weeks old, blood samples were taken from three additional birds from the same cohort. These were the three smallest birds in the cohort at the time, but they had not been in the group

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routinely sampled. Their mean body mass was 1.95 kg compared with 3.93 kg in the group of 12 at the same time. Their mean plasma thyroxine concentration was 0.4 nmol l^{-1} compared with 1.4 nmol l^{-1}.

These results suggested an association between mortality and low thyroxine. They did not prove a causal relationship; birds may have had low thyroxine because they were sick rather than the other way round. Nevertheless, an experiment was done to determine whether artificially increased thyroxine could reduce mortality (A. Dawson, D.C. Deeming and A.C.K. Dick, unpublished observations, 1996). A group of 22 ostriches were hatched, 10 were allocated to a treatment group and 12 were controls. When they were 4 days old they were weighed and a blood sample was taken. From then on, the ten experimental birds were given a single tablet each day of Elthoxin (Goldshield Healthcare) which

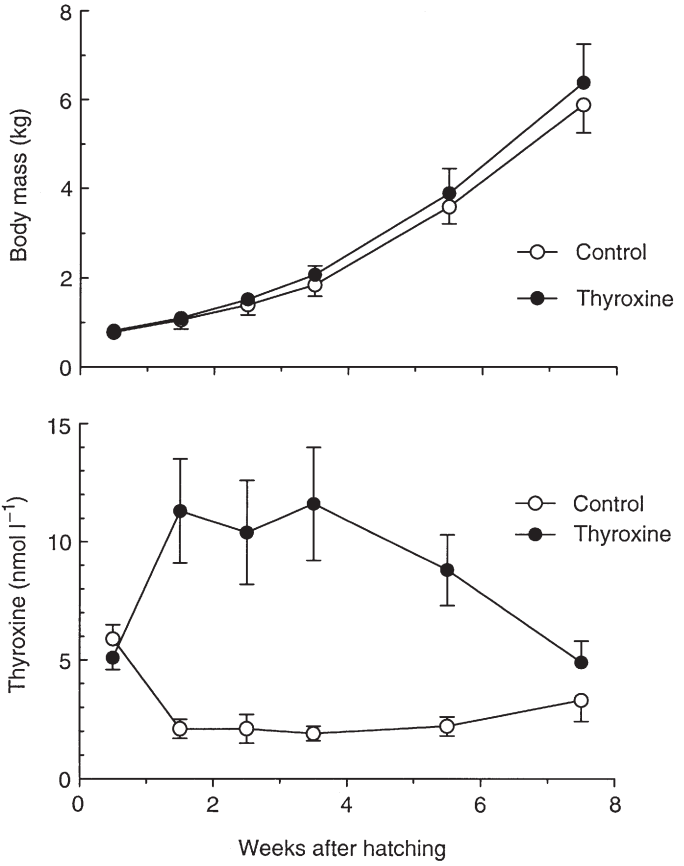

Fig. 3.7. Body mass (upper panel) and plasma thyroxine concentrations (lower panel) following hatching in ostriches treated with 100 mg thyroxine per day (n=10) or in untreated control birds (n=12). Each point represents the mean ± SE. Data of A. Dawson, D.C. Deeming and A.C.K. Dick (unpublished, 1997).

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provides 100 mg thyroxine. Controls were left untreated. All birds were weighed, and regular blood samples were taken, over the next 7 weeks. In controls, plasma thyroxine decreased between 4 and 10 days as before (Fig. 3.7); by contrast, in the treated birds it increased. From 4 weeks, thyroxine gradually decreased in the treated birds, presumably because the treatment remained constant but body mass increased. There was no difference in body mass between the two groups. However, six of the 12 controls died over this period whereas only two of the treatment group died. This experiment was too small to draw firm conclusions, but it suggested that thyroid supplementation did decrease mortality.

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Behaviour in Natural and Captive Environments

4

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One feature of behaviour invariably quoted when ostriches are discussed is their supposed habit of burying their head in the sand. Perhaps disappointingly, this myth has no basis in fact (Pocock, 1955) except for the juxtaposition of an ostrich's head to the horizon when feeding or lying down (Sauer and Sauer, 1966a). The behaviour of the ostrich in its natural habitat has been the subject of several studies, but work on the behaviour of ostriches in farming environments has only recently begun. This chapter reviews the behaviour of ostriches both in their natural habitats and in farming situations where the behaviour of captive ostriches is described by age groups (adults, juveniles and chicks under 3 months old).

NATURAL ENVIRONMENT

Social behaviour

Out of the breeding season the ostrich is a gregarious species (Sauer and Sauer, 1966a, b; Bertram, 1980, 1992; Burger and Gochfeld, 1988), forming groups of birds of mixed gender and age, particularly around water holes. In Namibia such groups can involve hundreds of birds (Sauer and Sauer, 1966a, b). Nevertheless, social groups based around specific family units do exist and survive beyond the mixing and disturbance observed at water holes (Sauer and Sauer, 1966a, b). There appears to be no specific structural unit, nor any temporal pattern to associations for social groups of ostriches, with adults mixing with adults and/or juveniles alike (Sauer and Sauer, 1966a, b). There does, however, appear to be a social

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hierarchy within these groupings, headed and maintained by an adult male or 'major' female (Sauer and Sauer, 1966b). Large flocks of birds allow individuals to preen and even sleep with greater ease than would be possible in smaller flocks (Sauer and Sauer, 1966b). During the breeding season much smaller groups of adult birds are more normal, with over 80% of sightings of ostriches by Bertram (1992) being of a single bird or a pair of ostriches.

Ostriches live in a mixed community in their natural habitats, with the possibility of encounters with a wide variety of other species of animal. Sauer (1970) investigated the interspecific behaviour of ostriches in Namibia by recording the outcome of contact with mammals and birds. Ostriches avoided close contact with other animals and almost 75% of interspecific behaviours were largely neutral, i.e. ignoring, tolerating or avoiding other species. This shyness has made the ostrich a difficult species to observe in natural situations (Sauer and Sauer, 1966a, b; Bertram, 1992). Agonistic behaviours towards other species formed 16% of the encounters and were aimed at defence and termination of an encounter (Sauer, 1970).

Feeding behaviour

A time–activity budget has been recorded for wild ostriches in the Namib Desert, Namibia (Williams *et al*., 1993). Radio-tagged ostriches were shown not to move during the night and were presumed to be sleeping. During daylight hours (06.30–19.00 h), approximately 60% of the time was spent walking, 20% pecking and 16% standing. Preening and sitting each occupied less than 3% of the time budget and all other behaviours combined accounted for less than 1%. Bertram (1992) showed that ostriches of both genders spent 33% of their time during daylight hours feeding, 29% travelling, 18% being alert and 9% preening.

Williams *et al*. (1993) also looked at the use of the habitat by ostriches. Adults spent 64% of their time on gravel plains (sparsely covered by perennial grasses) and 26% of their time on washes (dry river channels with shrubs and trees) where plant cover was almost twice as great. The birds pecked significantly more frequently on the washes than on the gravel plains, where the effort expended on foraging (number of steps per unit time foraging) was significantly higher than on the washes.

Adult ostriches are almost exclusively vegetarian, although they do swallow dry bones (Williams *et al*., 1993; Dean *et al*., 1994; Milton *et al*., 1994; Milton and Dean, 1995). Selection of food items is visual and involves the beak pulling at all parts of vegetation and stripping (not biting) leaves from shrubs and woody plants (Dean *et al*., 1994). A wide variety of vegetation is consumed, with the ostriches varying their diet according to plant life available in the habitat. Green annual grasses and forbs are preferred, although leaves, flowers and fruit from succulent and woody plants are also consumed (Williams *et al*., 1993; Milton *et al*., 1994). Dead plants, woody material and plants known to be toxic to mammalian herbivores are rarely eaten (Williams *et al*., 1993; Dean *et al*., 1994). Indeed, ostriches have been shown to have a significant preference for forbs low in phenolics and

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high in fibre (Milton *et al.*, 1994). A daily diet of 5–6 kg of fresh vegetation (70% water) is required by adult ostriches.

Ostriches need to consume stones in their diet (Milton and Dean, 1995) but they are also renowned for their ability to swallow unusual objects (Huchzermeyer, 1994), and reports include one on an adult ostrich which had consumed 2.5 m of barbed wire (Degen *et al.*, 1989). Milton and Dean (1995), Deeming and Dick (1995) and Samson (1996) all report instances of juvenile and adult birds having swallowed large numbers of metal objects, including nails.

Burger and Gochfeld (1988) report that in Kenya male ostriches had shorter feeding bouts than females (25.0 versus 37.5 s, respectively). Group size had a significant effect, with solitary ostriches spending much less time eating with shorter eating bouts (16.2 versus 34.1 s for solitary birds and those in groups) and they devoted less time per minute to eating to when solitary (20 s min^{-1} for one bird compared with 40 s min^{-1} for birds in groups of four to five birds).

Feeding and vigilance behaviours are mutually exclusive because once the head is lowered to feed, the ability of the bird to look around is lost. Bertram (1980) observed wild ostriches during the breeding season in Kenya and studied the relationship between group size and the length of time the head was held up. As group size increased (to three or four birds) then the rate at which the head was raised and the length of time the head was held up both declined. Males were more vigilant than females in all group sizes and this was presumed to be related to searching behaviour for predators and for potential mates or rivals.

Burger and Gochfeld (1988), also working in Kenya, found that male ostriches were more often solitary and spent more time with their head up. Both males and females spent significantly more time walking if in unisexual groups compared with mixed-sex groups. As group size increased the time spent with the head up declined for females (from 40 s min^{-1} for solitary birds to 12–15 s min^{-1} for birds in groups of six to ten birds). By contrast, vigilance in males only decreased to 20 s min^{-1} with the head up for groups of three to seven birds. In larger groups, the time increased again to an original level of 40 s min^{-1} observed in solitary birds, and there was a decrease in feeding by males in the largest groups. Burger and Gochfeld (1988) attributed the increase in male vigilance in larger groups to increased mate competition.

Courtship and breeding

Sauer and Sauer (1966a, b) describe the sexual behaviours of adult ostriches whilst still in social groups. Female birds show pre-nuptial courtship displays towards male companions involving posturing in front of potential mates. A dominant female exhibits aggressive behaviour against other females and any yearlings in the group, which often adopt a characteristic submissive posture (head down, neck in S-shape and tail down) to appease the aggressor. Males appear to develop courtship behaviours later than females, with a slow development of the characteristic red flush of the beak, neck, thigh and shin skin. Dominance by males in mixed groups is established by posturing, usually with the tail held erect,

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and aggression against companions. The erect phallus is also distended from the cloaca and displayed to other birds.

Males begin to establish territories where they make nest scrapes (Sauer and Sauer, 1966b). In Kenya, these territories vary between 11 and 19 km^2 although immature males hold smaller territories (Bertram, 1992). There is relatively little overlap between territories and the same area can be used by the male in successive years. Defence of the territory usually involves parallel walking, chasing and kantling (described below) by the males. By contrast, females cover a mean range of at least 25 km^2 and they enter territories held by a variety of males, although a few males are actively avoided by some females.

Courtship behaviours leading up to copulation (Sauer and Sauer, 1966b) involve a sequence of behaviours often initiated by the male 'booming' to attract a mate. Once the male and female come together they perform a synchronized feeding behaviour which can be easily interrupted by the birds going off to graze. The next stage is ritualized feeding by both birds at a chosen nest site. The male then struts with exaggerated strides, during which the neck is stretched forward and backwards with each step and the wings are swung alternately. The male then drops to the ground to kantle to the female; he sits on his haunches with his wings held forward and his neck held over his back, rhythmically moving his head and neck from side to side with his head hitting his back at the completion of each sideways stroke. The female shows precopulatory behaviour with her wings fluttering and held in a forward position and her head held down accompanied by a clapping of the beak. This culminates with the bird dropping to the ground with her tail raised and neck forward. The male responds by getting to his feet and approaching the female with his wings held forward. Just prior to mounting, the male stamps his feet on the ground several times. Mounting involves the male sitting astride and to the right of the female. Repeated thrusts of the phallus are often required before intromission. During copulation the male performs a kantle display to climax with his head being brought forward and a deep guttural grunt emitted. During the 30–60 s of mating the female usually remains impassive although she may hold her head forward and clap her beak. There is very little post-copulation behaviour.

Aberrant sexual behaviour has been reported for large groups of male ostriches in Namibia (Sauer, 1972). Typical courtship behaviours included kantling performed by males to males who did not reciprocate. Sauer (1972) interpreted this as a means of releasing sexual tension prior to breeding or as a method of suppressing aggression associated with a prolonged period of wet weather. Whether this interpretation is correct is unclear, because kantling is an aggressive behaviour in male–male confrontations over territory (Bertram, 1992). Since the behaviour was observed in large groups of males within which it is sometimes difficult to differentiate birds by age, it is possible that the behaviour was being displayed by young, inexperienced males.

The ostrich has a communal nesting system which is extensively described by Bertram (1992) and only briefly reviewed here. Each territorial male digs a number of nest scrapes which he shows to any female which enters his

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territory. In each territory a 'major' female pairs with the male and lays most of her eggs in the nest site she chooses. In addition, other 'minor' females visit the territory and may lay an egg within an already established nest. These birds may be 'major' females in another male's territory. The average number of minor females laying in a nest was three (range one to five). Each 'major' hen usually contributes about 11 eggs (range of 9–14) to her nest and the total number of eggs in the clutch (average of 26 with a range of 15–39) depends on the number of 'minor' hens laying in the nest. This breeding system is reported for birds throughout the natural range of the ostrich (Sauer and Sauer, 1966b; Jarvis *et al.*, 1985; Bertram, 1992) and hence is considered to be typical of the species.

Eggs are laid in the late afternoon or early evening (Sauer and Sauer, 1966b) and the clutch builds up over a period of up to 30 days (Bertram, 1992). During this period the nest is attended by both male and female, although full incubation does not proceed until the clutch is complete (Sauer and Sauer, 1966b). As the clutch is being laid the courtship behaviours of both males and females gradually diminish in frequency (Bertram, 1992). Incubation is carried out by both genders with the male bird sitting during the night (Bertram, 1992). At the first sign of danger the birds rely on camouflage to conceal them from predators, although they perform distraction displays or attack potential predators if necessary (Sauer and Sauer, 1966b; Bertram, 1992).

One unusual aspect of the ostrich breeding system is once the 'major' hen starts to incubate she rearranges the eggs and discards several from the nest until around 19–20 eggs remain (Bertram, 1979, 1992). These eggs lie in a ring around the incubating bird and do not develop. Contrary to the view of Sauer and Sauer (1966b), the major hen actively discards eggs laid in the nest by minor hens and retains her own. How she recognizes her own eggs remains unclear (Bertram, 1979). Further details of incubation behaviour are described by Deeming and Ar (Chapter 7).

Behaviour of offspring

Little is known about the behaviour of ostrich chicks under natural conditions. Hatching takes place over a period of 2–3 days, during which time the hatchlings remain brooded by an adult although they start to consume small stones during periods of activity (Sauer and Sauer, 1966b). Once the chicks leave the nest they are difficult to track in grassland (Bertram, 1992), but the parents of young birds brood them as protection against the elements and predators. Adults will feign a 'mock injury' to distract a potential predator from the chicks (Brown *et al.*, 1982; Bertram, 1992). Families of chicks are combined into creches, which may number up to 300 birds and are overseen by a single pair of adult birds (Hurxthal, 1979). When groups of chicks meet there is a vigorous behavioural contest between the guardians of each group over which adults will take charge of the enlarged creche. Usually younger chicks are accepted into groups of older chicks, but not *vice versa* (Brown *et al.*, 1982). By the time the chicks are a year old they

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have been abandoned by the adults and spend their time in a compact peer group (Bertram, 1992).

Other behaviours

Ostriches are reported to carry out a variety of maintenance activities including yawning and stretching (Sauer and Sauer, 1967). Yawning often precedes sleep and, together with stretching, takes place after waking. Ostriches are adept at behavioural thermoregulation. During hot weather they lose heat by panting and fluffing up their feathers to expose bare skin on their thorax and upper legs (Skadhauge and Dawson, Chapter 3).

FARMING ENVIRONMENT

Adults

Time–activity budgets

In a study conducted in South Africa, the behaviour of ostriches managed on ranches of natural vegetation surrounded by a boundary fence has been investigated and compared with sheep under the same conditions. Ostriches spend 43% of daylight hours walking, running and fighting, although sheep maintained under the same conditions spend only 19% of their time performing these activities (Milton and Dean, 1995). Male ostriches patrol boundary fences and even when provided with supplementary rations they forage from the veld. At stocking densities of 1–10 ha bird^{-1} year^{-1}, ostriches damage the veld through path formation and trampling of vegetation (Dean *et al*., 1994; Milton *et al*., 1994; Milton and Dean, 1995).

A simple time–activity budget over the period of daylight hours was recorded for a group of 120 adult ostriches (40:80 males:females) maintained in a 30 ha enclosure in Israel (Sambraus, 1994a). Standing and walking combined averaged 62.9% (n=24×30 min time periods) of the time–activity budget, with these behaviours increasing towards dusk (Fig. 4.1). Sitting and lying averaged 18.7% and occurred at a relatively low frequency during the morning but increased as the afternoon progressed before dipping just prior to dusk. Eating and drinking combined averaged 18.3% with a peak during the morning after the concentrate ration had been delivered.

Berendsen (1995) reports a time–activity budget for a group of 33 adult ostriches (9:24 M:F) maintained on a farm in Germany, but neither the time of year nor the time of day when observations were made were reported. The ostriches spent about 26% of their time feeding and in search of food although whether this activity was feeding on concentrate ration or foraging from the

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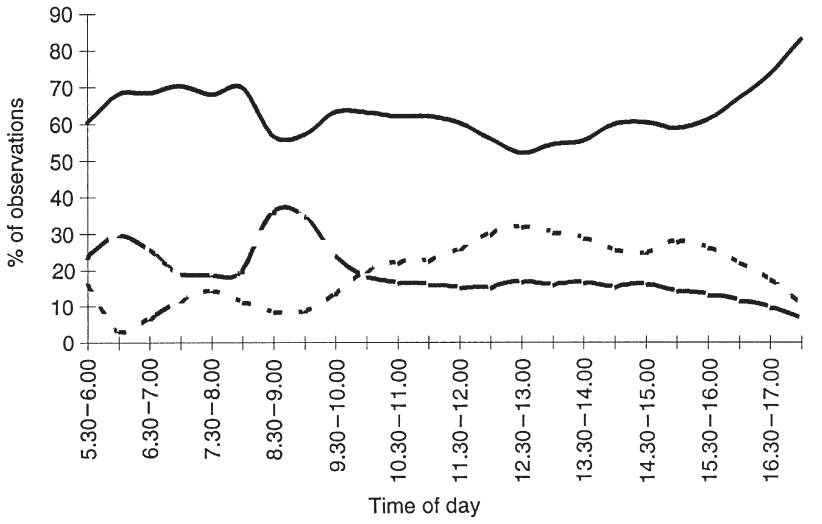

Fig. 4.1. The effect of time of day on three types of behaviour exhibited by a group of 120 adult ostriches (40:80 males:females) maintained on a farm in Israel. Short dashes, sitting/lying; long dashes, eating/drinking; solid line, standing/walking. Data from Sambraus (1994a).

pasture was not stated. Drinking took up only 1.1% of the time–activity budget. Fifteen per cent of the time was spent walking or running whereas 27% of the time was spent resting; by dusk 80% of the flock was resting. Standing occupied 18% of the time–activity budget. An average of 5% of the day was spent on preening but destructive feather pecking (presumably aimed at companions) was only 0.06% of the time budget. Fence pecking occupied 3% of the time. Less than 1% of the time–activity budget was spent in courtship behaviour, and aggressive behaviour accounted for 1.9% although the incidence of this was higher in the late afternoon.

More comprehensive time–activity budgets are available for breeding ostriches maintained on a farm in Britain during both summer (McKeegan and Deeming, 1997; Ross and Deeming, 1998) and winter (Deeming, 1998a). Six behaviours predominated in the time–activity budget: standing, pacing (i.e. walking near fence), walking, sitting, feeding (on concentrate ration) and foraging (from pasture). During summer months, significant differences existed between genders in ostriches maintained in pairs and trios (McKeegan and Deeming, 1997; Ross and Deeming, 1998; Fig. 4.2). Males both paced and walked significantly more than females, whereas the incidence of feeding and foraging were significantly higher in females (McKeegan and Deeming, 1997). Males and females maintained in two larger groups (11 and 22 birds, respectively) showed largely similar results, although in males the frequency of pacing was greatly reduced, with an increase in standing and sitting (McKeegan and Deeming, 1997). These

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differences were attributed to territoriality by males (considered difficult to maintain in the larger groups) and to increased energy requirements of females due to egg production (McKeegan and Deeming, 1997). Although not directly comparable, there was similarity between the time–activity budget of adult male ostriches in the group of 22 birds and that described for the group of birds observed by Berendsen (1995).

Few behaviours were affected by the time of day (McKeegan and Deeming, 1997) although the frequency of feeding increased, and the frequency of foraging decreased, in the period immediately after food delivery. In all group sizes the frequency of sitting behaviour was highest just before dusk.

Lambrechts *et al.* (1998a) carried out a time–activity budget of adult breeding ostriches maintained in Oudtshoorn, South Africa (Table 4.1). Although not directly comparable to the data collected by McKeegan and Deeming (1997), Lambrechts *et al.* (1998a) did find that the same six behaviours were most frequently observed and that there were gender differences (Table 4.1). Sitting was observed at a more frequent rate than in Britain, and females sat for more time than males. Standing was similar for both genders whereas the frequency of pacing was over twice as much in males than females. The frequency of foraging in females was almost three times higher than in males. The frequency of other behaviours was comparable in the two genders. That both McKeegan and Deeming (1997) and Lambrechts *et al.* (1998a) described largely similar patterns of time–activity budgets despite the different locations of the studies suggests that the behavioural repertoire of ostriches is rather conservative.

It is often assumed (Degen *et al.*, 1989; McKeegan and Deeming, 1997) that ostriches are inactive during the hours of darkness. Using a night-vision scope, Lambrechts and Cloete (1998) recorded nocturnal behaviour of adult ostriches

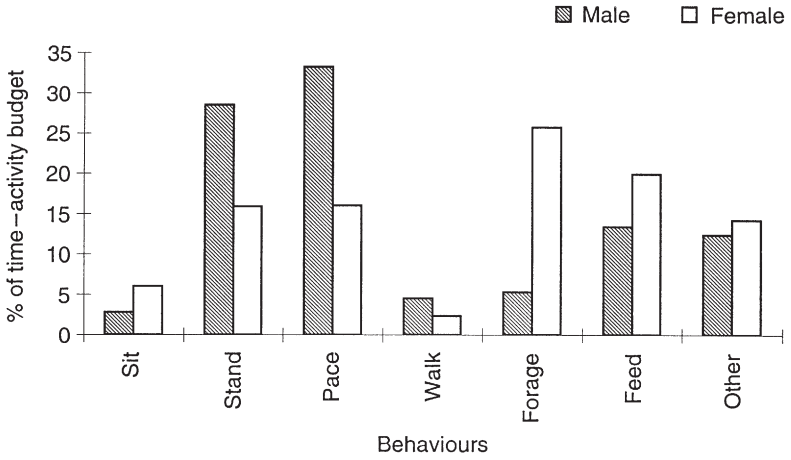

Fig. 4.2. Time–activity budget of male and female adult ostriches maintained as pairs and trios in breeding enclosures on a farm in Britain. Data from Ross and Deeming (1998).

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Table 4.1. A time–activity budget of male and female breeding ostriches maintained on farms in South Africa. Data derived from Lambrechts *et al.* (1998a).

Behaviour	Males	Females
Sit	14.5	23.1
Stand	32.3	31.7
Pace	31.6	12.8
Walk	3.3	4.6
Forage	5.3	15.0
Feed	5.2	4.8
Other (by difference)	7.8	8.0

in Oudtshoorn. Although a few maintenance and courtship behaviours were recorded, most of the birds sat at sunset and were inactive all night.

A time–activity budget for adult, non-breeding ostriches during winter months in Britain showed that gender differences were absent (Fig. 4.3; Deeming, 1998a). Active behaviours such as walking and pacing were a small part of the time budget, whereas intake of food was very important. During the morning the

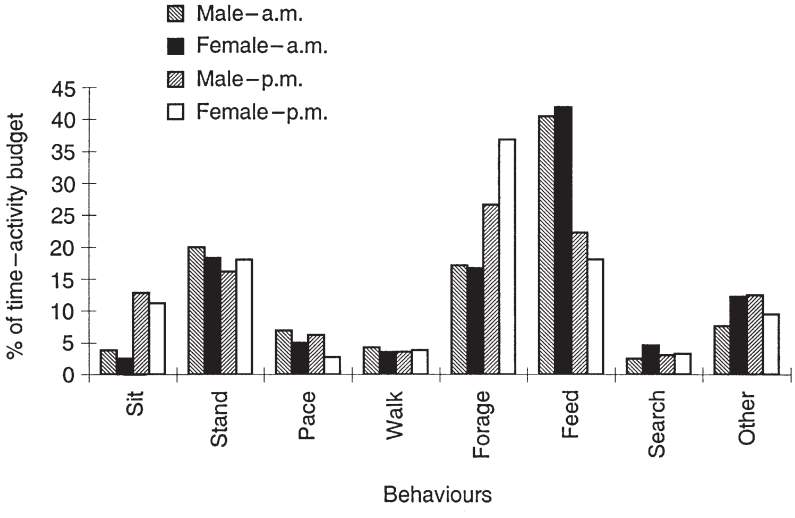

Fig. 4.3. The frequency of behaviours of male and female adult ostriches during the morning and afternoon as observed during winter months on a farm in Britain. Data from Deeming (1998a).

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amount of time spent feeding on concentrate ration was high whereas during the afternoon the time spent foraging on the pasture was high. This was attributed to the management's delivery of food during the morning and the ostriches' supplementation of their diet with grazing in the afternoon (Deeming, 1998a).

The effects of specific climatic conditions on ostrich behaviour have been investigated during spring and winter months in Britain (Deeming, 1997b, 1998b). During periods of rain, active behaviours such as pacing and foraging were decreased but feeding on concentrate ration was not significantly affected. In the spring, adult males and females spent over 50% of their time sitting if it was raining but only 10–20% if the weather was dry (Deeming, 1997b). The increase in sitting was due to precipitation rather than temperature although the birds usually chose to sit in the rain rather than in a shelter (Deeming, 1997b). Such behaviour has been observed in ostriches in Germany (Berendsen, 1995). Reviewing the behaviour and welfare of ostriches on farms in Germany, Reiner *et al.* (1996) found that only 20% of birds actively chose to seek shelter when the weather was inclement.

During the winter months rain also caused the birds to sit significantly more frequently than during dry weather (22% versus 2% for dry conditions), again associated with lower frequency of foraging activity. Intake of food, foraging and feeding combined occupied over 50% of the observations (Deeming, 1998b). In dry conditions during spring months, feeding and foraging only occupied 25–30% of the observed behaviours. During both spring and winter months, when the birds were not yet breeding, there were no gender differences in behaviour (Deeming, 1997b, 1998b). The effects of snow on behaviour have not been reported, but during icy conditions ostriches appear to walk more carefully (Reiner *et al.*, 1996).

Feeding behaviour

During the breeding season, feeding and scanning behaviours of captive male and female ostriches differ (Ross and Deeming, 1998). Studied during the 10 min period immediately after food delivery, male ostriches spent significantly less time than females feeding although the number of feeding bouts was significantly higher in males. Time spent scanning by females was much lower than in males. Compared with companion females, males also had a higher rate of head lifting during the period after food delivery. The higher number of head lifts for males in trios was considered to be due to the increased frequency of head lifting by the group as a whole. Interscan periods for males were mainly below 40 s with a maximum of 90 s, compared with a peak at 70 s and a range up to 160 s for females. These patterns of behaviour were attributed to increased vigilance by males of which females took advantage.

Ostriches kept on rangeland in Africa will consume concentrated ration when provided but will always consume natural vegetation whenever available, apparently preferring it (Dean *et al.*, 1994; Milton and Dean, 1995). Such

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ranched ostriches often degrade the natural vegetation through over-grazing and treading of paths (Dean *et al.*, 1994; Milton and Dean, 1995). On British farms, areas by gates and perimeters of enclosures are often worn clean of vegetation by adult ostriches walking in these areas, a problem exacerbated by prolonged wet weather when the ground tends to become waterlogged (Deeming, personal observations, 1993–1996). During summer months, a pair of adult ostriches are unable to graze down an area of pasture measuring 1200 m^2 and the grass often requires cutting (Deeming, personal observations, 1993–1996).

Misdirected feeding due to stress is often thought to be the cause of consumption of stones, straw, long grasses and roots which lead to proventricular impaction in ostriches of all ages (Huchzermeyer, 1997). Other behavioural indicators of stress or boredom in ostriches include pecking at the air, food and water troughs, and feathers and fences (Stewart, 1994; Sambraus, 1995a; Huchzermeyer, 1997; Lambrechts *et al.*, 1998b; Bubier, personal observations, 1995).

Social behaviour

In Namibia, Sambraus (1995b) studied the social structure of three groups of nine to ten adult ostriches of mixed gender (4:6 M:F). In each of the three groups the alpha and beta positions in the social hierarchy were held by older male birds although being male did not guarantee a high position in the social structure. Females generally occupied lower positions in the ranking order.

Little is known about agonistic behaviours in farmed ostriches. Aggression against females by adolescent males has been described by Stewart (1994) and aggression by adult birds is commonly directed towards younger chicks (Bolwig, 1973).

Courtship behaviour

The pattern of courtship behaviour of captive ostriches closely resembles that observed in the wild (Bolwig, 1973; Stewart, 1994; Berendsen, 1995; Hicks-Alldredge, 1996; Deeming, 1997a; Bubier *et al.*, 1998). Frequency of mating by ostriches in captivity in Britain is low, with only 20 attempts at copulation being recorded in 99 h of observations (McKeegan and Deeming, 1997). Both the incidence of courtship and copulation behaviours in a group of 120 adult ostriches in Israel were higher during the first 3 h after dawn compared with the rest of the day (Sambraus, 1994c). In a study which compared rates in the presence and absence of humans, high rates of copulation were reported in ostriches in the presence of a human standing adjacent to the enclosure fence (Bubier *et al.*, 1998).

In farming situations, breeding enclosures can be small and hold a pair or trio of birds. In Europe some enclosures hold relatively large groups of ostriches in a

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1:2 M:F ratio. In South Africa and Israel, large breeding camps (hundreds of hectares) are established with 150–200 birds, again in a 1:2 M:F ratio. In the latter two systems the birds are left to choose their own mates (Hicks-Alldredge, 1996). In Britain, Deeming (1996) showed that pairs and trios were more productive than larger groups, but more research in this field is needed.

Behavioural problems with regard to the choice and number of mates have been suggested by several authors to pose a problem in commercial production (Stewart, 1994; Hicks-Alldredge, 1996; Deeming, 1997a), although few studies back up these assertions. In Britain, ostriches in enclosures containing one male with two females had low values for egg production and fertility, both of which significantly improved when one of the females in each enclosure died (Deeming, 1996). In Israel, farmed ostriches exhibited aberrant courtship behaviours, with females both displaying and attempting to mount other females (Sambraus, 1994c). Kantle displaying by a female to another female in an adjacent enclosure has been observed in Britain (Deeming, personal observation, 1996). The significance of these anecdotal reports is not clear, but it is clear that mate selection in captive ostriches requires further investigation.

The courtship response of ostriches to humans can be very marked. In a study by Bubier *et al.* (1998), birds were observed for 10 min periods from distant locations where the birds could not see the human, and then for 10 min periods with the human standing next to the fence. Significant differences in the frequency of both male and female courtship behaviours were observed. Male kantling and wing swinging and female soliciting did not occur during data sessions when the ostriches were observed from a distance and were only observed when the human was next to the fence. Adult birds were also observed for 10 min periods before and after exposure to a human next to the perimeter. No significant differences in the courtship behaviours in these periods were observed suggesting that contact with humans did not stimulate courtship behaviour thereafter, although the incidence of copulation whilst the human was present was higher than observed before or after contact. This study suggests that ostriches raised on farms may be imprinting on humans. If this is the case, this would cause problems at maturity when adult ostriches might then direct their courtship displays at humans rather than at mates, as observed in this study.

Spray marking one female ostrich in a trio with stock-marker paint has been shown to disrupt the social behaviours of the three birds during the breeding season (Chapman and Deeming, unpublished observations, 1996). Male birds spent significantly more time with the unmarked female and expressed significantly more agonistic behaviour towards the marked female.

Lambrechts and Cloete (1998) split pairs of adult ostriches into two groups of ten based on whether they had produced less than 30 eggs, or more than 60 eggs, in the previous breeding season. Time–activity budgets revealed gender differences similar to those reported by McKeegan and Deeming (1997) and Lambrechts *et al.* (1998a). Observations over a period of 6 months during the breeding season revealed that consumption of concentrate feed by males was significantly higher in the low productivity group, whereas the frequency of mating

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in this group was significantly lower. Whether these results are a reflection of mate compatibility in these birds remains to be determined.

The behaviour of breeding adult ostriches is reported to be influenced by exogenous application of an L-carnitine–magnesium supplement (Lambrechts *et al.*, 1998a). Compared with birds in the control group, frequency of sitting was lower in both genders in the treatment group. The frequency of mating in males and the frequency of foraging in females were also significantly increased by the treatment. Although the treatment was designed to affect the energy metabolism of the birds, the full significance of these results requires further investigation.

Other behaviours

Care of the plumage has been considered to be very important in maintaining good feather condition in ostriches kept in Europe (Sambraus, 1994b). Frequency of preening in a group of 120 adult ostriches maintained as one group (40:80 M:F) in Israel was higher during the morning than the afternoon. By contrast, the incidence of dust bathing was very low during the morning but increased steadily during the afternoon to a peak around dusk (Sambraus, 1994b). Preening and dust bathing represented a small part of the time budgets of adult birds (<5 and <0.4%, respectively) observed in Britain during the summer months (McKeegan and Deeming, 1997). During winter months preening took up less than 1.5% of the time budget of adult birds, and dust bathing was not observed (Deeming, 1998a).

Sambraus (1995a) also reports on the incidence of pecking of body feathers in the same group of 120 ostriches in Israel. Bad cases of feather pecking can lead to the back of the bird being stripped of feathers. Although both genders can be affected, females were more likely to peck and be pecked. Feather pecking appears to be a vice for some ostriches and is one that is hard to break (Bubier and Deeming, personal observations, 1995–1996). During the summer months in Britain, feather pecking occurred at low incidence (<1% of time–activity budget) in one group of 11 ostriches with a higher frequency of pecking by females; other groups of birds did not exhibit this behaviour (McKeegan and Deeming, 1997). Deeming (1998a) found that during winter months pecking at other birds was a small part (<1.5%) of the time–activity budget of a different group of male and female ostriches maintained on the same farm (Deeming, 1998a). By contrast, Samson (1996) found that feather pecking was frequently observed in ostriches kept confined indoors over the Canadian winter.

Waltzing behaviour described for wild ostriches is also performed by captive birds (Stewart, 1994), with this twirling behaviour often being performed when birds recover from being startled or when they have just been released from overnight accommodation (Deeming, personal observations, 1993–1996).

Sleep in ostriches appears to occur either with the bird holding its neck raised or with the bird lying prone with its neck outstretched straight in front of it (Stewart, 1994; Deeming, personal observations, 1993–1996). Adult ostriches

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tend to sleep with their heads up whereas young chicks tend to sleep in the prone position (Deeming, unpublished observations, 1993–1996).

Behaviour of juveniles

Behaviour of farmed ostriches older than 3 months but not yet sexually mature has received little attention to date. In Israel, Degen *et al.* (1989) described a time–activity budget for 5- to 6-month-old ostriches (mean body mass 57.4 kg). These birds were maintained in pairs, offered only concentrate feed and kept in outdoor enclosures on packed ground without natural vegetation. During daylight hours over 60% of the birds' time was spent walking, with sitting forming the next largest part of the time–activity budget (20%). Walking in this context included a lot of pacing along the fence-line but this was not quantified separately. At night the birds sat, and presumably slept, for around 12 h. Only 6.6% of the daylight time was spent eating concentrate ration whereas 1% was spent drinking. Pecking at the ground (termed 'foraging' by Degen *et al.*, 1989) formed only 5% of the time–activity budget and the birds actually consumed soil at a rate of 130 g day^{-1}. The birds in each pair usually performed behaviours in synchrony. Time of day had little significant effect on the time–activity budget of the ostriches although sitting was highest during the first hour of daylight (0600–0700 h) and preening highest between 0700 and 0900 h.

The study by Degen *et al.* (1989) was conducted in an environment free from natural vegetation, and the data may reflect this deprived environment. Thus the time–activity budget may be atypical and hence is of little interest to those seeking to develop good welfare standards. There is a pressing need for additional research into the time–activity budgets of juvenile ostriches.

The influence of the age of ostriches and the response to humans was investigated to assess the effect of these two factors on the behaviour and the position of the birds within an enclosure (Lay and Deeming, unpublished observations, 1995). Individual birds, maintained in groups of a single age, were observed: (i) in the presence of the human observer within 2 m of the enclosure perimeter; and (ii) from a hide where the human observer could not be seen by the birds. Five birds from each of three groups, aged 2, 4 and 6 months (a total of 15 juveniles), together with adults maintained in pairs, were observed in two trials: (i) recording the frequency of individual behaviours in 10 min sessions; and (ii) recording the position of the birds within the enclosure (front or rear of the enclosure) during four 10 min sessions spread over a 2-week period.

In the presence of the human observer there was an increase in standing and a decrease in feeding and foraging activity (Lay and Deeming, unpublished observations, 1995). Although older birds spent more time in the front half of their enclosure (i.e. that part adjacent to the fence where most human traffic occurred), there was no significant effect of age on positioning in the absence of the human (Table 4.2). Birds at 2–4 months old did not show any significant

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preference for their location within an enclosure. Once a human was present the youngest ostriches remained equally distributed in the enclosure, but the 6-month-old and adult birds spent significantly more time in the half of the enclosure next to the observer (Table 4.2). These results suggest that the presence of humans is influencing behaviour in all age groups although the extent of this disruption requires further investigation.

Behaviour of chicks aged less than 3 months

Most studies of ostrich chick behaviour to date have been carried out in captive birds held in the northern hemisphere, and research on behaviour of chicks in their native Africa has not been published. de Kock (1996a) does report that chicks reared by foster parents (Verwoerd *et al.*, Chapter 8) do not show abnormal behaviours such as eating sticks. The more natural environment appears to relieve stress and frustration observed in chicks reared by hand (de Kock, 1996a, b).

A time–activity budget has been described for ostrich chicks aged between 7 and 14 days old (Bubier *et al.*, 1996). Observations were recorded in an indoor rearing barn maintained at temperatures in the range 24–32°C and with pelleted food provided both in plastic troughs and scattered over the concrete floor. The activity of 20 chicks was recorded for 10 min sessions over a 1-week period with a total of 200 min. The time–activity budget (Table 4.3) showed that walking took up 23.1% of the chicks' time with only 6.7% of their time standing; 11.2% of the time was spent under the heat lamp provided in their enclosure (set at 32°C). A time-consuming activity for a few chicks was pecking at objects other than food, food or water trays, or 'toys' provided to stimulate activity in the birds. This type of pecking tended to be highly repetitive within bouts and highly habitual, with individual chicks performing this type of pecking often in a day and over

Table 4.2. Mean proportion (±SD) of 10-min periods spent by ostriches of different ages in the front half of an enclosure when the human observer was hidden in a hide (human absent), and when the observer was within 2 m of the enclosure perimeter (human present). One-way analysis of variance was performed on $\log_e$ transformed data. Lay and Deeming, unpublished data (1995).

Age	Human absent	Human present
2 months	0.548±0.229	0.548±0.129
4 months	0.557±0.136	0.348±0.199
6 months	0.637±0.420	0.808±0.180
Adult	0.783±0.222	0.848±0.090
Significance ($F_{3,19}$)	NS	***

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Table 4.3. Time–activity budget (as percentage of time observed) of 7- to 14-day-old ostrich chicks maintained on a farm in Britain. Data from Bubier *et al.* (1996).

Activity	Time (%)
Feeding from floor	27.7
Walking	23.1
Under brooder lamp	11.2
Pecking at objects	10.2
Standing	6.7
Drinking	5.8
Feeding from tray	3.5

many days. This type of stereotypical behaviour suggests that chicks are having problems. In this case, they appeared to be having difficulty locating and consuming food presented as pellets.

Ostrich chicks are naturally gregarious and normally do not fare well if reared in solitude. The warbling call of young birds appears to be performed only at times when the birds feel isolated or insecure (Deeming *et al.*, 1996b). Deeming and Ayres (1994) showed that when chicks were sorted into groups by mass on day 9 post-hatching, this affected the rate of growth thereafter, with the group of smallest birds actually growing at a faster rate than the group of largest birds. In order to study whether this growth response was due to differences in behaviour, perhaps a pecking order, Lambert *et al.* (1995) recorded the effect of variation in size on the frequency of pecking from individual chicks at the toes and heads of companion birds. Negative correlations between pecking rates and the growth rate of the chicks showed that the birds which pecked the most had the slowest rates of growth and in a few cases the individuals died. Head pecking may remain as a long-term vice in some birds (Stewart, 1994).

Although Lambert *et al.* (1995) and Samson (1996) described toe and head pecking, and Samson (1994, 1996) describes feather pecking, as aggressive behaviours, such activities are better considered as misdirected feeding behaviours and a response to specific environmental factors, usually less than optimal rearing conditions (Stewart, 1994; Bubier *et al.*, 1996). Once feather pecking is habitual in a bird it is difficult to stop the behaviour even if the environmental conditions are improved.

Chicks spent the largest amount of time eating pellets that were spread on the floor, pecking at the ground and specks of dust as well as engaging in coprophagy (Bubier *et al.*, 1996). The amount of time spent feeding from a food

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trough was significantly smaller than the time spent pecking at the ground (3.5 and 27.7%, respectively). The frequency of feeding bouts from the floor was also significantly higher than from the bowl, suggesting that this may be a more efficient way of feeding young chicks.

This aspect of feeding in chicks was investigated further by Paxton *et al.* (1997) who documented the factors affecting pecking and feeding behaviours in captive chicks aged between 10 and 50 days. Pecking activity was classified into different categories: pecking directed at food items on the ground; pecking directed at food in trays; drinking actions and 'other' pecking behaviour not directed towards food or water. There was significant repeatability (i.e. consistency over time) for feeding from the trays and 'other' pecking, but not for drinking or pecking at food items on the floor. Feeding from the ground significantly increased as the chicks got older but the amount of feeding from a tray did not increase (Fig. 4.4). Furthermore, chicks appeared to be more willing to feed from partially empty trays because, compared with full trays, there was enhanced contrast between the bottom of the tray and individual pellets (Paxton *et al.*, 1997). With time, ostrich chicks learn to feed on pellets from a tray, although it appears that the tray may be the visual cue for feeding rather than the pellets (Deeming *et al.*, 1996b).

Although the height of the boundary walls did not appear to influence pecking either at the environment or at other chicks, the enclosure in which chicks were kept significantly affected feeding from the ground and trays (Paxton *et al.*, 1997). The significance of the enclosure was not its position in the barn but rather the feeding and pecking behaviour of the specific groups of companions. There were significant correlations between different pecking behaviours in young chicks (13–20 days), but in older chicks increased feeding on pellets scattered on the ground showed significant negative correlations with feeding from

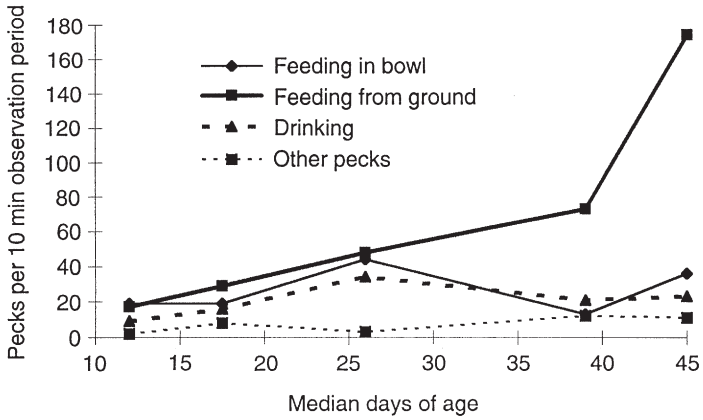

Fig. 4.4. The change in frequency in different pecking behaviours with increasing chick age maintained on a farm in Britain. Data from Paxton *et al.* (1997).

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the bowl and drinking. Furthermore, over the course of the experiment, pecking at the side of the food tray was observed to spread from one chick to other chicks in the pen. Addition of an experienced older chick may enhance feeding efficiency by example (Huchzermeyer, 1997; Paxton *et al.*, 1997). The susceptibility of young chicks to imitation of companions may mean that prompt removal of the first chick to exhibit pecking at non-food items may benefit the development of appropriate feeding behaviour in the remaining birds.

Food preferences of young chicks have been studied both in semi-natural conditions and under artificial rearing conditions. In a pilot study to test the feeding behaviour of young ostrich chicks given access to natural vegetation, Cooper and Palmer (1994) showed that two 3-week-old chicks showed a preference for selected plant species and exhibited little change in the composition of their diet with increased experience. When presented with fresh cut branches of 12 specific plants there was a marked preference for the foliage of *Aspilia mossambicensis* (*Compositae*) and *Indigofera schimperi* (*Leguminosae*). Eight plants were completely rejected. When the chicks were older they were given supervised access to typical savanna grassland where they freely chose emergent grass shoots, A. *mossambicensis* and I. *schimperi*, which constituted 95% of their diet. The birds appeared to use a visual cue for food selection and were attracted to dark green foliage.

A colour preference test for 9-day-old chicks in an artificial rearing system was performed using strips of coloured tape (Bubier *et al.*, 1996). Pecking at green stimuli was ten times higher than pecking at white stimuli (15.5 ± 8.9 versus 1.5 ± 2.2 pecks min^{-1}) whereas pecking at other colours (red, blue, black and yellow) was at a low level (all <0.5 pecks min^{-1}). Pecking at green was significantly higher than at all other colours with the exception of white.

Another study examined the preference of chicks for chopped fresh lucerne leaves or pellets of concentrate feed (Deeming *et al.*, 1996a). Chicks less than 21 days old were placed in an arena where food was presented in designated areas. Given a choice, the birds spent 73.5% of their time in the lucerne section of the arena. This was significantly higher than the time spent in a control area without food or in the pellet area (10.5 and 16.3%, respectively), although all the food was eaten. Lucerne leaves were always eaten as the first choice until they were all consumed and irrespective of time of day. By contrast, pellets were eaten to a lesser extent. Consumption of pellets was higher during the morning than during the afternoon. Failure to recognize food items such as pellets is suggested as a cause of starvation by several authors (Huchzermeyer, 1994; Deeming *et al.*, 1996b; Lambrechts *et al.*, 1998b).

Whilst ostrich chicks are generally considered to be vegetarian, it has been reported that they will consume insects if given the opportunity, although it appears that chicks without parental guidance take several weeks to learn to identify insects as food (Milton *et al.*, 1993). Chicks of other avian herbivores, e.g. grouse, will prey on insects during the first few weeks of life (Savory, 1989). Feeding of mealworms (coleopteran larvae) to chicks is also reported to be a stimulus for feeding in young chicks (Huchzermeyer, 1994; Deeming *et al.*, 1996b).

Coprophagy has been observed in both wild (Holtzhausen and Kotzé, 1990)

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and captive chicks (Kriebich and Sommer, 1995; Bubier *et al*., 1996; Deeming *et al*., 1996b; Samson, 1996; Paxton *et al*., 1997). An interest in white objects may be related to the white urates which accompany the faeces of adults, and whilst it is likely that in the wild the young birds are inoculated with beneficial microflora through coprophagy, possible ingestion of pathogens in captive environments remains a concern for good husbandry (Deeming *et al*., 1996b). The suggestion that coprophagy represents pica (Samson, 1996) is questionable. The youngest chicks will readily accept small stones in their diet (Deeming *et al*., 1996b).

FURTHER RESEARCH

Our knowledge of ostrich behaviour in captive environments is patchy and there are key areas where additional research is needed. In particular, knowledge of the social and feeding behaviour of chicks and juveniles could assist in developing more appropriate husbandry techniques. For adult birds, an understanding of the factors determining mate selection and mating frequency will be important when attempting to maximize individual bird performance.

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Basic Concepts and Recent Advances in Digestion and Nutrition

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Despite the worldwide interest in ostrich farming and although it is a well established industry in South Africa, knowledge of the nutritional requirements of ostriches is not well defined. Historically, nutritional recommendations for poultry were extrapolated to develop strategies for ostriches which often resulted in the application of unrealistic nutrient values. This became evident from various nutrition-related problems encountered by commercial ostrich farmers in the raising of feedlot birds and breeders on concentrated diets. The use of poultry energy values for ostriches has led to a high incidence of obesity in breeders and marked-age ostriches. The tendency of ostriches to consume, under normal conditions, between 1 and 3% of their total feed consumption in the form of soil has led to nutritional problems associated with mineral content. Certain soils in the USA have high levels of iron and molybdenum, both of which interfere with copper absorption through negative chelation. Thus copper deficiencies have been observed in ostriches fed on diets containing what would appear to be adequate levels of copper. Common pathology has been primarily aortic rupture and problems with egg shell formation, although poor growth in chicks and abnormal feather colour have also been observed. Consumption of soil is non-existent in modern poultry production and minimal in poultry raised in outside pens.

For a better understanding of the nutritional needs of any species, it is important to understand its natural diet and the physical and functional properties of its gastro-intestinal tract (GIT). Here we briefly describe reports of the diet of wild ostriches. The anatomy of the GIT is described by Bezuidenhout (Chapter 2), and information on how it changes in ostriches with age and diet is provided in this chapter.

The current competitive environment with an increasing supply of birds has fuelled the need for scientific feeding to ensure profitable production of ostriches.

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Hence accurate evaluation and knowledge of the nutrient contents of the raw materials for formulating diets, and knowledge of nutrient needs during various stages of growth and production, are essential. This information should include the following (Oldham and Emmans, 1990): (i) the extent to which an ingredient can provide essential nutrients that can be retained by ostriches and that result in growth and production; (ii) the potential utilization of various ingredients and the extent to which one ingredient can substitute for another; and (iii) an assessment of changes in animal performance through nutrition.

NATURAL DIET OF OSTRICHES

The wild ostrich has evolved to be a selective grazer (Sauer and Sauer, 1966). Milton *et al.* (1994) looked at the selection of food by the wild ostrich in southern Africa, and found that plant selection was influenced by the relative abundance of vegetation and the bird density. Ostriches selected against plant species with high fat, phenolic, tannin, sodium or calcium oxalate content. Cooper and Palmer (1994) studied food preferences starting with 1-week-old chicks free to roam in acacia savanna. Food selection was primarily a visual choice, with chicks being attracted to bright green foliage, and a secondary response apparently being taste. Ultimately selection was for selected forbs and new grasses, and mature grass leaves were not consumed. Dean *et al.* (1994) observed adult ostriches in different regions in southern Africa and found that shoots accounted for 39% of total consumption whilst whole plants, flowers, leaves and fruit accounted for 25, 16.6, 12.2 and 4.1%, respectively, of the diet. These authors describe ostriches in the wild as 'patch selective foragers' because the birds prefer annuals to perennial grasses or shrubs. Adult and sub-adult ostriches tended to select low-growing plants and rarely ate woody materials (Milton *et al.*, 1994). The average crude protein of the selected plants was 12% and avoided succulent species with sodium concentrations higher than 9% (dry matter basis).

Despite reports that ostriches consume a variety of animal species (reviewed by Cramp *et al.*, 1977), Milton *et al.* (1994) found no evidence that the ostriches they studied were omnivorous. By contrast, Williams *et al.* (1993) found only very small quantities of animal materials such as insect parts, antelope faeces and small bones in the stomach contents of wild-caught, adult ostriches. It is likely that animal material forms a very minor part of the natural diet of ostriches.

THE GASTRO-INTESTINAL TRACT

The GIT of ostriches is distinct from that of other birds (Bezuidenhout, Chapter 2). Cho *et al.* (1984) reported that in a 30-day-old ostrich the intestinal length (small intestine plus large intestine) was 2.83 m in length. The small intestine

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represented 37% (1.04 m) of the total length, whilst the caeca and large intestine each accounted for 6% (0.16 m) and 57% (1.62 m), respectively, of the intestinal length. By comparison, an adult domestic fowl (*Gallus gallus*) has a total intestinal length of 0.68 m, with the small intestine, caeca and rectum comprising 90% (0.61 m), 7% (0.05 m) and 3% (0.02 m), respectively, of the intestinal tract (Calhoun, 1954).

Bezuidenhout (1986) examined the GIT of 20 ostriches (aged 2–52 weeks) and found the duodenum to be 0.8 m in length whereas the jejunum and ileum were 1.6 m and 4 m in length, respectively. Each caecum was 0.95 m in length, and the rectum was 16 m in length. Of the entire length, proportions were 3.3% for the duodenum, 6.6% for the jejunum, 16.5% for the ileum, 7.4% for the caeca and 66% for the rectum.

Baltmanis (1996) and Baltmanis *et al.* (1996, 1997a, b) report on a study comparing two diets. Birds were fed either a concentrate diet or a supplement and lucerne (*Medicago sativa,* alfalfa) and Bermuda grass (*Cynodon dactylon*) hay. The crude fibre contents were 8.2 and 14% for the concentrate and hay–supplement diets, respectively. The concentrate contained 11.1% acid detergent fibre (ADF) and 14.8% neutral detergent fibre (NDF), whereas the hay–supplement diet contained 19.6 and 24.9% ADF and NDF, respectively. The birds were taken to 114 kg or 15 months (whichever came first) at which point they were slaughtered and processed for hide, meat yield, GIT dimensions and meat evaluation.

Baltmanis *et al.* (1996, 1997a) worked with ostriches having a slaughter mass of 91 to 127 kg. Full and empty masses, as well as length of the GIT segments, were determined at slaughter (Table 5.1). The large intestine was significantly longer in moderate fibre-fed birds while the rest of the intestinal segments were shorter in these birds. Empty and full mass of the intestine were markedly different between the birds fed the two diets. As would be expected, the greatest increases in full mass were seen in the caeca and large intestine (Table 5.1). The empty mass of the intestinal tract (including gizzard and proventriculus) was 20% higher in moderate fibre-fed birds. This increase in intestinal mass can have a large effect on maintenance energy requirements since the intestinal tract is one of the most metabolically active organs in the body.

Degen *et al.* (1994) found that the contraction cycle of the proventriculus, gizzard and duodenum in ostrich chicks (7–8 weeks old) was similar to those reported by Duke *et al.* (1972) and Sklan *et al.* (1978) in turkeys (*Meleagris gallipavo*) and fowl, respectively. Retrograde movement of part of the duodenal contents into the gizzard increases the time feed is exposed to pancreatic and gastric secretions. The reacidification that occurs in this retrograde movement reactivates peptic digestion.

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Table 5.1. The influence of dietary fibre on the length and masses of the various component parts of the gastro-intestinal tract (GIT) of ostriches. Data are means (SEM) from Baltmanis *et al.* (1997a).

	Low fibre[1]			Moderate fibre[1]		
Component of GIT	Length (m)	Mass full (kg)	Mass empty (kg)	Length (m)	Mass full (kg)	Mass empty (kg)
Proventriculus		2.16 (0.17)	0.80 (0.04)[b]		3.03 (0.29)	1.16 (0.06)[a]
Gizzard		2.79 (0.18)[b]	2.08 (0.17)[b]		4.24 (0.16)[a]	2.82 (0.12)[a]
Duodenum	1.07 (0.10)	0.40 (0.03)	0.22 (0.04)	0.96 (0.02)	0.35 (0.02)	0.23 (0.04)
Jejunum	1.64 (0.22)	0.63 (0.05)	0.48 (0.04)	1.54 (0.04)	0.64 (0.03)	0.52 (0.04)
Ileum	4.20 (0.19)	1.51 (0.06)	0.89 (0.03)[a]	3.78 (0.02)	1.37 (0.07)	0.72 (0.04)[b]
Caecum	0.85 (0.02)	0.74 (0.05)	0.32 (0.01)	0.89 (0.02)	0.98 (0.10)	0.23 (0.01)[b]
Large intestine	9.26 (0.32)[b]	4.02 (0.24)[b]	1.28 (0.09)[b]	10.45 (0.22)[a]	8.73 (0.95)[a]	1.76 (0.02)[a]

[1]The low- and moderate-fibre diets contained 20.3 and 21.1% protein, 9.5 and 12.7% acid detergent fibre, 13.9 and 15.6% neutral detergent fibre, respectively. Mean age and body mass of the birds at slaughter were 365 and 441 days, and 113.2 and 98.2 kg, respectively. Means within row and within measurement with different superscript differ ($P<0.05$).

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DIGESTION

Extensive research has been done on pancreatic enzyme characterization (see review by Oelofsen *et al.*, 1991). By contrast, there is little information available on levels of digestive enzymes or on age-related changes in enzyme levels. In preliminary work done on birds aged 3 weeks old (Angel and Sell, unpublished data, 1993) the levels of sucrase and maltase in the duodenum, jejunum and ileum were similar to those found in turkeys at 5 days old. Maltase and sucrase activity in the jejunal mucosa was 10.1 and 0.39 μM of substrate hydrolysed mg^{-1} protein h^{-1}, respectively. Trahalase, the mucosal membrane enzyme involved in the digestion of trahalose, an insect-based carbohydrate, was absent suggesting that ostriches have evolved away from the consumption of insects as part of their diet. Milton *et al.* (1993) reported consumption of termites by captive ostrich chicks, but the value of insects in the diet has to be questioned as ostriches cannot utilize trahalose.

Information on intestinal pH in the different portions of the GIT of ostriches is limited. Swart *et al.* (1993a) measured a pH around 2 in the proventriculus and gizzard, although this rapidly increased to around pH 7 in the small intestine, increasing slightly to pH 8 in the large intestine.

Like other higher animals, the ostrich lacks cellulase to digest plant fibre components and has to rely on plant fibre fermentation. This requires a slow rate of passage of the digesta and an area within the GIT where microbes can colonize and reproduce without being swept away by the passage of digesta. Ruminants have a pre-gastric adaptation, the rumen, that allows microbes to colonize and digest fibre within the intestinal tract. The passage rate in ruminants is slow, 38–50 h, and allows for extensive fermentation. Post-gastric adaptations of the GIT for plant fibre fermentation are mainly modifications of the hindgut. Among birds, grouse and ptarmigans (*Lagopus* spp.) have the ability to change the size of the caeca based on availability and digestibility of foodstuffs (Moss, 1983). Moss and Trenholm (1987) found that gut length in red grouse, specially of the caeca, increased as the intrinsic digestibility of the diet decreased. Gassaway (1976) found that the rock ptarmigan could obtain approximately 18% of the standard metabolic rate from volatile fatty acids (VFAs).

Ostriches are undoubtedly the best post-gastric fibre fermenters among birds. Passage rate in the ostrich is similar to that of ruminants. Swart *et al.* (1993a) reported a passage rate in 42-day-old ostriches (5–10 kg body mass) of 39 h, and in birds weighing 42–50 kg, 47.9 h. Swart *et al.* (1987) found that the concentration of VFA was high in the proventriculus and gizzard (158.8 and 139.3 mM, respectively). The small intestine had low levels of VFA (65–67 mM) and concentration increased in the hindgut. Concentration in the caeca was 141 mM, and 171–195 mM in the proximal rectum. Acetate was the most important of the individual VFAs found, which indicates fermentation of foodstuffs high in plant cell walls. VFA production rates in the rectum are higher than those reported by Herd and Dawson (1984) for the emu (*Dromaius novaehollandiae*).

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Swart *et al.* (1993a) reported hemicellulose and cellulose digestion in 42–50-kg (210 days old) ostriches of 66.2 and 39.3%, respectively, and an NDF digestibility of 45.6%. Previously, Swart *et al.* (1987) had reported an NDF digestibility of 63%. Angel (1996) found NDF digestibility to change with age with 3-week-old ostriches digesting only 6.5% of the NDF and 30-month-old ostriches digesting 61.7% of the NDF. Swart *et al.* (1993a) found that VFA production in the hindgut of ostrich chicks could account for 52 and 76% of the daily metabolizable energy intake in 7- and 46-kg birds, respectively. Swart *et al.* (1993b), in a study using four ostrich chicks from 42 to 210 days, found that maintenance energy requirement was 0.44 MJ W^{-1}, $kg^{0.75}$ day^{-1}. They also found that these birds utilized metabolizable energy for tissue deposition poorly at 0.32 MJ W^{-1}, $kg^{0.75}$ day^{-1}.

Swart *et al.* (1993c) studied differential tissue deposition in growing ostriches. Twelve chicks were sacrificed at 60 days of age (mean mass of 9.1 kg), six chicks at 90 days old (20.2 kg) and six ostriches at 120 days old (30.6 kg). All sacrificed birds were analysed chemically for body composition. Relative to total body composition, protein content remained fairly constant throughout the 60 days studied. By contrast, fat levels increased from 8.1 to 22.6% with moisture content decreasing from 74.6 to 66%. From 60 to 90 days of age the feed conversion ratio was 2.52, and from 90 to 120 days of age it was 4.07. Conversion of feed energy to deposited energy actually improved as feed conversion worsened. Thus these birds appear to improve their efficiency from an energetics standpoint while conversion of total feed to total gain deteriorates.

Bezuidenhout (1993) suggested that due to the long rectum, reflux of urine up into the caeca and upper rectum does not occur (Skadhauge and Dawson, Chapter 3). In other birds reflux of urine into the caeca does occur (Duke, 1989), and urates can serve as a supply of nitrogen for bacterial fermentation. Duke *et al.* (1995) concluded that the retrograde movement of urine in the ostrich is negligible and so nitrogen recycling from the urine for use by microbes in the caeca and upper rectum is not a factor in the nutrition of ostriches.

FEEDSTUFF EVALUATION

Swart (1988) concluded that the end products of fibre fermentation could contribute to the ostrich's metabolizable energy (ME) requirements, and so the use of ME values derived from poultry in diet formulation for ostriches results in an underestimation of the true ME content of ingredients for ostriches. This conclusion was supported by various studies with ostriches in which the true metabolizable energy contents of various ingredients, corrected to zero nitrogen retention (TME_n), were determined (Cilliers, 1994, 1998; Cilliers *et al.*, 1994, 1995, 1997, 1998b, c, d). These experiments were simultaneously replicated in domestic fowl, and this comparison clearly demonstrated the enhanced digestibilities of ingredients in ostriches as compared with the fowl, which is almost certainly a reflection on the differences in their digestive tracts.

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Comparison between ostriches and domestic fowl

Data were obtained by means of the balance method, i.e. with continuous feeding and total excreta collection (Cilliers, 1994). For ostriches, excreta collection harnesses were fitted around the neck, resting on the back and kept together by Velcro at the tail end. Adjustable straps without buckles enabled free movement in the crates. Canvas bags with plastic linings were attached to each harness with Velcro and fitted snugly over the entire tail region ensuring quantitative collection of excreta (Cilliers *et al*., 1994). Male domestic fowl were individually housed in wired cages with raised floors where droppings were collected in trays.

For ostriches, unpalatable materials were mixed with a basal diet (B) of lucerne meal in order to ensure high levels of intake. For the male fowl, maize meal was used as the basal diet. The energy contents of the test diet (basal diet + test ingredient) and basal diet were then used indirectly to determine the true energy content of the test material. More palatable ingredients (e.g. maize) were used as sole ingredients in other test diets allowing direct calculation of energy content. The basal diet (B) was mixed with the unpalatable test materials (TM) in the following ratios (B:TM): 100:0, 80:20 and 60:40. Each feed mixture was fed at two to three intake levels, i.e. *ad libitum*, and restricted to 15 and 30% of *ad libitum* so as to ensure a range of food intake and excreta production for analysis. The TME_n contents of ingredients were calculated by means of the regression method, where the complement of slopes yielded estimates of the true portions that were metabolized and nitrogen retention per kg consumption of the test ingredient.

Regression analysis yielded a highly significant relationship ($P<0.001$) for each of the 21 sets of TME_n values for ostrich and fowl for the various ingredients studied (Table 5.2). Linear models offer the possibility of calculating TME_n values for ostriches using fowl data until such time as information becomes available on different feedstuffs for ostriches. All data were pooled to determine one model (Cilliers and Hayes, 1996): ostrich $TME_n = 6.35 + 0.645 \times$ fowl TME_n ($r^2 = 0.80$). This model is a useful tool in adjusting raw material contents according to values easily established with fowl in routine analysis.

Alternative feed ingredients

Traditionally, maize has been used as the primary dietary source in commercial monogastric diets due to its high concentration of energy. Grains such as barley, oats and triticale have been restricted in monogastric diets due to their lower energy content resulting from a high fibre content. Furthermore the presence of anti-nutritional factors in these ingredients also limits their use in diet formulation for monogastrics (Annison, 1993; Jeroch and Danicke, 1995).

Cilliers *et al*. (1997) determined that ostriches were capable of utilizing the more fibrous energy sources more efficiently than the domestic fowl. The higher energy contents indicated that the non-starch polysaccharides in these sources such as ß-glucans and arabinoxylans had little, if any, effect on the available

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Table 5.2. TME_n contents of various ingredients evaluated for ostriches and fowl (data from Cilliers, 1994, 1998).

Source	Protein (g kg^{-1})	Moisture (g kg^{-1})	TME_n ostriches (MJ kg^{-1})	TME_n fowl (MJ kg^{-1})
Maize	90.5	53.9	15.22	14.07
Oats	114.7	92.1	12.27	10.63
Malting barley	93.1	103.2	13.92	11.33
Triticale	136.3	69.0	13.21	11.82
Corn and cob meal	75.2	97.5	13.45	*
Soybean oilcake	445.2	83.9	13.44	9.04
Sunflower oilcake	365.6	82.1	10.79	8.89
Lupins (*Lupinus albus* cv. Buttercup)	362.8	98.0	14.61	9.40
Canola seed (full fat)	234.0	65.0	22.50	13.51
Canola oilcake	315.0	78.0	13.76	9.51
Fishmeal (local high fat)	619.9	87.0	15.13	13.95
Ostrich meat and bone meal	505.9	102.0	12.81	8.34
Lucerne hay	176.1	71.4	8.91[2]	4.03
Wheat bran	165.0	90.7	11.91	8.55
Grape residue	46.0	102.0	7.81	*
Molasses meal	40.0	110.0	7.77	*
Hominy chop	89.0	92.0	11.49	*
Lucerne hay[1]	176.1	71.4	8.99	4.03
Phragmites australis (common reed)	104.5	105.0	8.67	2.79
Atriplex nummularia (salt bush)	118.2	78.0	7.09	4.50
Agave americana[3] (Alivera)	35.0	921.3	12.2	*

*Not determined for the test sample.
[1]Mean value of ten different measurements.
[2]Lucerne value determined during the evaluation of drought resistant plants.
[3]Value on a dry matter basis.

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energy of these ingredients for ostriches. The latter was confirmed by no significant differences in growth rates observed between birds fed diets with different ingredient combinations (Cilliers, unpublished results, 1997). Efficient utilization of fibrous ingredients by ostriches makes the use of corn and cob meal a feasible option in diet formulation, especially in grain-producing areas where sufficient quantities of roughage are often a problem.

For the economic evaluation of proteinaceous ingredients, the energy and amino-acid content as well as nutrient availability are deciding factors on the use of an ingredient in diet formulation. TME_n values of various protein sources for ostriches and fowl were determined by Cilliers (1994) and Cilliers *et al.* (1998c). Enhanced digestibility of the hulls in soybean oilcake and sunflower oilcake made a substantial contribution to the energy values of these ingredients. The use of these ingredients therefore reduces the required levels of energy sources in diets, enabling the use of more regionally available and inexpensive sources of roughage. Ingredients such as sunflower oilcake are not favoured for monogastric diets because of their poor amino-acid profile and higher fibre content, but these characteristics make these ingredients economically attractive in diet formulation for ostriches.

In the evaluation of sweet lupins (*Lupinus albus* cultivars Buttercup and Swartland) for ostrich diets, TME_n was superior to that of soybean, sunflower and oilcake (Cilliers, 1994). Apart from the more efficient utilization of the fibrous hull by ostriches versus fowl, the improved energy content could probably be related to an improved utilization of the fat content in lupins by ostriches. This speculation was confirmed by the findings of Brand *et al.* (1998) who determined substantially higher TME_n values for full-fat canola and canola oilcake in ostriches as compared with fowl. It is important to note that the high fibre ingredients, when used in poultry diets, can and often do cause changes in the digestibility of other nutrients in the diets. This is especially true when these ingredients are used at moderate to high levels in the diet. Thus the ingredient energy differences referred to here have other contributing factors apart from fibre utilization.

The more efficient digestibility of dietary fat was the only cause of the improved energy measured for fishmeal and meat and bonemeal in ostriches, as opposed to values determined for fowl (Cilliers, 1994). The fat content for fishmeal was 120 g kg^{-1}, which explains the higher energy value of this fishmeal (13.95 MJ kg^{-1}) compared with the energy value (8.2 MJ kg^{-1}) for the average fishmeal used for poultry. The TME_n figures presented for fishmeal by Cilliers (1994) would be an overestimate for the average available sources of fishmeal.

Cilliers (1994) concluded that various protein sources could economically be used in diet formulation for ostriches. The high energy levels and pricing of lupins and full-fat canola favour these ingredients for diets that require lower levels of essential amino acids. Evaluation is needed of maximum-use levels for ingredients containing anti-nutritional factors. In a number of growth studies with sweet lupins (*L. albus* cv. Swartland), no detrimental effect was observed up to dietary levels of 150 g kg^{-1} (Cilliers, unpublished data, 1997).

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Lucerne hay is the source of roughage most commonly used in diets for ostriches. Cilliers *et al.* (1994) compared energy levels of high-fibre ingredients for ostriches and fowl, and reported TME_n values for lucerne of 8.6 and 4.03 MJ kg^{-1}, respectively. Trends toward a more diversified and a more economical feed supply to non-ruminants necessitate a reduction in feed costs. Poor availability of good quality lucerne, especially in certain regions, raises the question whether it would not be more economical to use food by-products in diets for ostriches. Cilliers (1994) concluded that wheat bran could be a useful alternative for lucerne in the ostrich diet. This will also be a more economically feasible option than in diets for other monogastrics, due to the higher energy value this ingredient has for ostriches as compared to the fowl. Other by-products such as grape residue, apple pomace and mill screenings could make useful contributions in diets for ostriches when available (Cilliers and Sales, 1999).

The potential use of *Phragmites australis* (common reed), *Atriplex nummularia* (salt bush) and *Agave americana* (alivera) as dietary supplements for ostriches were evaluated by Cilliers (1994) and Cilliers *et al.* (1998c). These ingredients are readily available in the more arid areas of South Africa where many ostriches are raised. TME_n values of 8.67 and 7.09 MJ kg^{-1} for common reed and salt bush, respectively, compared favourably to TME_n contents of 8.9 MJ kg^{-1} determined for lucerne. It was concluded that these ingredients could be utilized as supplementary sources of roughage in diets for ostriches.

Cilliers (1994) conducted a growth study with ostriches with masses of 80–100 kg, using salt bush, common reed and lucerne as sources of roughage in similar nutrient-value diets. After an initial adaptation period of 7 days, similar growth rates and feed conversion rates were determined on the three experimental diets. Alivera leaves were cut daily from the main plant and chopped into small blocks before feeding to the birds. The evaluation of the true energy content of this ingredient yielded an energy value of 12.2 MJ kg^{-1} that contributed approximately 80% of the value of maize (Cilliers and Sales, 1999). In more extensive feeding conditions, alivera leaves could substitute for maize as a dietary energy supply for birds from 6 months onwards (>70 kg).

Cilliers and Sales (1999) found that the cost of molasses meal meant that it had little economic value in diets for ostriches apart from its laxative, pelleting and palatability characteristics. With a TME_n value of 7.77 MJ kg^{-1}, molasses meal is an inferior product to many other ingredients, e.g. common reed and salt bush, which are very much cheaper. However, in the USA, Central and South America, molasses meal is a by-product which has to be disposed of which makes it a cheap ingredient in ostrich feed.

Potential use of pastures and silage for ostriches

When formulating a completely balanced ration it is assumed that the diet is the sole source of nutrient supply, but it is common practice among ostrich farmers to feed ostriches on pasture, hence diluting the balanced diet and leading to

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impaired growth and feed conversion. Pasture could, however, make a substantial contribution to the nutrient requirement of ostriches provided it is supplemented by a concentrate suitable for the pasture type and stage of growth.

Formulation of concentrates which took into account the nutrient contribution of lucerne pastures gave superior results, and growth rates compared favourably to birds receiving complete diets in feedlots (Cilliers, 1998). As birds initially have high nutrient requirements, the composition of pasture concentrates should comprise a minimum of 67% of total feed requirement for growing ostriches from 4 to 6 months (45–70 kg). Nutrient supply from pastures can be gradually increased to 50–55% for birds between 6 and 10 months (70–95 kg), while nutrient intake from pastures after 95 kg could comprise 60% of total requirements.

It is important to note that not all pastures are suitable for ostriches. Baltmanis (1996) showed that Bermuda grass was not accepted well by ostriches. Birds lost mass when fed a supplement and pastured on Bermuda grass, because consumption from the pasture was low to nil. Angel and Hicks-Alldredge (unpublished data, 1997) showed that over the winter months the use of winter wheat pasture with 0.45 kg of a supplement supported body mass gains similar to those of ostriches fed complete diets. Birds were started on the dietary treatments when they were 7 months old and had an average body mass of 81 kg. At 10 months old, birds fed on pasture and supplement had gained an average of 30 kg. At an average body mass gain of 34 kg, the body mass gain of birds fed the complete balance diet was not significantly different. Feed costs, including pasture management, for the last 3 months of production for forage-fed birds were 80% lower than for birds fed the complete diet.

The use of silage as a source of roughage for ostriches has tremendous potential for the ostrich industry. Cilliers *et al.* (1998d) investigated the potential use of maize silage for feeding to growing ostriches (50–70 kg) over a 40-day trial period. Experimental groups receiving silage (average intake was 2 kg bird^{-1} day^{-1}) were supplemented by a concentrate formulated to complement the maize silage at 1.25 kg bird^{-1} day^{-1}, whilst the control group consumed an average of 2 kg of the balanced diet suitable for their age. It was evident that ostriches needed an adaptation period to adjust to the nutrient supply from silage (Table 5.3). Although reduced mass gains were experienced over the 40-day trail period, a potential saving per kg gain of nearly 20% was possible using silage as source of nutrients (Table 5.3).

The effect of age on TME_n values of various ingredients

Angel (1993, 1995) studied the effect of age on the apparent ME contents of a complete diet and found that apparent fat digestion was very low at 3 weeks of age and increased rapidly up to 10 weeks of age, after which no significant differences were observed (Table 5.4). Apparent NDF digestibility followed a similar trend, with the 3-week-old birds utilizing NDF very poorly and showing a rapid

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Table 5.3. Growth of ostriches (50–70 kg) over a 40-day trial period comparing consumption of silage with standard rations (Cilliers, 1998).

Variable	Silage group	Control group
Days between weighing	Average daily gain (kg bird^{-1} day^{-1})	Average daily gain (kg bird^{-1} day^{-1})
Period 1: 9 days	0.290	0.396
Period 2: 13 days	0.312	0.453
Period 3: 18 days	0.458	0.477
Total period (40 days)	0.353	0.442
Cost	Rand kg^{-1} gain^{-1}	Rand kg^{-1} gain^{-1}
Period 1	10.35	11.33
Period 2	9.63	9.90
Period 3	6.54	9.41
Total trial period	8.04	9.95

Table 5.4. Effect of ostrich age on apparent digestibility of neutral detergent fibre (NDF) and fat, and on apparent metabolizable energy (ME) of the diet (Angel, 1995).

	Apparent digestibility		
Age	Fat (%)	NDF (%)	Apparent ME (MJ kg^{-1})[1]
3 weeks	44.5^{a}	6.5^{a}	7.2^{a}
6 weeks	74.3^{b}	27.3^{b}	9.3^{b}
10 weeks	85.4^{c}	51.2^{c}	10.9^{c}
17 weeks	91.2^{c}	58.1^{cd}	11.5^{d}
30 months	92.8^{c}	61.7^{d}	11.8^{d}
SEM[2]	2.7	2.4	0.13

[1]The diet was formulated to contain 8.3 MJ kg^{-1} based on fowl metabolizable energy values and 11.6 MJ kg^{-1} based on metabolizable energy values published by Cilliers (1994). The diet contained, by analysis, 24.1% protein, 7.3% fat, 33.9% NDF, 20.8 acid detergent fibre, and 89.1% dry matter.
[2]Standard error of the means. Means within a column with different superscripts differ ($P < 0.05$).

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increase in digestibility up to 17 weeks of age, after which no significant differences were seen (Table 5.4). This translated into a very low apparent ME value of the diet at 3 weeks of age and a rapid increase in the amount of energy obtained by ostriches up to 10 weeks of age, after which no significant changes were seen. The ME value of the diet, based on ostrich ME values (Cilliers, 1994), was 11.6 MJ kg^{-1} while the same diet had a calculated ME, based on poultry ME values of 8.3 MJ kg^{-1}. The 3-week-old ostrich obtained an ME of only 7.2 MJ kg^{-1} of diet, while the 17-week-old bird obtained an ME of 11.5 MJ kg^{-1} of diet (Table 5.4).

Cilliers (1994) conducted most of his TME_n studies on birds at 8 months of age and older, and the question should be raised to what extent these values are applicable to younger birds. It is known that for ingredients containing high levels of fibre, fat and non-starch polysaccharide, different ME values were determined for broilers, pullets and mature birds (Farrell *et al*., 1991).

Cilliers *et al*. (1998a) used barley (known for its anti-nutritional factors) and lucerne (high fibre content) in a comparative study between mature (<105 kg) and immature ostriches (6 months old; 50–60 kg). TME_n values of 9.16 and 9.26 MJ kg^{-1} were determined for lucerne and 13.94 and 13.92 MJ kg^{-1} for barley with immature and mature ostriches, respectively. It was concluded that the same TME_n values would be suitable for ostrich diet formulation for age groups older than 6 months. These results agree with those of Angel (1995), where birds older than 17 weeks obtained the same ME from the diet as adult ostriches. More work is required to evaluate the true TME_n of feedstuffs especially for chicks under the age of 2 months.

The additivity of TME_n values in ostriches

In least-cost formulation, where a TME_n value is assigned to an ingredient independent of the nature of the diet, it is assumed that all values are additive (Miller, 1974). This theory, and the accuracy of TME_n values determined for ostriches and fowl, were evaluated by comparing theoretical (individual determined) values to a value determined for a combination of various ingredients in one diet. The calculated and determined values for ostriches and fowl (Cilliers *et al*., 1998b) did not differ significantly from determined values (Table 5.5). It was concluded that accurate TME_n values were now available for diet formulation for ostriches where TME_n values for the ingredients used were available.

AMINO ACID METABOLISM

Accurate measurements of the digestible amino-acid contents of raw materials are desirable for least-cost formulations of diets. Due to the lack of information, in the past digestible amino-acid values for ostriches were also derived from fowl. A study was conducted to compare apparent and true digestibility of amino acids

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Table 5.5. Comparison between calculated and determined TME_n values (MJ kg^{-1}) for an experimental diet in male domestic fowl (adults) and ostriches (8 months of age), showing that determined TME_n values were additive and assigned to ingredients independently of its inclusion level in a complete diet. Data from Cilliers *et al.* (1998b).

Source	Calculated value by cumulative calculating individual values	Determined value by balance method
Ostriches	11.69	11.25
Domestic fowl	8.28	8.02

in a high-protein (209 g kg^{-1}) diet between immature ostriches (7 months) and adult fowl (Cilliers *et al.*, 1997). Amino-acid digestibilities were calculated by the regression method and yielded a mean value for true digestibility of 0.837 (range 0.780–0.862 as a proportion of 1) for ostriches whilst a value of 0.795 (range 0.723–0.825) was measured for fowl. Individual digestibilities are summarized in Table 5.6. True retention of dietary protein was higher for ostriches than in fowl, but the reverse was true for lipid retention (Table 5.6). Again the ostrich is better able to digest amino acids than the fowl, thus using digestibility values from poultry in diet formulation for ostriches will slightly underestimate the true amino-acid content. Results presented in Table 5.6 emphasize the importance of an assessment of amino-acid digestibilities for individual ingredients.

Determination of metabolizable energy and amino-acid requirements for maintenance and growth

According to Ferguson *et al.* (1994) the use of prediction equations to model growth and production is one of the best approaches to estimating nutrient requirements for poultry. There is no reason why the same principles cannot be applied to ostriches, provided the nutritional constants are known whereby animal requirements are converted to feed requirements.

Cilliers (1994) and Cilliers *et al.* (1998d) estimated the efficiency of conversion of feed energy and amino acids for maintenance and growth. To obtain these factors a comparative slaughter technique was applied, where an initial group of 7-month-old growing ostriches was slaughtered and growth measured as retained carcass energy and carcass protein (amino acids) in the remainder. Birds were fed a balanced diet of which the TME_n and true amino-acid availability was also determined by the balance method. Retained energy (RE) during the trial period (MJ $kg^{-0.75}$ body mass) was regressed against TME_n intake according to the following model: $RE\ (kg^{0.75}) = a + b \times ME_{intake} kg^{0.75}$, where the coefficient b estimates

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Table 5.6. True digestibilities (as proportion of 1) of various amino acids in a balanced high protein diet. Data from Cilliers *et al.* (1997).

Nutrient	Ostriches	Domestic fowl
Threonine	0.831	0.804
Serine	0.849	0.823
Alanine	0.937	0.919
Valine	0.862	0.810
Methionine	0.816	0.776
Phenylalanine	0.809	0.723
Histidine	0.854	0.806
Lysine	0.832	0.755
Isoleucine	0.829	0.817
Tyrosine	0.816	0.764
Arginine	0.780	0.736
Cysteine	0.806	0.781
Leucine	0.859	0.825
Protein	0.646	0.609
Lipid	0.870	0.892

the efficiency of TME_n utilization for RE (kpf) in growing birds and $a \times b^{-1}$ predicts daily requirements for maintenance energy (TME_n) per $kg^{0.75}$ body mass (Chwalibog, 1991). The same procedure was applied to estimate amino-acid requirements for maintenance and to calculate the efficiency of amino-acid utilization for carcass protein synthesis.

Retained carcass energy was also regressed on effective energy (EE), the unit proposed by Oldham and Emmans (1990) to correct TME_n for differences in heat loss of fats, carbohydrates and protein during metabolism: $EE = TME_n - 4.67 \times$digested protein$- 3.8 \times$faecal organic matter$+ 12 \times$digested N-free extract. Maintenance energy requirement (EE_m) was also calculated according to a formula proposed by Emmans and Fisher (1986) in which maintenance requirement was based on the protein content of the carcass (Table 5.7). The determined TME_n and amino-acid availability results were used to calculate actual amino acid and energy intake from feed fed to experimental groups.

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Table 5.7. Relationship between carcass energy retention and energy intake in ostriches in a TME_n system (Cilliers, 1998).

RE	Intercept	SD	Slope	SD	R	Efficiency of utilization (kpf)
In the TME_n system						
$kgBM^{0.75}$	–0.176	0.018	0.414	0.022	0.97	0.414
MJ day^{-1}	–3.528	1.011	0.443	0.056	0.862	0.443
In effective energy system[1]						
RE	–0.176	0.010	0.568	0.031	0.95	0.568

[1]Effective energy (Emmans, 1989) for maintenance, using carcass protein content: EE_m (MJ day^{-1}) = $P_m^{-0.27} \times 1.63P = 20.66^{-0.27} \times 12.48$ (± 0.363)$\times 1.63 = 8.980 \pm 0.227$ MJ day^{-1} (Mean for 12 birds) where P_m = mature protein mass (kg), value used was for mature birds weighing 120 kg and protein content of 17.2%; P = current protein mass of a bird, the value used was for a 65 kg animal with a carcass protein content of 19.2%.

Regression equations relating retained energy on energy consumption are given in Table 5.7.

Regressions were highly significant and the efficiency with which TME_n was converted to carcass energy (slope of the regression line) amounted to 0.414 and 0.443 for RE expressed per $kg^{0.75}$ or as MJ day^{-1}, respectively. TME_n requirement for maintenance was 0.425 MJ $day^{-0.75}$ (i.e. 0.176/0.414) or 7.964 MJ $day^{-0.75}$ (i.e. 3.528/0.443). The daily EE requirement for maintenance, based on carcass protein content (Emmans and Fisher, 1986), amounted to 8.90 MJ day^{-1} (Table 5.7). Although substantially different, these two values, 7.96 and 8.90, can at least be regarded as being of the same order.

Net efficiency of amino-acid utilization

Results on daily maintenance requirements (mg kg^{-1} gain day^{-1}) and the net efficiency of utilization for the various amino acids are listed in Table 5.8. These values were calculated with feather growth included, i.e. for the whole bird. The net efficiency of amino-acid utilization varied between 0.569 (leucine) and 0.968 (alanine). For lysine and methionine, amino acids often limiting in those materials available for ostrich diets, the values amounted to 0.733 and 0.780, respectively, which correspond well to equivalent values reported for the fowl (0.7 and 0.8, respectively; Boorman and Burgess, 1986).

Retention in various body components was separately measured in feathers,

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Table 5.8. Result of maintenance needs and retention (mg kg^{-1} EBM day^{-1}), and net efficiency of utilization for protein and amino acids in ostriches (calculated according to mean empty body mass of 65 kg for the period). Data from Cilliers *et al.* (1997).

Nutrient	Maintenance	Retention rates	Net efficiency
Protein	678	3276	–
Threonine	57	60	0.710
Serine	53	56	0.615
Alanine	86	02	0.968
Valine	65	72	0.702
Methionine	38	33	0.780
Phenylalanine	68	74	0.654
Histidine	47	45	0.877
Lysine	91	109	0.733
Isoleucine	60	63	0.682
Tyrosine	51	51	0.904
Arginine	96	118	0.948
Cysteine	21	19	0.569
Leucine	91	111	0.569

hide, legs and skeleton (Cilliers *et al.*, 1998d). These data were proportionally pooled and combined as total growth and retention. During the latter part of this study it was noticed that the ratio of hide to body mass increased with age in contrast with ratios of other components, e.g. legs and feathers, which remained constant. Future research should therefore be directed at defining differences in growth rate and difference in the conversion of feed amino acids to the different body components.

Predicted energy and amino-acid requirements for ostriches

Results on carcass characteristics (Cilliers, 1994; Cilliers *et al.*, 1996, 1998d) were used to estimate nutrient requirements for ostriches at different ages. A Gompertz growth curve constructed for ostriches reared from 1 day old to 520

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days old (Cilliers *et al.*, 1995) was used as the basis for these predictions. It is fully realized that figures in Table 5.9 assume a constant body composition during the period of prediction, i.e. that of a 7-month-old bird, and this cannot be correct for energy contents for birds of all ages, although it may represent typical amino-acid profiles and total protein levels. Nutrient requirements in Table 5.9 must thus be seen as a first attempt to furnish guidelines in a field where scientific knowledge on nutrient requirements is almost non-existent. It was also assumed that the efficiency of nutrient utilization is constant for different age groups. Further research will be needed to test these assumptions for ostriches of different ages, and it is expected that these values will be refined.

It should be noted that figures presented in the Gompertz curve used in calculations were based on data collected over years on the experimental farm at Oudtshoorn, South Africa (Cilliers *et al.*, 1995). Although conditions at the time of determination were seen as optimal, this study did not take into account feeding of diets to attain maximum rate of growth. Diets fed to birds during the growth period to establish potential growth curves differed substantially from what is used today. Hence a substantial improvement in rate of maturing would now be possible. As requirements were estimated per unit gain, requirements should remain unchanged.

Despite the potential of possible errors due to assumptions, requirement estimates (Table 5.9) were remarkably similar to estimates made from the Emmans (1989) formula, which uses mature protein content and the protein content of the body at a particular stage to determine energy and amino-acid needs for maintenance and growth. In Table 5.9 values are given for a TME_n requirement of 10.4 and 19.36 MJ day^{-1} for 90 and 300 days of age. The corresponding Emmans' values are in close agreement and amounted to 9.3 and 19.3 MJ day^{-1}, respectively (Cilliers, 1994).

Future work will have to establish whether energy to amino-acid ratios remain constant per unit body mass and whether the ratio of hide to carcass to legs to feathers is constant during the different phases. Cilliers *et al.* (1998d) found that the ratio of hide to empty body mass changed from 48.5 to 55.6 g kg^{-1} during the experimental period. It will be essential to determine whether the efficiency of nutrient utilization remains constant for different age groups. Efforts should be directed towards quantifying the relative growth of the different body components and the relationship between nutrient intake and product output and composition.

IMPLICATIONS OF UREA CONTAMINATION OF OSTRICH DIETS

Urea has been recognized for many years as toxic to poultry (Jones and Combs, 1953). In recent years conflicting evidence as to the role of urea in poultry nutrition has been generated. Urea is rapidly absorbed intact from the upper intestine of the fowl (Chowdhury *et al.*, 1996), and thus previous reports by Okumura *et al.* (1976) that the microbial load played an important role in the use of urea in fowl may be in doubt.

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Table 5.9. Calculated TME_n, effective energy and lysine requirements for maintenance and growth in ostriches at various growth intervals (E and F formula for Emmans and Fisher, 1986), from Cilliers *et al.* (1998b).

Age (days)	Body mass (kg)	Body mass for period (kg)	Feed intake (kg bird^{-1} day^{-1})	Carcass energy gain (MJ day^{-1})	For growth (MJ day^{-1})	Maintenance (MJ day^{-1})	Total (MJ day^{-1})	Diet level TME_n (MJ kg^{-1})	E and F Formula	Lysine (g day^{-1})
1	0.8									
30	3.3	1.8	0.25	2.400	2.671	0.673	3.34	13.6	13.23	2.48
60	9.1	6.6	0.49	5.333	5.938	1.757	7.70	15.7	14.10	5.80
90	16.6	14.6	0.75	6.475	7.211	3.182	10.39	13.9	12.34	7.77
120	25.0	23.6	0.91	6.856	7.635	4.547	12.18	13.4	12.01	9.11
150	36.2	33.6	1.35	8.380	9.332	5.925	15.26	11.3	10.36	11.65
180	47.9	45.4	1.65	9.599	10.689	7.429	18.12	11.0	10.32	14.01
210	58.2	57.5	1.81	8.570	9.544	8.869	18.41	10.2	9.70	14.44
240	67.4	68.1	1.90	7.540	8.398	10.077	18.48	9.7	9.43	14.63
270	75.8	77.6	1.95	6.970	7.761	11.122	18.88	9.7	9.54	15.13
300	83.7	86.5	2.00	6.551	7.296	12.064	19.36	9.7	9.69	15.71
330	88.6	93.6	2.40	4.036	4.500	12.791	17.29	7.2	7.32	14.06
360	91.9	96.0	2.45	2.740	3.054	13.246	16.30	6.7	6.84	13.34
390	95.2	101.6	2.50	2.740	3.054	13.609	16.66	6.7	6.90	13.73
420	98.4	105.2	2.50	2.606	2.960	13.964	16.92	6.8	7.06	14.05
450	101.2	108.4	2.50	2.265	2.545	14.287	16.83	6.7	7.08	14.04
480	103.2	111.1	2.50	1.752	1.951	14.548	16.50	6.6	6.99	13.82
510	105.1	113.2	2.50	1.447	1.612	14.754	16.37	6.5	6.97	13.76
540	106.7	115.0	2.50	1.371	1.527	14.934	16.46	6.6	7.04	13.89
570	109.1	117.2	2.50	1.961	2.206	15.148	17.35	6.9	7.43	14.71
600	110.7	119.4	2.50	1.295	1.442	15.356	16.80	6.7	7.25	14.29

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There have been several reports since 1995 of accidental urea consumption by ostriches. These occurred mainly due to feed contamination or through the use, for ostriches, of cattle supplements containing urea. A series of studies were undertaken (Angel *et al.*, 1999) to determine the effect of urea on performance and toxicity signs. Birds were fed 0.4, 0.8 and 1.6% urea either for 30 days or for the duration of the growing phase. Transient increases in blood urea nitrogen were observed, but no effects were seen on growth rate, feed efficiency or carcass weight. A separate study was carried out where a single dose of urea (17 g urea kg^{-1} body mass) was given to 2-month-old ostriches. Birds were bled every 2 h after dosing for 8 h. Again, only a transient increase in blood urea nitrogen was seen with no deleterious effects observed.

PRACTICAL FEED-FLOW PROGRAMMES

Due to the nature of ostrich farming, various feed-flow programme approaches are encountered (e.g. Table 5.10) and husbandry practices vary from intensive zero-grazing systems to extensive farming on pastures or in arid areas (Verwoerd *et al.*, Chapter 8). Choice of diets is determined by: (i) stage of marketing; (ii) final aim in slaughter or breeder birds; (iii) slaughter age; (iv) purpose of slaughter bird, i.e. for meat, feather or hide production; (v) availability of ingredients, pastures and silage; and (vi) economy. The majority of birds in South Africa are slaughtered at 14 months of age with a mature feather plucking. Ideal body size for leather production is 95 kg, and any gain above this results in unnecessary deposition of fat for which farmers are occasionally penalized. Furthermore, no additional money is paid for hides exceeding 145 dm^3 which corresponds to a body mass of 95 kg. With recent changes in the ostrich market (Deeming, Chapter 1), there has been a rapid change to a younger slaughter age (8–10 months) as a result of changed demand for the type of product. This will allow a substantial saving in production costs due a reduction in feed requirements because the post-finisher diet will be omitted.

CONCLUSIONS

The ostrich is well adapted to its natural diet of vegetation, and because of post-gastric microbial fermentation it is very efficient at extracting nutrients and energy. Our understanding of ostrich nutrition for farmed birds is, by contrast, still in its infancy. Considerable further research is needed to validate requirement information for major dietary components, and there is an urgent need to establish vitamin and mineral requirements for different ages. In light of work on fatty acid profiles of ostrich egg yolks by Noble *et al.* (1996), basic information on nutrient requirements of breeders is needed. A large and focused study on the effect of age on hide quality is lacking at this time.

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Table 5.10. A typical feed-flow programme currently used by the majority of ostrich producers in South Africa. From Cilliers (1998).

Age group	Mass interval (kg)	Diet type	Feed intake (kg period^{-1})
Day old to 2 months	0.8–18	Pre starter with 20.5–22% protein	22–25
2–4 months	18–45	Starter with 18–20% protein	55–60
4–6 months	45–70	Grower with 15.5–17% protein	90–95
6–10 months	70–95	Finisher with 13–14% protein	230–250
10–14 months	> 95	Post-finisher or maintenance diet with 10–12% protein	300–320

As the industry focuses on production feeding, guidelines will have to be developed for each specific end point. Development of cost-effective feeding methods in different areas of the world will have to be a primary focus of research if this industry is to survive in the long term. As genetic improvements generate an ostrich with greater growth capacity and better feed conversion potential, nutrient requirements will change and thus feeding guidelines will need to follow.

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6

Reproduction

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The increasing demand for ostrich products experienced in recent years and the resultant pressure on breeders for accelerated production have focused attention on the reported low productivity in the industry (Table 7.1). Reports on the extent of the problem vary and although certain individual operations claim high fertility and hatchability rates, the industry in general is beset by a poor reproductive performance. This aspect is described in more detail by Deeming and Ar (Chapter 7).

Whereas intensive studies on the reproductive system of domestic poultry have been carried out and reported on in the literature, very little information is currently available on reproduction in ostriches. Many basic questions remain unanswered and certain avenues of research are hampered by a lack of elementary data, particularly with respect to female reproduction. Here the current understanding of reproductive biology is reviewed with the exception of behaviour which is described by Deeming and Bubier (Chapter 4).

ANATOMY OF THE MALE REPRODUCTIVE SYSTEM

The male reproductive organs in the ostrich resemble those of other birds, and comprise the testis and ductus epididymis. There is also a well developed phallus (MacAlister, 1864; Duerden, 1912; Fowler, 1991; Hicks, 1993).

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The testes

The testes are situated on either side of the caudal vena cava, ventral to the cranial division of the kidneys (MacAlister, 1864; Duerden, 1912; Cho *et al.*, 1984; Bezuidenhout, 1986). They lie near the adrenal glands and are suspended from the body wall by a fold of mesentery (Duerden, 1912). The testes vary considerably in size and appearance depending on the age and sexual status of the cock. In very young chicks they can be seen as two white, worm-like bodies, about 10 mm in length, lying ventral to the cranial division of the kidney near the midline (Duerden, 1912). Soley (1992) reported similar findings in 2- to 3-month-old birds and noted that the left testicle is positioned slightly caudal to the right testicle and lies ventromedial to the cranial division of the left kidney. The right testis is situated ventrolateral to the cranial division of the right kidney. In 14-month-old birds, the testes are cream-coloured, finger-like structures, 35–45 mm in length with a central circumference of 40 mm (Soley, 1992). At 18 months they are reported to reach the size of a finger (Duerden, 1912; Hallam, 1992). During the breeding season the testes are about 160 mm long and 50 mm wide (MacAlister, 1864; Bezuidenhout, 1986; Hallam 1992) and oval in shape (Cho *et al.*, 1984). These observations were corroborated by Soley (1992) who described the testes of sexually active mature males as tan-coloured, elongated, oval structures measuring 140–160 mm in length and 184–220 mm in circumference at their widest point. Both testes completely cover the ventral aspect of the cranial and middle divisions of the kidneys (Fig. 6.1) and extend from the caudal border of the spleen as far as the cranial tips of the caudal divisions of the kidneys. The cranial pole of the left testis lies at the caudal border of the last rib and is related craniomedially to the spleen. The cranial pole of the right testis lies approximately 25 mm caudal to the last rib (Soley, 1992).

MacAlister (1864) noted that the testes are enclosed by a strong fibrous tunica albuginea whereas Soley (1992, 1997a) described a thick, testicular capsule consisting chiefly of a well-developed tunica albuginea covered by a layer of cuboidal cells representing the lining of the peritoneum. Although the tunica albuginea is very cellular in appearance, it is composed mainly of fibrous connective tissue. In places this layer displays a laminated arrangement of the regular dense connective tissue. Scattered smooth muscle cells are also observed. Numerous arteries and veins as well as attendant non-medullated nerves are present, particularly in the region beneath the peritoneal lining. Profiles of the intracapsular component of the rete testis are also observed. A thin, inner cellular layer (tunica vasculosa) containing numbers of small blood vessels is situated adjacent to the testis parenchyma. Numerous fine septa project from this layer and push between the seminiferous tubules for a short distance before merging with the peritubular connective tissue. Larger septa, which penetrate much deeper within the testis parenchyma, are occasionally observed emanating from the tunica albuginea. These structures contain large blood vessels and non-medullated nerves. Despite the size of these septa, distinct lobulation of the testes is not observed.

The testis parenchyma typically consists of closely packed seminiferous

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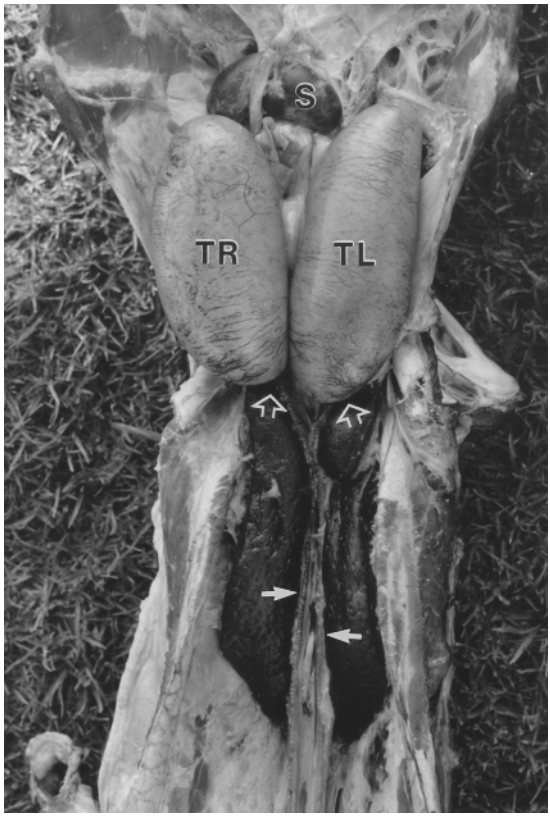

Fig. 6.1. A ventral view of the reproductive tract of a sexually mature male ostrich during the breeding season. The left (TL) and right (TR) testes completely cover the cranial and middle divisions of the kidneys and extend to the cranial border of the caudal divisions (open arrows). The deferent ducts (arrows) appear as convoluted tubes running with the ureters along the medial borders of the caudal renal divisions. S, spleen. 10 mm = 30 mm.

tubules separated by a thin layer of peritubular connective (boundary) tissue (Figs 6.2 and 6.3). This tissue closely invests the seminiferous tubules and is continuous with the inner cellular layer of the tunica albuginea. It consists of an inner fibrous layer immediately below the seminiferous epithelium, and an outer layer of alternating cellular and acellular lamellae. The cellular lamellae are composed of myofibroblasts (Soley, 1990a, 1992). The continuity of the boundary tissue between neighbouring seminiferous tubules is often broken by the presence of blood and lymphatic capillaries, as well as by occasional Leydig cells. Larger blood and lymphatic vessels, as well as groups of Leydig cells and individual mast cells, are observed to form interstitial tissue between groups of seminiferous tubules. The Leydig cells typically display a large vesicular nucleus with a prominent

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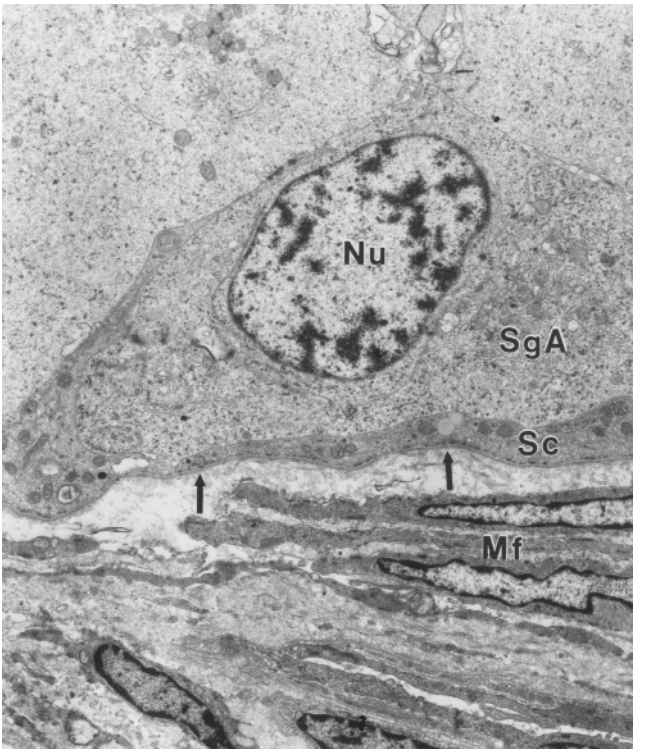

Fig. 6.2. Transmission electron micrograph of a type A spermatogonium (SgA) situated at the base of the seminiferous epithelium. The nucleus (Nu) contains dispersed clumps of heterochromatin, many of which are peripherally situated. Fine extensions of Sertoli cell cytoplasm (Sc) almost completely separate the spermatogonium from the underlying basal lamina (arrows). A number of myofibroblasts (Mf) are situated in the boundary tissue. ×7000.

nucleolus and abundant cytoplasm filled with profiles of smooth endoplasmic reticulum (Soley, 1992).

In sexually mature birds examined during the breeding season, the seminiferous epithelium varies between 75 and 150 μm in thickness and consists of columns of developing germ cells associated with evenly spaced Sertoli cells. The latter are long, columnar elements which stretch from the basement membrane to the lumen of the seminiferous tubules. In respect of general shape, organelle content and association with the germinal component of the seminiferous epithelium, ostrich Sertoli cells are similar to those of other vertebrates and share the basic features described in other birds (Soley, 1992). A prominent layer of cells with dark-staining cytoplasm, which are identified as spermatogonia, appears to lie against the basal lamina immediately surrounding the seminiferous tubules. However, both light (LM) and transmission electron microscopy (TEM) reveal

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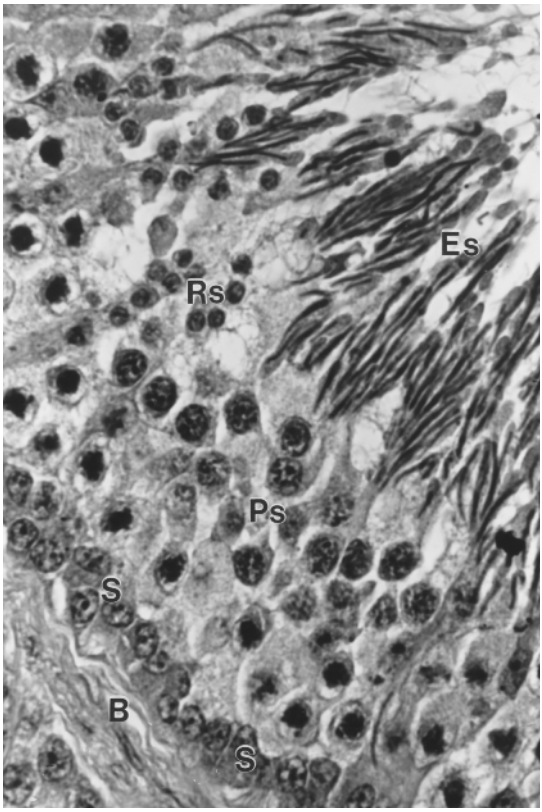

Fig. 6.3. A light micrograph of the germinal epithelium lining a seminiferous tubule in the testis. A row of spermatogonia (S) with relatively pale nuclei line the base of the tubule immediately adjacent to the surrounding boundary tissue (B). A wide layer of primary spermatocytes (Ps) in various stages of the first meiotic division are the most prominent cells. Small groups of secondary spermatocytes/early round spermatids (Rs) are also visible, whilst masses of elongated spermatids (Es) line the luminal surface of the tubule. ×750.

that fine extensions of the Sertoli cells effectively separate the spermatogonia from the basal lamina, leaving only small regions of open contact between the two.

The removal of the testes to control aggressive behaviour in male birds has been reported. According to Smit (1963), initial castration (caponizing) techniques were risky and led to numerous fatalities amongst birds. Sikarskie (1987), however, developed a relatively safe surgical technique employing a single left lateral approach for the removal of both testes. This technique is best carried out at the onset of the breeding season when the testes increase in size, but should not be performed during peak gonadal development due to the increased risk of haemorrhage.

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The epididymis

In the ostrich the epididymis is a large structure attached to the dorsomedial surface of the testis (Bezuidenhout, 1986; Soley, 1992). In some texts the presence of a well developed epididymis is not noted (Duerden, 1912; Cho *et al.*, 1984) although MacAlister (1864) described it as being large, extending about 75 mm caudal to the testis. In juvenile birds, the epididymis projects well beyond the cranial and caudal poles of the testis, is larger than the testis, and lies lateral to the testis on the dorsal body wall (Budras and Meier, 1981; Soley, personal observations, 1988). In adult birds during the breeding season the testes exceed the length of the epididymis by 20 mm cranially and caudally (Budras and Meier, 1981) although variations have been noted (Soley, 1992).

The epididymis is divided into a cranial appendix epididymis and a main part which is attached to the testis along most of its length by the mesepididymidis, except for the caudal extremity which remains free and is continued caudally as the ductus deferens. In transverse section the main part is described as being nearly square (Budras and Meier, 1981) or triangular in profile (Soley, 1992). The appendix represents approximately the cranial two-fifths of the entire length of the epididymis. Caudally it is attached to the testis, whilst cranially its narrower free end is intimately connected to the adrenal gland (Budras and Meier, 1981; Soley, 1992).

The origin, development and structure of the epididymis of the ostrich has been studied in detail by Meier (1979) and Budras and Meier (1981), with additional histological information being supplied by Soley (1992). The appendix epididymis contains the ductus aberrans (the cranial continuation of the ductus epididymidis) and the ductuli aberrantes. The latter are reported to give rise to lipoid-rich noduli epididymidis (Meier, 1979; Budras and Meier, 1981) which demonstrate morphological evidence of steroid hormone synthesis (Budras *et al.*, 1980). The main part of the epididymis contains ductuli efferentes and the ductus epididymidis. These elements of the excurrent duct system are linked to the testis by the rete testis which consists of intratesticular, intracapsular and extratesticular components. The extratesticular rete comprises small pockets of rete tubules in the epididymis and long tubules/channels housed in cords of fibrous connective tissue which link the testicular capsule (containing the intracapsular rete) with the epididymis (Budras and Meier, 1981; Soley, 1992). The ostrich rete testis appears simply to link the seminiferous tubules with the ductuli efferentes.

The rete testis is joined to the highly convoluted ductuli efferentes which are divided into two regions (proximales and distales; Budras and Meier, 1981; Soley and Els, 1992). Soley (1992) describes an intermediate region of the ductuli efferentes which is characterized by intense secretory activity. The highly elongated columnar cells in this region are filled with spherical bodies (granules) of varying size, and the lumen of the duct contains free granules and cytoplasmic masses filled with granules (Soley, 1992). Whether this region represents a temporary transformation of either the proximal or distal efferent duct, or forms a specialized region of the ductuli efferentes, is not known. The intense secretory activity, how-

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ever, may indicate that this region makes an important contribution to the seminal fluid. The distal ductuli efferentes are joined to the ductus epididymidis via short connecting ducts, the ductuli conjugentes (Budras and Meier, 1981). The ductus epididymidis is highly convoluted and characteristically displays a pseudostratified, non-ciliated columnar epithelium (Budras and Meier, 1981; Soley, 1992). The ductus epididymidis constitutes the bulk of the epididymis (Soley, 1992).

The ductus deferens leaves the caudal part of the epididymis as a fairly straight tube and runs parallel to the ureter, near the midline (Fig. 6.1). The ductus deferens opens into the urodeum lateral to the ureter (MacAlister, 1864; Duerden, 1912; Bezuidenhout, 1986), via the deferent duct papilla (Soley, 1992). In sexually active birds during the breeding season the ductus deferens is readily identified by its highly convoluted nature and white colour. During semen collection the deferent duct papillae are frequently found to be turgid with accumulated semen.

The phallus

The ostrich has an intromittent organ commonly called a phallus (Boas, 1891; King, 1981a; Fowler, 1991) although some authors refer to it as a penis (Duerden, 1912; Grimpe, 1930). The phallus is attached to the ventral wall of the cloaca and comprises a base and a conical shaft (Fig. 6.4; Müller, 1838; Gerhardt, 1933, as quoted by King, 1981a; Duerden, 1912). In adult males the flaccid phallus is about 20 cm long, bright red in colour and lies in a phallic pocket in the ventral wall of the proctodeum (Gerhardt, 1933 as quoted by King, 1981a; Fowler, 1991). When in its pocket the phallus is bent in the middle of its shaft (on its ventral aspect) forming a knee-shaped arch (Müller, 1838). The phallus is bulky and occupies most of the proctodeum, apparently blocking the ureters and sealing the cloacal lumen (Geoffroy-Saint-Hilaire, 1822). Consequently it has to be partly protruded to allow for defecation and urination (Geoffroy-Saint-Hilaire, 1822; Müller, 1838; King 1981a; Fowler, 1991). When erect, the phallus is about 40 cm long (Gerhardt, 1933, as quoted by King, 1981a; Berens von Rautenfeld, 1977; Fowler, 1991) and projects from the cloaca in a ventrocranial curve and slightly to the left, with the phallic sulcus on the dorsal aspect (King, 1981a; Fowler, 1991). The phallus consists of: paired fibrous bodies; the phallic sulcus; the elastic vascular body; and muscles of the phallus.

The paired fibrous bodies are two dorsally situated structures (Geoffroy-Saint-Hilaire, 1822; Müller, 1838; Boas, 1891) which form the bulk of the phallus. They lie next to one another, are fused in the cranial half of the phallus (closer to its base), but remain separate in the caudal half (closer to the tip) where they are joined by fibrous connective tissue (Müller, 1838; Boas, 1891). The left body is thicker and longer than the right body, causing the observed asymmetry (Grimpe, 1930; King, 1981a) which causes the erect phallus to deviate to the left (Müller, 1838; Fowler, 1991).

The phallic sulcus originates near the papillae of the ductus deferens

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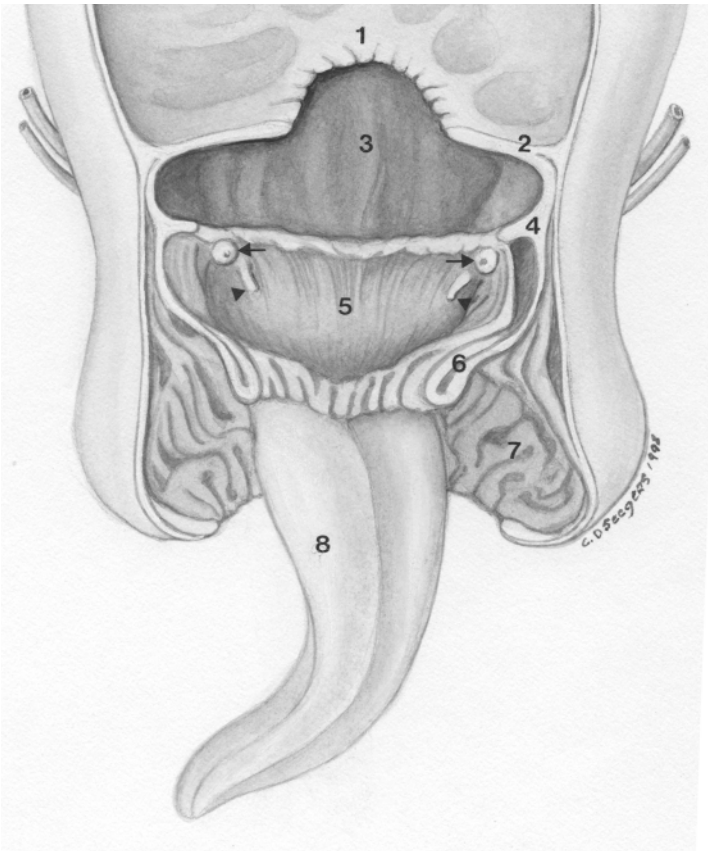

Fig. 6.4. Schematic representation of the cloaca of a young male ostrich illustrating the opening of the urogenital system in the urodeum. The cloaca has been slit open dorsally and the sides partially reflected laterally to reveal the various compartments of the cloaca. The size of the phallus has been exaggerated and the organ has been extended caudally, accentuating the size of the urodeum which contains the paired seminal papillae (arrowheads) and openings of the ureters (arrows). In the normal position the base of the phallus would lie closer to the seminal papillae. 1, Terminal portion of the rectum (colon); 2, recto-coprodeal fold; 3, coprodeum; 4, uro-coprodeal fold; 5, urodeum; 6, uro-proctodeal fold; 7, proctodeum; 8, phallus with dorsally positioned phallic groove.

and ends at the tip of the phallus. The dorsal groove between the two fibrous bodies forms the basis for the phallic sulcus. According to Müller (1838), the walls of the sulcus are formed by erectile tissue which becomes thicker towards the base. The erectile tissue extends well beyond the lips of the sulcus to form the two erectile cushions on each side of the root of the fibrous bodies (Boas, 1891). The phallic sulcus serves to transport sperm from the ductus deferens to the cloaca of the female during copulation (Duerden, 1912).

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The elastic vascular body lies in the midline on the ventral aspect of the phallus and is confined to the distal free half of the phallus (Müller, 1838; Boas, 1891; Gerhardt, 1906; Grimpe, 1930; King, 1981a). It originates at about the middle of the phallus and extends distally where it is almost solely responsible for forming the tip of the phallus. It consists of a thick outer layer of elastic tissue and an inner core of erectile tissue. The elasticity of the body is probably responsible for the ventral curvature of the phallus during erection and for the bent condition of the phallus when flaccid (Müller, 1838).

The levator phalli muscle is responsible for extruding the phallus from its proctodeal pocket and also for the cranial redirection of the free phallus (Müller, 1838; Gerhardt, 1933 as quoted by King, 1981a). There are two pairs of retractor phalli muscles, although the one pair is very small (Müller, 1838). However, Gadow (1887) describes only a single pair which arise from the floor of the pelvis and attach to the ventral aspect of the phallus. They are responsible for retracting the phallus into its pocket.

The mechanism of erection remains unknown. King (1981a) discusses the confusion created by the references made to cavernous tissue in the phallus by Müller (1838) and Boas (1891). Gerhardt (1933) as quoted by King (1981a), mentions that Grimpe in 1923 suggested that erection is achieved by lymphatic engorgement. However, failure to convincingly demonstrate the presence of a paracloacal vascular body (King, 1981a) appears to disqualify this suggestion. By contrast, Berens von Rautenfeld (1977) describes and illustrates a well developed lymphatic system in the phallus which is responsible for erection. It consists of a large lymphobulbus phallus situated on either side of the seminal groove which is linked to the somatic lymphatic system, and in turn to the general circulation. Each lymphobulbus phallus is flanked by a clearly demarcated branch of the vena pudenda interna. As this area is free of sensitive nerve endings, it is a useful site for injecting drugs (Berens von Rautenfeld, 1977; Huchzermeyer, 1998).

SPERMATOGENESIS

Spermatocytogenesis

Two types of spermatogonia can be identified in the seminiferous epithelium (Soley, 1992). Type A spermatogonia are few in number and display a relatively small oval or slightly elongated nucleus containing evenly distributed fine strands of heterochromatin. The nucleus, which contains a prominent nucleolus, is generally positioned parallel to the basal lamina of the tubule. Type A spermatogonia are typically flattened cells with a broad base of contact with the perimeter of the seminiferous tubule (Fig. 6.2).

Type B spermatogonia reveal a large, round (7–8 μm), elongated or irregularly shaped nucleus containing conspicuous masses of peripheral heterochromatin and one or two nucleoli. They are round or polygon-shaped cells with

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smaller regions of contact with the boundary of the seminiferous tubule.

Some spermatogonia demonstrate features which made it difficult to classify them as either A or B type cells and may represent intermediate types. Preleptotene spermatocytes are similar in appearance to type B spermatogonia but are situated further away from the basal lamina. Round primary spermatocytes are encountered in various stages of development and exhibit features characteristic of vertebrate primary spermatocytes. The large, spherical nuclei of leptotene, zygotene and pachytene spermatocytes, although differing in appearance, are of similar size (Fig. 6.3). Synaptonemal complexes occur in the nuclei of zygotene and pachytene spermatocytes. The latter are visible in almost any section of the seminiferous epithelium of the ostrich. Secondary spermatocytes resulting from the first meiotic division display a relatively large nucleus (6 μm in diameter). The chromatin material is diffusely distributed although a peripheral rim of heterochromatin can be observed. The type and distribution of cytoplasmic organelles is similar to that of round spermatids (see below).

Spermiogenesis

Based on light and electron microscopic observations it is possible to recognize eight stages of spermiogenesis in the ostrich. These are described in detail by Soley (1992) and are summarized here.

Stage 1 spermatids are round cells with a centrally positioned spherical nucleus. The most obvious features under light microscopy are the presence of a dense granule (the acrosomal granule) in the vicinity of the nucleus; a diplosome consisting of a long and a short centriole oriented obliquely with respect to the nucleus; and a tendency for the nuclear membrane to appear thickened due to the accumulation of chromatin material along its inner aspect. The nucleus also displays scattered clumps of chromatin with intervening clear areas. Electron microscopy reveals an organelle-rich region of the cytoplasm containing the diplosome and the acrosome granule as well as numerous small round and oval mitochondria, dictyosomes, profiles of smooth and granular endoplasmic reticulum, polyribosomes, vesicles, multi-vesicular bodies and occasional lipid droplets. TEM also shows that the free end of the long distal centriole has usually established contact with the plasmalemma of the cell from which the axoneme emerges.

Stage 2 spermatids are similar to stage 1 spermatids, but on both LM and TEM the acrosomal vesicle housing the acrosomal granule and the cytoplasmic end of the diplosome are seen to have established contact with the nuclear membrane in close proximity to each other. The diplosome is still oriented obliquely with respect to the nucleus and a dense structure identified as the chromatoid body is associated with the proximal centriole. The acrosome vesicle is housed within a crater-like depression of the nucleolemma and appears electron-opaque due to the dispersion of its contents. The nuclear membrane lining the crater appears electron-dense.

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Stage 3 spermatids also display morphological features similar to the previous two stages, but the developing acrosome and the centriolar complex are stationed at opposite poles of the nucleus. The acrosomal vesicle appears flattened and the diplosome and emerging flagellum sometimes display an oblique attachment to the nucleus.

Stage 4 spermatids are slightly elongated cells containing an irregularly shaped nucleus which assumes a dumb-bell, kidney- or pear-shaped appearance. The nucleus contains scattered clumps of coarse material which are often concentrated beneath the nuclear membrane. The acrosome is a flattened structure attached to the one pole of the nucleus whilst the centriolar complex is connected to the other pole and generally oriented parallel to the long axis of the cell. A cylindrical nuclear invagination which contains an acrosomal rod appears at the apical tip of the nucleus immediately beneath the developing acrosome. The circular manchette begins to develop during this stage and peculiar radial bodies are observed in the cell cytoplasm.

Stage 5 spermatids are similar in all respects to stage 4 spermatids except for the nuclei which are longer and narrower and display a scalloped appearance due to multiple constrictions of the nuclear membrane. The nucleoplasm has a finely granular homogeneous appearance. The plasmalemma of the cell is closely applied over the acrosomal region. A band of dense material identified by TEM as the dissipating chromatoid body is observed at the base of the nucleus.

Stage 6 spermatids are conical with a narrow apical region of cytoplasm surrounding the tip of the nucleus. The long, narrow nucleus is 2 μm in diameter, displays smooth contours, and contains evenly dispersed finely granular chromatin. Occasional dense granules are seen in the karyoplasm. The caudal cytoplasm is reflected around the developing flagellum forming a short flagellar canal. The annulus can be detected by both LM and TEM. The acrosome is crescent-shaped and the circular manchette well developed.

Stage 7 spermatids differ little from the previous stage. The nucleus is longer and slightly narrower and stains more densely. In thin sections the nucleoplasm displays a progressive accumulation of rod-like granular material which is occasionally seen in a spiral formation. The flagellar canal deepens and the circular manchette reaches maximum development. The acrosome forms a small cap-like structure at the apical tip of the nucleus. Maximum nuclear length is attained during this stage.

Stage 8 spermatids are situated close to the lumen of the tubules and display a long, slender (1 μm in diameter) dark-staining nucleus. On TEM the nucleoplasm consists of coarse, densely packed granules or, in nearly mature sperm, a homogeneous electron-dense mass. A well developed longitudinal manchette is present, the acrosome assumes the form characteristic of mature sperm, and caudal displacement of the cytoplasm is observed. After dissolution of the longitudinal manchette, mitochondria surrounded the proximal and distal centrioles to complete the formation of the midpiece.

During all stages of spermatogenesis the developing germ cells are linked by intercellular bridges. In general appearance these bridges are similar to those

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described in other birds and mammals, display a similar organelle content, and maintain cytoplasmic continuity between the attached cells. Specialized bridges, characterized by an extensive system of endoplasmic reticulum cisternae, are observed in dividing spermatocytes (Soley, 1992). Numerous residual bodies surrounded the newly formed sperm cells. These structures are generally round cytoplasmic units of variable size containing excess mitochondria, as well as large accumulations of membrane-associated material, radial bodies and reticulated bodies. Multinuclear cells are a consistent feature of ostrich seminiferous epithelium, although they are infrequently observed in some birds. These cells are generally situated close to the basal lamina of the tubules and form large cytoplasmic aggregations containing a variable number of nuclei. Cytoplasmic continuity is not always a feature of the multinuclear cells and they sometimes appear as a circumscribed bundle of closely packed cells. Multinuclear cells appear to be systematically moved towards the lumen of the tubule and show signs of degeneration, which suggests that they are not viable components of the seminiferous epithelium (Soley, 1992).

Ultrastructural features of spermiogenesis in the ostrich have been well documented (Soley, 1990b, 1991, 1992, 1994a, 1996, 1997b; Baccetti *et al.*, 1991). The main features include: the existence of a circular and longitudinal manchette which play a role in nuclear shaping; the formation of a deep endonuclear canal housing a slender perforatorium; a stationary annulus which does not appear to receive contributions from the chromatoid body; the formation of a ribbed fibrous sheath around the principal piece of the tail in a similar fashion to that observed during mammalian spermiogenesis.

Sperm morphology

Light microscopic features of the sperm cell (Fig. 6.5) have been described by a number of authors (Retzius 1911; Berens von Rautenfeld, 1977; Soley, 1992). The cells are 70 μm in length and vermiform (worm-like) in appearance. The slender head is gently curved, although crescent-shaped and convoluted forms are also observed (Soley, 1992). It measures 13 μm in length, and is composed of a nucleus (11 μm) and an apical cone-shaped acrosome (2 μm). The nucleus gradually tapers towards the tip and measures 0.5 μm in diameter at its widest point. The base of the nucleus abutting the midpiece is narrower than the main body of the nucleus.

The tail is 57 μm long and clearly divided into a midpiece, principal piece and end piece (Fig. 6.5). The midpiece is short (3 μm) and slightly larger in diameter than the nucleus, and reveals no special features. The principal piece forms the longest segment of the tail (51 μm). Its diameter is approximately 0.4 μm immediately beneath the midpiece but decreases progressively towards the end of the tail. The tail terminates in a short (2–3 μm) end piece which in most sperm is difficult to visualize accurately. These linear measurements are based on scanning electron microcopy (SEM) studies (Soley, 1992; Soley and Roberts, 1994)

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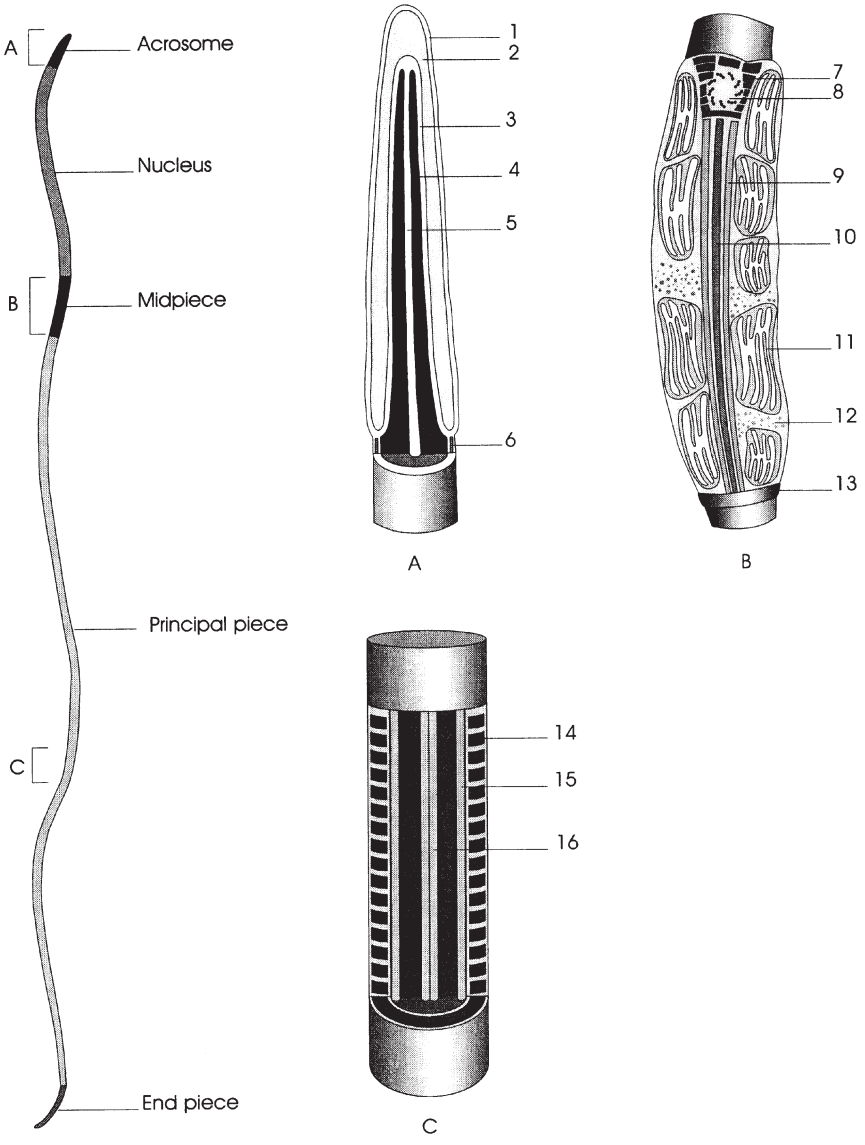

Fig. 6.5. Schematic representation of a spermatozoon illustrating the various components of the head (acrosome and nucleus) and tail (midpiece, principal piece and end piece). Insets A, B and C represent finer details of the structure of the acrosome, midpiece and principal piece, respectively, and are not drawn to scale. 1, Plasmalemma; 2, acrosome; 3, sub-acrosomal space; 4, nucleus; 5, endonuclear canal housing the perforatorium or acrosomal rod (not illustrated); 6, posterior ring; 7, segmented connecting piece; 8, proximal centriole; 9, wall of distal centriole; 10, rod of dense material lying within distal centriole; 11, mitochondrion; 12, inter-mitochondrial cement; 13, annulus; 14, ribs of fibrous sheath; 15, outer doublet microtubules of axoneme; 16, inner microtubular pair of axoneme.

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and probably do not reflect the true dimensions of the various components of the sperm cells as the preparation of material for SEM is known to result in a high degree of shrinkage (van der Horst *et al.*, 1991).

The ultrastructure of ostrich sperm cells has also been thoroughly investigated using both SEM and TEM (Soley, 1989, 1992, 1993, 1994b; Baccetti *et al.*, 1991; Soley and Roberts, 1994). SEM largely corroborates the features of ostrich sperm revealed by LM, whilst TEM has revealed important details of the internal structure. The cells display a short, conical acrosome which covers the tapered tip of the long, cylindrical nucleus (Fig. 6.5). A nuclear invagination housing an acrosomal rod extends deep within the karyoplasm. A centriolar complex is situated beneath the head and consists of a short proximal centriole and a long (3.0 μm) distal centriole which extends the complete length of the midpiece. The central cavity of the distal centriole contains a pair of microtubules embedded in a rod of electron-dense material. The midpiece is surrounded by a mitochondrial sheath. Concentrations of fine granular material are present between the mitochondria. The principal piece of the tail is demarcated from the midpiece by a distinct annulus and characterized by a ribbed fibrous sheath enclosing a typical axoneme. Rudimentary coarse fibres are observed between the fibrous sheath and the doublet microtubules of the axoneme in the proximal region of the principal piece. The end piece contains a disorganized collection of axonemal microtubules.

Ostrich sperm differs in a number of respects from that of other non-passerine birds (the absence of a typical perforatorium; the presence of a ribbed fibrous sheath; a deep nuclear invagination; the structure and length of the distal centriole) but shows a close similarity to sperm of the rhea and crested tinamou, both representatives of primitive avian families. These observations add further support to the theory that the ratites and tinamous constitute a monophyletic group, although ostrich and rhea sperm are more closely allied.

Bertschinger *et al.* (1992) report that the most common major sperm defects include midpiece reflexes, coiled tails reminiscent of the 'Dag defect' in mammals, partial or complete aplasia of the mitochondrial sheath, persistent cytoplasmic droplets, and abnormally shaped heads. In ostrich sperm the cytoplasmic droplet is generally positioned in the neck region of the cell (Soley and Els, 1993; Soley *et al.*, 1996) similar to the proximal droplet identified in mammalian sperm and which is viewed as a major defect. There are indications, however, that the site of sperm release during spermiation in the ostrich is the head region (Soley, personal observations, 1998) which would imply movement of the droplet to a distal position, a situation considered to be a minor anomaly in mammals. The presence of sperm with translucent and swollen heads has been reported in some samples (Soley, 1992; Bertschinger *et al.*, 1992) and there is a significant correlation between translucent heads and the incidence of dead sperm (Bertschinger *et al.*, 1992). Irons *et al.* (1996) report an increase in this type of defect late in the breeding season and associate the anomaly with poor individual motility. Whether this phenomenon indicates a loss of nuclear contents, a change in the composition of the chromatin, or a decrease in the density of the chromatin due to swelling, is not known (Soley, 1992).

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Semen collection, evaluation and artificial insemination

Semen collection in ostriches has been described by Berens von Rautenfeld (1977) and Bertschinger *et al.* (1992). Birds are confined in specially constructed plucking crushes available on farms, which facilitate semen collection without causing injury to the birds or handlers. The phallus is removed from the cloaca and held in the extruded position with the aid of a piece of cloth which provides a firmer grip. The fingers of the free hand are then inserted beneath the uro-proctodeal fold covering the entrance to the urodeum which contains the deferent duct papillae. Gentle massage of the latter generally results in emptying of the distal ends of the ducts. The ejaculate, which runs down the phallic groove, is collected using a pre-warmed collection tube. Both Bertschinger *et al.* (1992) and Irons *et al.* (1996) report that the collection of semen, and the volume of the ejaculate, is significantly improved by administering an intravenous injection via the basilic vein (Bezuidenhout and Coetzer, 1986) of 5 IU oxytocin 2–4 min prior to collection. In difficult or excitable birds it is sometimes necessary to give a second injection of oxytocin at the same dose approximately 10 min after the first. This treatment has proved to be perfectly safe and usually produces prompt results.

A number of papers have provided data on semen evaluation parameters (volume, colour, consistency, pH, individual motility, sperm morphology, sperm concentration) in ostriches (Berens von Rautenfeld, 1977; Hicks, 1990; Bertschinger *et al.*, 1992; Irons, 1995; Irons *et al.*, 1996; Hemberger, 1996). Ostrich semen does not demonstrate mass motility, and individual motility is also poor in comparison to mammalian sperm (Bertschinger *et al.*, 1992). Irons (1995) and Irons *et al.* (1996) point out that, due to limitations imposed by the collection technique, the samples obtained by this method may not represent a physiological ejaculate. The mean volume of semen obtained by this collection technique is only 0.6 ml (Bertschinger *et al.*, 1992, Irons, 1995; Irons *et al.*, 1996; Hemberger, 1996), although the use of oxytocin improves the mean volume to 1.4 ml (Bertschinger *et al.*, 1992). The methods used to obtain a physiological semen sample from male emus (Malecki *et al.*, 1996, 1997) may be difficult to apply to ostriches due to the sheer size and aggressive nature of the birds.

Although artificial insemination (AI) in ostriches is being investigated in a number of countries, very little published information is available. Berens von Rautenfeld (1977) described the technique of AI in ostriches but presented no results. Hemberger (1996) claimed successful egg production (average fertility of 83.2%) following AI with semen diluted with a new medium, 'triladyl–ostrich egg yolk–saline 0.7 sperm diluent'. The actual number of hens inseminated and the number of fertile eggs laid, is not mentioned, however, making it difficult to judge the success of the project. Irons (1995) correctly points out that basic information pertaining to numerous facets of reproduction will have to be elucidated before techniques such as AI can be optimally applied.

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ANATOMY OF THE FEMALE REPRODUCTIVE SYSTEM

In contrast with the situation in the male, very few detailed studies have been carried out on the female reproductive tract of the ostrich. Numerous books and papers simply report that anatomically and physiologically this organ system conforms to the general avian pattern. The cost factor involved in sacrificing female birds in production during the breeding season undoubtedly impacts negatively on this type of research.

The reproductive tract of the female ostrich consists of the ovary and oviduct, of which usually only the left ovary and oviduct develop (Duerden, 1912; Fowler, 1991). The homologue of the male phallus is the clitoris or female phallus which, in the ostrich hen, is 20–30 mm (Berens von Rautenfeld, 1977; Fowler, 1991) or even 40 mm (Gerhardt, 1933, as quoted by King, 1981a) in length. This structure projects from a genital mound on the floor of the proctodeum (Fowler, 1991) and is also visible during urination and defecation (Gerhardt, 1933, as quoted by King, 1981a). It has a clearly visible phallic sulcus on its dorsal surface (Müller, 1838).

The ovary

The left ovary is suspended from the dorsal body wall and is situated ventral to the cranial division of the left kidney (MacAlister, 1864; Duerden, 1912; Cho *et al.*, 1984; Bezuidenhout, 1986) and dorsal to the abdominal air sacs (Hicks, 1993). The size, shape and position of the ovary varies depending on the breeding cycle. In young chicks the ovary is small (about 12 mm in length) and pale in colour (Duerden, 1912). Cho *et al.* (1984) describe the ovary of immature birds as a single thin, flattened elliptical to rectangular-shaped structure situated on the ventral side of the kidney. In mature birds the ovary resembles a bunch of grapes (Figs 6.6 and 6.7). It consists of a stroma in which numerous follicles of varying size are embedded. There is no information on the formation of follicles or the development of the oocyte in the ostrich, although it is assumed to follow a similar pattern to that described in detail for other birds (Hodges, 1974; Gilbert, 1981). The diameter of the ovary varies from 1 to 8 cm (Duerden, 1912; Smit, 1963; Fowler, 1991). During the breeding season, from 12 to 16 ova attain maturity (MacAlister, 1864; Duerden, 1912). Each mature ovum is contained in a capsule and is attached to the surface of the ovary by its own stalk. The timing of ovulation and the duration of egg passage in the oviduct of the ostrich are not known (Irons, 1995), although the fact that a hen will generally lay an egg every second day suggests that the passage along the oviduct takes approximately 48 h.

The oviduct

The oviduct comprises the infundibulum, magnum, isthmus, uterus and vagina (Figs 6.6 and 6.7; Duerden, 1912; Muwazi *et al.*, 1982), is richly supplied with

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blood, and is suspended from the dorsal body-wall by a fold of peritoneum known as the broad ligament (MacAlister, 1864; Duerden, 1912). In young birds it is a straight, narrow tube, pale in colour, and lies ventral to the left kidney (Duerden, 1912). In the mature hen it is large (approximately 1.2 m long), convoluted, and has a rich blood supply (Duerden, 1912; Fowler, 1991). The infundibulum is fan-shaped and lies close to the ovary. It receives the ovulated ova (Duerden, 1912) and is the part of the oviduct where fertilization takes place, approximately 15 min after ovulation (Hicks, 1993). The infundibulum, magnum and isthmus are lined internally by a tall, simple columnar epithelium which becomes pseudo-stratified in some areas. Ciliated and non-ciliated cells are present, and simple branched tubular glands are found in the lamina propria (Muwazi *et al.*, 1982). Albumen and the two shell membranes are secreted by these parts of the oviduct (Duerden, 1912), the membranes being formed in the isthmus and the thick albumen around the oocyte in the magnum (Hicks, 1993).

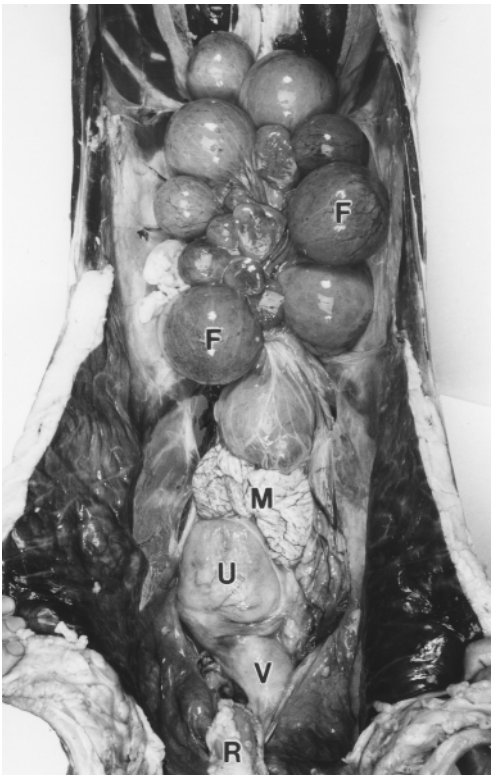

Fig. 6.6. Ventral view of the female reproductive tract of a sexually mature ostrich *in situ*. The ovary contains numerous large follicles (F) and fills the cranial half of the abdominal cavity. The visible parts of the oviduct are the magnum (M), shell gland (uterus) (U) and vagina (V). The rectum (R) has been reflected caudally. 8 mm = 42 mm.

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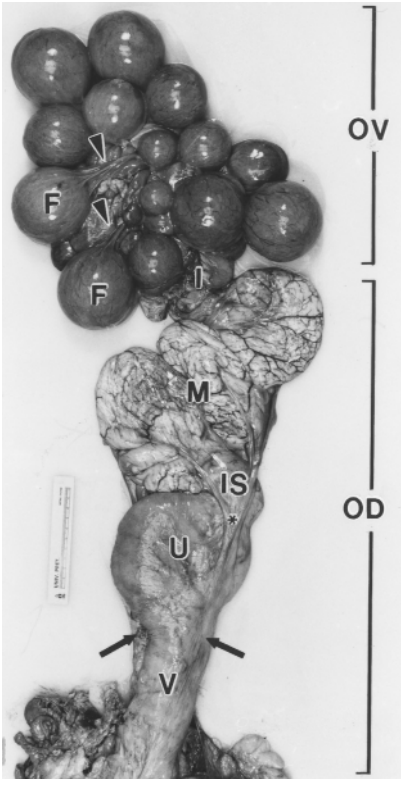

Fig. 6.7. Ventral view of the mature female reproductive tract removed and partially separated to illustrate the various components. The ovary (OV) displays many follicles in different stages of development. The larger follicles (F) are attached to the surface of the ovary by a stalk or pedicle (arrowheads). The oviduct (OD) consists of the infundibulum (I), magnum (M), isthmus (IS), uterus (U) and vagina (V). Note utero-vaginal junction (arrows) where the sperm host glands (sperm storage tubules) are located and the prominent muscular cord (asterisk) which forms part of the ventral ligament of the oviduct. 8 mm = 50 mm.

The wall of the uterus is thick due to the presence of a well developed muscular tunic (MacAlister, 1864; Fowler, 1991). The mucosa of the uterus and vagina contains approximately 80 longitudinal folds that are 5–20 mm in height (Bezuidenhout *et al.*, 1995). A distinct difference between the mucosa of the uterus and that of the vagina is evident. The mucosa of the uterus is darker in appearance than that of the vagina and the transition from one to the other is abrupt and well demarcated (Fig. 6.8; Bezuidenhout *et al.*, 1995). The epithelial lining of the uterus and vagina is a pseudostratified columnar epithelium consisting of both ciliated and non-ciliated cells (Muwazi *et al.*, 1982; Bezuidenhout *et al.*, 1995). Large numbers of uterine glands are present in the lamina propria of the uterus. These glands are absent in the vagina (Muwazi *et al.*, 1982;

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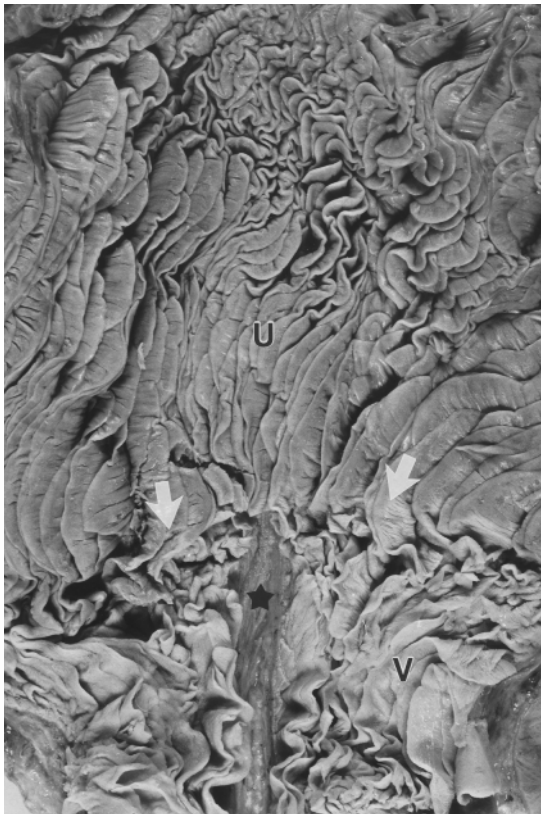

Fig. 6.8. The lumenal surface of the distal oviduct illustrating the transition (arrows) between the uterus (U) and the vagina (V). The utero-vaginal junction is the site where numerous sperm storage tubules are found. Note the well developed mucosal folds in both the uterus and vagina. The vaginal mucosa is pale in comparison to that of the uterus. A number of vaginal folds have been removed (star) to reveal the underlying connective tissue. 10 mm = 20 mm.

Bezuidenhout *et al.*, 1995). The calcitic shell of the egg is deposited in the uterus (Duerden, 1912).

Many sperm-storage tubules (sperm host glands), some containing sperm, are present in the lamina propria of the vagina (Bezuidenhout *et al.*, 1995; Groenewald *et al.*, 1996). These tubules are more abundant in the area nearest to the utero-vaginal junction. They are lined by a non-ciliated simple columnar epithelium (Fig. 6.9; Bezuidenhout *et al.*, 1995). The reported presence of sperm-storage tubules in the infundibulum of the oviduct of some bird species has not been confirmed in the ostrich. The vagina opens into the urodeum next to the opening of the left ureter (Duerden, 1912).

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ANATOMY OF THE CLOACA

The cloaca of the ostrich (Figs 3.2, 3.3 and 6.4) consists of three compartments: the coprodeum, urodeum and proctodeum (Duerden, 1912). The rectum is continued as the rectal pouch which enters the coprodeum (Fowler, 1991). Geoffroy-Saint-Hilaire (1822) and Gadow (1887) reported the presence of an extra rectal pouch. The rectal pouch is separated from the coprodeum by the rectocoprodeal fold, which is very well developed (Geoffroy-Saint-Hillaire, 1822; Gadow, 1887; Jolly, 1915). The coprodeum is a large sac which may be covered by a dark, tough membrane (Fowler, 1991). The ventral part of the coprodeum forms a large dilation which may act as a 'bladder' (Skadhauge, personal communication, 1998;

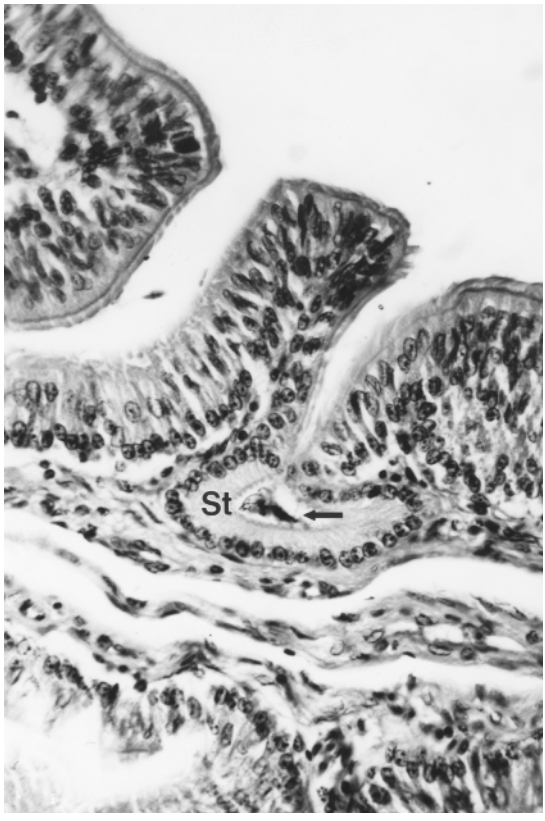

Fig. 6.9. Light micrograph showing a section of a vaginal fold close to the uterovaginal junction displaying a sperm storage tubule (St). The dark mass (arrow) in the lumen of the tubule represents sperm heads. Note the transition from the ciliated pseudo-stratified columnar epithelium of the vagina to the non-ciliated simple columnar epithelium of the sperm storage tubule. ×350.

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Bertschinger, personal communication, 1998; Soley and Groenewald, personal observations, 1997; Skadhauge and Dawson, Chapter 3). The coprodeum and urodeum are partly separated by a coprourodeal fold (Geoffroy-Saint-Hilaire, 1822).

The urodeum is short and contains the openings for the ureters, the left oviduct in the female and the two ductus deferens in the male. The openings of the oviduct and the two ductus deferens are situated ventral to those of the ureters. The opening of each ureter is situated on the summit of a small papilla (Geoffroy-Saint-Hilaire, 1822), whilst each ductus deferens opens into the urodeum at the end of a caudally pointed papilla as is the general situation in birds (King, 1981b). The uroproctodeal fold separates the urodeum from the proctodeum (Fowler, 1991).

The proctodeum forms the most caudal part of the cloaca and all excretions (urine and faeces) pass through it to the vent. The bursa of Fabricius (cloacal bursa) is located in the dorsal wall of the proctodeum. In the male the phallus lies on the ventral wall (floor) of the proctodeum.

The surface of the bursa displays numerous fossae separated by broad septa (Forbes, 1877). According to Gadow (1887) it is separated from the proctodeum by a valvular fold. Geoffroy-Saint-Hilaire (1822) and Forbes (1877) reported that the opening of the bursa is so wide that the proctodeum and cloacal bursa effectively form a single cavity. Gadow and Selenka (1891) postulated that most ratites will retain the bursa at its full size for life, a claim contradicted by the work of Forbes (1877). Geoffroy-Saint-Hilaire (1822) and Gadow and Selenka (1891) claimed that the bursa acts as a container for urine and that the ostrich therefore possesses a true urinary bladder. Some doubt as to the validity of these observations has been expressed (King, 1981b), and the dorsal location of the bursa would seem an unlikely position for a 'bladder' in the context of cloacal structure in the ostrich. According to Berens von Rautenfeld and Budras (1982), the bursa of Fabricius in the ostrich and emu forms an integral part of the dorsolateral wall of the proctodeum and does not originate as a dilation of the proctodeum.

Gender determination

Gender determination can be performed by examination of the cloaca for the presence of a phallus or clitoris. It is usually performed in juvenile ostriches and can be done by visual examination, by digital examination and by proctoscopy (Samour *et al.*, 1984; Gandini and Keffen, 1985; Fowler, 1991). Numerous authors note that sexing birds should be carefully and gently performed to prevent cloacal prolapses (Smit, 1963; Weeks and Bush, 1974; Berens von Rautenfeld, 1977; Samour *et al.*, 1984; Gandini and Keffen, 1985; Huchzermeyer, 1998).

Gandini and Keffen (1985) describe the technique for eversion of the ventral wall of the proctodeum in small birds (0.8–15 kg body mass) for visual examination. The presence of a phallus with a sulcus and visible blood vessels is used

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to distinguish males from females. Stewart (1989) points out that in young chicks the phallus and clitoris are of similar size. However, the phallus is conical in cross-section and reveals a seminal groove, whereas the clitoris is laterally compressed and lacks the groove. Stewart (1989) also notes that chicks can be sexed at any age, although the technique is easier in 1- to 3-month-old birds. Fowler (1991) describes the masculine chick phallus as being round in cross-section, 10–40 mm in length and displaying a dorsal sulcus. The female chick phallus is flat in cross-section, 5–10 mm long and may have a minimal dorsal groove. A genital mound is also present. Berens von Rautenfeld (1977) also points out that the male phallus has a palpable corpus fibrosum (cartilaginous matrix of Jensen *et al.*, 1992) which is not present in the female phallus.

In larger birds (15–54 kg body mass) digital examination is performed by introducing a finger into the vent and palpating the ventral wall of the proctodeum for the presence of a phallus. Samour *et al.* (1984) used a proctoscope in addition to digital examination. A human proctoscope can be employed to examine for the presence of a phallus on the ventral floor of the proctodeum.

CONTROL OF REPRODUCTION

Ostriches are generally considered to be seasonal breeders. However, they may also be opportunistic breeders, and in Israel egg-laying has been reported in each month of the year (Degen *et al.*, 1994). According to Mellett (1993), the breeding season in the southern hemisphere starts in March/April and extends into the spring (September) or later, although in South Africa the season traditionally runs from June to February. Wild birds in Zimbabwe are observed to lay from July to December/January, whilst domesticated South African hybrids continue laying until at least the end of February (Jarvis *et al.*, 1985). In the USA, ostriches are summer breeders but the season may extend from as early as January to as late as October (Stewart, 1989). Birds in the northern USA lay from May to September, whilst in the south birds may produce all year round (Hicks, 1992). According to some sources the breeding season is synchronized photoperiodically (Hicks, 1992; Mellett, 1993) and coincides with increasing daylight length. The observation by Jarvis *et al.* (1985) that wild ostriches in Zimbabwe lay eggs from July to December irrespective of rainfall appears to support the role of day length in regulating the breeding season. Other studies, however, note that the onset of breeding, or peaks in reproduction, coincide with periods of good rainfall and the consequent improvement of food resources (Sauer, 1972; Leuthold, 1977). Degen *et al.* (1994) argue that the onset of reproductive activity is triggered by the availability of sufficient food over a length of time and not necessarily by rainfall. South African ostriches show peak reproductive activity between August and November and lay mainly between July and December, but can continue to lay eggs until February. Degen *et al.* (1994) predicted that seasonal changes in repro-

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ductive hormone levels in domestic ostriches would be gradual, similar to those of domestic chickens rather than those of wild birds.

Reproductive endocrinology has received little attention in the ostrich (Skadhauge and Dawson, Chapter 3). Very little information is currently available regarding the endocrine control of male reproduction. It has been demonstrated (Degen *et al.*, 1994) that, in the ostrich, plasma luteinizing hormone (LH) levels are approximately three times higher in males than in females, and males show a more dramatic seasonal variation than females. Degen *et al.* (1994) determined that LH levels show an increase 1 month before the onset of the breeding season in both males and females, and then decline steadily for the remainder of the season. Testosterone levels in males show an increase 1 month after the onset of the breeding season, later than the increase in LH levels, and remain elevated for approximately 4 months. In South African birds, plasma testosterone levels in the cock peak in May (461 nmol l^{-1}) and show the lowest levels at the end of the breeding season in January (63 nmol l^{-1}; Bertschinger *et al.*, 1991).

Plasma LH levels in female birds show an increase 1 month before the onset of the breeding season and then decline steadily for the remainder of the season. By contrast, oestradiol levels, which influence egg formation, are elevated from the first month of the laying season until a month before the end of the season. There is a peak in oestradiol levels during the third month of the season which corresponds to the peak in egg production (Degen *et al.*, 1994).

FACTORS AFFECTING FERTILITY

Male infertility

Male infertility may result from using immature males (Jensen *et al.*, 1992; Irons, 1995). There are no accurate methods for determining the age of ostriches, and birds are often mated when too young (Irons, 1995). Although both sexes reach puberty at 2 years of age, reproductive maturity is only achieved in males at about 4 years old (Stewart, 1989). Females generally mature about a year earlier than males. Males can also be out of season and out of cycle. They are known to lag behind females regarding the onset of sexual activity at the beginning of the breeding season, during which time many infertile eggs are laid (Irons, 1995).

Poor libido and exhaustion of males during protracted laying periods are also factors that affect fertility. It is known that both male and female ostriches observe periods of reproductive quiescence during the breeding season. These periods may last 3 or 4 weeks and are characterized by a break in egg laying by the female and a loss of the red coloration of the male (Stewart, 1989). It is common practice in South Africa to separate males and females at this time. This forced breeding break is said to be instrumental in improving overall seasonal fertility. The arbitrary determination of this period on some farms may play a significant role in lowered egg production and fertility. A preliminary study by Soley *et*

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al. (1991) revealed that birds not subjected to a forced rest period (physical separation) within the breeding season showed a more positive relationship between good semen quality and the number of fertile eggs than birds forced to rest. Contrary evidence has been presented by Hastings (1991), who reported high infertility levels (30–60%) in seven of eight breeding pairs which were kept together all year.

Nutrition plays a major role in infertility. The most common problem is obesity in the male, which leads to decreased fertility (Irons, 1995). Deficiency of vitamins and minerals including vitamins A and E and selenium have been linked to infertility (Hastings, 1991; Hicks, 1993). Severe malnutrition is not usually a major problem, but can cause decreased fertility.

Behavioural disorders often lead to a failure to copulate. The most common problems are excessive aggression, obsessive territorial behaviour, incompatibility between males and females, and human imprinting in males (Hicks, 1993; Irons, 1995; Huchzermeyer, 1998). The role of human imprinting on reproductive success has elicited an interesting debate. Some evidence suggests that courtship behaviour directed at humans (by both male and female birds) may interfere with productive mating between ostriches (Deeming and Bubier, Chapter 4). Some reports suggest that the presence of a chosen human partner is in fact essential to stimulate copulation and to induce ovulation in females (Huchzermeyer, 1998). More information on the effects of misdirected courtship behaviour/lack of mate recognition is required to determine the impact of this phenomenon on reproductive performance.

Environmental stresses such as extreme climatic conditions (particularly high temperatures), the presence of predators and the influence of high voltage power lines have been shown to adversely affect fertility (Hicks, 1993; Jensen *et al.*, 1992). Anatomical causes of infertility include anomalies of the phallus such as absence of the seminal groove (Hicks, 1993).

Semen evaluation is deemed to be essential for the determination of male fertility (Bertschinger *et al.,* 1991, 1992). There is a definite seasonal pattern in semen quality with a peak (mean high of 77.4% morphologically normal sperm) being reached during the middle of the breeding season. Using a single semen examination for determining the breeding status of a bird can be misleading. Semen samples examined at the beginning and end of the breeding season are not true indicators of a bird's potential. A correlation has also been established between semen quality (based on percentage normal sperm) and egg fertility (Soley *et al.*, 1991).

Diseases of the reproductive system affect the reproductive capabilities of the male. Prolapse of the cloaca; prolapse of, or injuries to, the phallus; and infectious diseases such as testiculitis have been described (Jensen *et al.*, 1992; Huchzermeyer, 1998).

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Female infertility

Maturity of females is of lesser importance in poor fertility, but can play a role (Irons, 1995). However, nutrition does have an effect on laying – poor nutritional status and obesity can result in non-laying (Huchzermeyer, 1998). Low serum calcium levels and malnutrition are also responsible for egg binding (Jensen *et al.*, 1992; Huchzermeyer, 1998).

Behavioural disorders and environmental stresses similar to those affecting males also result in decreased fertility in females. Aggressive pen mates adversely affect egg laying. Human imprinting in females also plays a role, and it has been shown that females will stop laying in the absence of the farm owner or manager (Huchzermeyer, 1998; Deeming and Bubier, Chapter 4). It is also recognized that social interactions within and between breeding groups exert an important influence on reproductive behaviour, and ultimately on egg fertility rates (Stewart, 1989).

Reproductive disease is one of the most common factors affecting the reproductive capabilities of the female. Prolapse of the cloaca, prolapse of the vagina and peritoneal hernias all adversely affect egg laying (Hicks, 1992, 1993; Huchzermeyer, 1998).

Egg binding (retention) is the inability of the hen to expel the egg after formation of the shell and is a condition that can result in low egg production and infertility. Low serum calcium levels, malnutrition, cold weather, lack of exercise, nervous disturbances, tumours of the oviduct, oviduct infections, soft-shelled eggs, fright and excessive size of the egg have been given as reasons for egg binding (Jensen *et al.*, 1992; Hicks, 1993; Huchzermeyer, 1998). The situation is further complicated if the hen continues to ovulate. This results in the accumulation of eggs behind the blockage, with consequent swelling and even rupture of the oviduct.

Infections of the oviduct caused by various infective organisms reduce fertility, and oophoritis, salpingitis and metritis have been described (Jensen *et al.*, 1992; Hicks, 1993; Huchzermeyer, 1998). The symptoms of oviduct infections vary from the formation of abnormal shells to a total lack of egg production. Metritis in particular may lead to the formation of yolkless eggs, eggs with roughened surfaces, ridges, the absence of a mucin coat and soft-shelled eggs (Hicks, 1993). Egg-yolk peritonitis (the release of ova into the peritoneal cavity) and tumours have also been reported to affect reproduction (Jensen *et al.*, 1992; Hicks, 1993).

IN CONCLUSION

It is obvious from this review that a great deal of basic information is still required to provide a meaningful understanding of ostrich reproduction, particularly with a view to the application of AI in the ostrich industry. In male birds a technique

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will have to be devised for the collection of physiological semen samples so that accurate information regarding semen volume, sperm concentration and sperm motility can be obtained. Close observation of sexual behaviour, to accurately determine the number of matings per day, most favoured time of mating, etc., will also assist in defining possible AI techniques. The endocrinology of male reproduction will also have to be thoroughly studied, as well as the factors (e.g. daylight length, presence of birds of the opposite sex) influencing hormonal levels. As pointed out by Irons (1995) this type of information could be utilized for formulating hormone treatments aimed at manipulating reproductive functions. In female birds the role and function of sperm storage tubules will have to be determined, as well as whether sperm storage sites are possibly situated elsewhere in the oviduct. The timing of ovulation, identification of the stimuli which lead to ovulation, and characterization of the hormonal events surrounding ovulation (Irons, 1995) are also facets requiring scientific investigation. A thorough study of reproductive anomalies in both sexes is also urgently required.

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Factors Affecting the Success of Commercial Incubation

7

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A review of scientific reports of fertility and hatchability of ostrich eggs incubated in different countries (Table 7.1) shows that results are highly variable. Fertility ranges from very poor (<50%) through to good (>85%), but there are no reports of fertility at the higher levels commonly experienced in the poultry industry (90–95%). As a consequence, hatchability of eggs incubated is poor with maximal values at around 60%. Hatchability of fertile eggs is higher, but again at best only around 70% of fertile eggs are producing live chicks. There can be considerable variation in hatchability between farms (Deeming, 1995a) and between laying seasons (Philbey *et al.*, 1991). Whilst it is certain that individual farming operations will achieve better results than shown in Table 7.1, these data do illustrate two general problems in ostrich production, i.e. low fertility and reduced hatchability, which appear to be prevalent in farming operations worldwide. The aim of this chapter is to review those factors affecting successful artificial incubation of ostrich eggs.

Whilst the emphasis of this chapter is on problems with commercial, artificial incubation, these can be better appreciated given an understanding of the natural nesting environment of the ostrich. Therefore, the chapter starts with a brief description of the environment in which nests are built by wild ostriches and some of the environmental parameters measured under incubating ostriches. The bulk of the chapter is based around the factors which affect commercial egg production and incubation and how these impact on hatchability. Where possible, suggestions are made about how existing problems could be investigated and possibly solved.

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Table 7.1. Examples of hatchability of ostrich eggs incubated in commercial operations around the world.

Country of incubation (country of origin)	Percentage fertility	Percentage hatchability of eggs incubated	Percentage hatchability of fertile eggs	Reference
South Africa	–	50	–	Smith *et al.* (1995)
South Africa	72.9	61.8	–	van Schalkwyk *et al.* (1996)
South Africa	81.9	46.2	56.4	Cloete *et al.* (1998)
South Africa	70	70–80	–	Verwoerd *et al.* (1998)
Great Britain	74.8	24.1	31.9	Deeming (1996a)
Great Britain	42.6	27.9	48.5	Deeming (1996b)
Great Britain (Namibia)	86.7	60.0	69.2	Deeming *et al.* (1993)
Great Britain (Namibia)	67.9	39.0	58.2	Deeming *et al.* (1993)
Great Britain (Namibia)	69.2	49.2	71.1	Deeming and Ayres (1994)
Great Britain (Zimbabwe)	77.8	37.2	51.5	Deeming (1995a)
Great Britain (Bophuthatswana)	82.4	47.6	57.7	Deeming (1996b)
Great Britain (the Netherlands)	84.2	34.9	41.5	Deeming (1996b)
Australia	51.3	58.4	–	More (1997)
Australia	67.9	45.5	67.0	More (1996b)
Zimbabwe	30.0	3.3	11.1	Foggin and Honywill (1992)
USA	63	–	66	Wilson *et al.* (1997)
Israel	55	43	77	Ar and Gefen (1998)
Israel	73	58	80	Anon. (1999)

– not reported.

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NATURAL INCUBATION

Ostrich nests are found in a variety of different habitats dictated by geographical range (Deeming, Chapter 1) and include open, grassy areas, dry river beds and even woodland (Cramp *et al.*, 1977; Brown *et al.*, 1982; Jarvis *et al.*, 1985a). The nest is a simple, shallow hollow, free of lining material, usually dug in the ground by the male bird alone and often located at the approximate centre of his territory (Cramp *et al.*, 1977; Brown *et al.*, 1982). Favoured sites may be used over several years (Sauer and Sauer, 1966).

The laying season in Zimbabwe is mainly between June and October, although nests can be found at any time of the year (Jarvis *et al.*, 1985a). In Namibia most ostrich nests are found between August and October (Sauer and Sauer, 1966). Although Jarvis *et al.* (1985a) could find no particular relationship between rainfall and nest building, it is clear from their data that many nests are established during the dry season, with hatching occurring during the rainy season. In general, nests are usually established during the dry season prior to the first rains which allow for growth of vegetation, a source of food for chicks (Sauer and Sauer, 1966; Brown *et al.*, 1982). Jarvis *et al.* (1985a) showed that the number of nests in Zimbabwe found between August and December showed an approximate 6-week difference between peaks, although it was unclear why this was so. Ostriches reared outdoors in Israel lay eggs between January and October. Since the natural distribution of ostriches is on both sides of the Equator in arid areas, it seems that their laying season is 'opportunistic' rather than determined by daylight length, and thus, like the domestic fowl (*Gallus gallus*), they are good candidates for domestication and all-year-round laying.

The clutch is established by the 'major' hen who will lay the bulk of her eggs in the nest dug by the resident male. Other 'minor' females also enter the male's territory and contribute eggs to the nest, although the male may not be the father (Bertram, 1992). Eggs are generally laid during the late afternoon or early evening (Sauer and Sauer, 1966). The major female contributes between eight and 14 eggs, although clutch sizes can vary from 16 to 36 eggs (Bertram, 1992). Not all of the eggs deposited in the nest are incubated, because only around 20 eggs can be accommodated under the birds, and so a proportion are removed from the nest by the major hen (Bertram, 1992). It would appear that the major female excludes only the eggs of minor hens, although there is no suggestion made by Bertram (1979, 1992) as to how the bird can recognize her own. None of these excluded eggs hatches, and they are often taken by predators (Bertram, 1992).

The nest is attended by adult birds as the clutch is being laid (Bertram, 1992). Nest attendance by the birds is limited in the first week of laying although the birds are present during the hottest part of the day. As the clutch enlarges, the birds spend more time at the site, with the female being present during daylight hours and the male during the night. After 21 days of laying, the nest is almost never left unattended. During this time of clutch building, the birds do

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attempt to protect the eggs from predators but in many cases the nest is lost. Of 53 nests found during the study by Bertram (1992), only 22 (41.5%) reached incubation and at least seven of these were subsequently lost due to predation or fire.

One problem with leaving the eggs in an open nest is exposure to the sun, which causes the top surface of the egg to reach around 45°C at midday whilst the centre of the egg reaches over 40°C during the late afternoon (Bertram, 1992). Although the bright colour and the lustre of ostrich eggs may make them obvious to aerial predators, e.g. the Egyptian vulture (*Neophron percnopterus*), it does reflect 98% of the radiated red and near infra-red light from the sun. The eggshell also reflects 99.9% of the violet and ultra-violet light leading to selective (small) heat penetration into the egg, which is increased when the shell membranes are wet immediately after laying (Ar and Gefen, 1998). Whether this property is critical is unknown, although it can be calculated that it amounts to a heat load of 0.3–0.4 mW per egg at noon. Better camouflaged brown eggs reached a higher temperature (3.5°C higher than white eggs) during exposure to the sun (Bertram and Burger, 1981a). During the period prior to incubation, ostrich eggs lost on average 2.88 g day^{-1} (Bertram and Burger, 1981b), which for a 1500 g egg laid at the start of the clutch equates to almost 4% of its initial egg mass. None of the eggs left in an unattended nest for more than 15 days' exposure showed any embryonic development by the start of incubation (Bertram, 1992). By contrast, Jarvis *et al.* (1985b) reported that there is some development of embryos prior to proper incubation but these observations need clarification.

Incubation is carried out by the female during the day and the male during the night. As the female relieves the male only some 2 h after sunrise and leaves the nest well before sunset, the male carries out the bulk (61–70%) of the incubation (Siegfried and Frost, 1974; Bertram, 1992). It is the presence of the male sitting on the eggs throughout the night which appears to be the start of incubation proper (Bertram, 1992).

The temperature of the nest air and eggs, together with humidity readings within the nest, have been recorded in several studies (Siegfried and Frost, 1974; Bertram and Burger, 1981b; Swart *et al.*, 1987; Swart and Rahn, 1988). Nest air temperature was recorded as 31.5–31.8°C by Siegfried and Frost (1974), but averaged 36.1°C over the whole incubation period in the study of Swart *et al.* (1987). Males maintain nest air temperature at higher levels than females, despite the lower ambient temperatures during bouts of incubation (Siegfried and Frost, 1974; Swart *et al.*, 1987). These values are of limited usefulness for incubator setting since they vary with the site of measurement, e.g. they tend to be higher near the brood patch and lower close to the soil.

Temperature of the egg also varies in relation to the brood patch of the bird and the stage of development (Swart *et al.*, 1987; Swart and Rahn, 1988). The top of the egg is only 0.5–0.6°C lower than the brood patch temperature (37.8–38.2°C) throughout incubation, but the centre and bottom of the egg are several degrees lower at the start of incubation. Infertile eggs have a temperature profile that does not alter with time, but as embryos develop, the egg contents

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increase in temperature and approach the temperature of the brood patch (Fig. 7.1; Swart and Rahn, 1988). Since the young embryo tends to float to the top of the yolk to a position just under the shell, its incubation temperature is almost certainly closer to that of the brood patch than to the mean egg temperature.

The relative humidity measured in an ostrich nest averaged 41% (SD 5%, range 32–52%) with fluctuations which matched that of the relative humidity of the ambient air (Bertram and Burger, 1981b). The moisture content within the nest was higher than the ambient air (2.1 versus 1.6 kPa, respectively). Similar results were described by Swart *et al.* (1987), although the water content of the air in the nest during female, diurnal incubation, and the ambient air were lower (1.3 versus 0.99 kPa) than male, nocturnal incubation (1.57 versus 1.12 kPa for nest and air humidity, respectively). Swart *et al.* (1987) showed that although nest humidity was higher, about 60% of the variation in nest humidity could be explained by variations in ambient humidity. On average, the nest humidity throughout incubation recorded by Swart and Rahn (1988) was 1.76 kPa, compared with the ambient air of 0.63 kPa. These values are at the lower end of the range of nest humidities so far recorded for a variety of birds from a variety of nesting habitats (Rahn, 1991).

Changes in the gaseous environment have not been recorded in an ostrich nest, but can be inferred from humidity changes between the nest and ambient, egg water loss and embryonic oxygen consumption. This calculation reveals a maximal decrease in nest oxygen of up to 0.1%. It can be assumed that any stale air that develops during the sitting behaviour of the adults is released once the adult stands to turn the eggs or to swap incubation duties with its partner. Egg

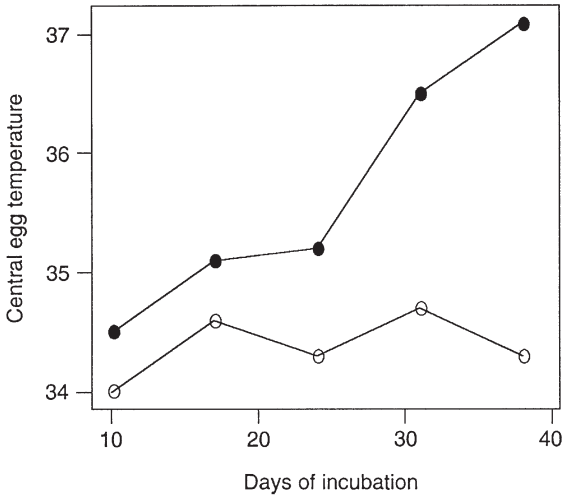

Fig. 7.1. The relationship between egg temperature and day of incubation in infertile (❍) and fertile (●) ostrich eggs incubated by adult birds. Redrawn using data from Swart and Rahn (1988).

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turning appears to be relatively infrequent in the ostrich, with the position of the eggs being regularly changed only when the male and female swap roles on the nest, although the adult will swivel on the nest, and sometimes stand and roll the eggs with its beak (Sauer and Sauer, 1966; Siegfried and Frost, 1974).

Hatching in the nest occurs after an average incubation duration of 42–43 days and over 4–5 days (Sauer and Sauer, 1966; Jarvis *et al.*, 1985a; Bertram, 1992). Jarvis (1994) reports that adult birds aid chicks in externally pipped eggs to hatch by crushing the shell with their sternum, but this report requires clarification. The chicks call out during hatching (Sauer and Sauer, 1966) although it is unclear to what extent this helps to synchronize the hatch of the clutch.

It should be noted that if we accept the fact that in nature, population sizes are more or less stable, then on average each adult ostrich is replaced during its life span by only one other, and all others must perish as eggs, chicks or young. Thus different rules would apply to incubation success in nature, compared to artificial incubation 'success'.

COMMERCIAL ASPECTS OF EGG PRODUCTION

Chemical composition of eggs

Although the chemical composition of ostrich eggs has been described in some detail (Osuga and Feeney, 1968; Feeney and Allison, 1969; Deeming, 1993; Angel, 1995; Sales *et al.*, 1996), very little research has been involved in determining whether nutritional components of ostrich eggs influence hatchability, although cases of club-down, normally associated with riboflavin deficiency in the egg, have been reported (Deeming, 1997).

One interesting project compared the lipid composition of egg yolks from farmed ostriches with that of yolks from eggs laid by birds living wild on a game ranch and with access to natural vegetation (Noble *et al.*, 1996). There were no differences in the total lipids and proportions of lipid fractions, but significant differences were observed in the fatty acid profiles of the yolks. In the yolks from wild birds, all of the lipid fractions exhibited substantial concentrations of 18-carbon polyunsaturated fatty acids. In eggs from farmed birds the amounts of linolenic acid were only 10% of those observed in wild eggs. Similar levels of linolenic acid were also recorded in the yolks of ostrich eggs laid in Germany (Reiner *et al.*, 1995). It has not been possible to date to link poor hatchability of farmed eggs with these differences in yolk composition, but it is known in poultry that an imbalance in essential fatty acids influences hatchability (Noble *et al.*, 1986). Further research on nutritional deficiencies in ostrich embryos is required.

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Egg size

The ostrich egg is unusual for its large size, averaging 1545 g with a range of mass of 1–2 kg (Deeming, 1993). One sample of almost 17,000 eggs from Israel had an average mass of 1461 g (SD 163 g; Ar *et al.*, 1996). This makes the ostrich egg the largest laid by a living bird, yet it is also one of the smallest in proportion to the body mass of the female (Rahn *et al.*, 1975; Bertram, 1992; Deeming, 1993). This large egg size is interesting in a general zoological context, but it also has an important impact on commercial artificial incubation.

The range in mean egg mass for all other species of birds (from hummingbird to emu) is around 700 g with a range in incubation periods of around 40 days. Allometric relationships (Rahn and Ar, 1974) suggest, however, that the duration of incubation of a 1500 g ostrich egg should be 58.8 days when based on egg mass alone, or 50 days when water vapour conductance of the eggshell is included in the calculation. By contrast, the ostrich embryo has an incubation period of 42 days and typical variation around this mean is only 2–3 days, despite the considerable range in egg mass. Therefore, compared with other birds, the duration of incubation is considerably shorter than predicted from egg mass.

Ar and Gefen (1998) have shown that the rate of organ differentiation during the first half of incubation is fast, relative to that described for the fowl (Table 7.2). Moreover, the relative rate of growth during this period is much slower in the ostrich embryo. At 65% of the incubation duration, the ostrich embryo has attained a dry mass of only 19% of the dry hatchling mass, compared with a value of 32% in the fowl embryo. By contrast, during the last 35% of the incubation duration, the rate of mass gain is much faster than for other species. Furthermore, the ratio of true hatchling to residual yolk is 44:56 in the ostrich hatchling compared with 54:46 in the fowl (Ar and Gefen, unpublished observations, 1998). The ostrich embryo appears to have been able to accelerate development and hatches with relatively more residual yolk than typical precocial species. The reasons behind this strategy are unclear, but may lie with reduction of predation pressure on adults during incubation.

The differences in egg mass in the ostrich have interesting implications for the rates of embryonic growth in individual eggs. Hatchling mass (65.6% of initial egg mass) from a 1200 g egg would be 787 g, compared with 1180 g hatchling from a 1800 g egg. The difference in incubation period is only 3 days (Deeming *et al.*, 1993). For the fowl egg, mass has no influence on embryonic mass at 12 days (Burton and Tullett, 1985) and so at 21 days of development the ostrich embryos in the two egg sizes will have a mass of around 19 g (Ar and Gefen, 1998). Therefore, the average rate of growth of these two embryos during the second half of development would be 37 g day^{-1} for the 1200 g egg, and 55 g day^{-1} for the 1800 g egg. This variation in embryonic growth rates poses the questions: how is the rate of embryonic growth controlled?; and how does the embryo 'know' how large its egg is (and hence its final body mass)? Such questions certainly apply in other species but the effects are exaggerated in the ostrich, making it ideal for research in this field.

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Table 7.2. A comparison of timing of developmental stages between ostrich and fowl embryos. From Ar and Gefen (1998).

Hamburger and Hamilton (1951) stage		Days (and percentage time) from initiation of incubation			
		Fowl (37.5°C)		Ostrich (36.5°C)	
18–23	Beginning of allantois development	3–4	(14–19)	7–8	(17–19)
21–22	Appearance of eye pigmentation	3–4	(14–19)	7–8	(17–19)
27	Initiation of grooves between fingers	5–5.5	(24–26)	11–12	(26–29)*
	Appearance of nostrils			13–14	(31–33)
34	Appearance of nictitating membrane	8	(38)	13–14	(31–33)*
34	Completion of the scleral papilla circle	8	(38)	15–16	(36–38)
34	Initiation of feather germs on head dorsal side and thighs	8	(38)	15–16	(36–38)
35	Bending of the maxilla over the mandible	8.5–9	(40–43)	17–18	(40–43)
38	Eyelid covers about 2/3 of eyeball	12	(57)	21–22	(50–52)*
38	Appearance of scales on leg	12	(57)	21–22	(50–52)*
46	Hatching	21	(100)	42	(100)

* Denotes a deviation from the fowl model.

The problem of egg mass is of particular importance in artificial incubation. Ideally, incubators should accommodate a majority of eggs which vary little from the average, so that in multi-stage incubators (i.e. batches of eggs containing several stages of development within the same machine), single settings for temperature and for humidity would produce a suitable incubation environment for most of the eggs. The wide range in egg mass in the ostrich poses a problem for incubation. It will not be possible to provide an optimum environment for eggs of 1200 or 1800 g within an incubator set for an average egg mass of 1500 g. The different surface area:volume ratios of the differently sized eggs mean that temperature profiles of the eggs may differ, with larger eggs of higher metabolic rate retaining more heat. A 15% loss of the initial mass for a 1500 g egg will be achieved for one humidity setting, but it is likely that this setting will be unsuitable for smaller and larger eggs of different water content and shell conductances, which may lose too much and too little mass, respectively. In practice, larger ostrich eggs do have a lower hatchability (Krawinkel, 1994; Deeming, 1995a,

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1997). Ar *et al.* (1996) showed that hatchabilities of large and small eggs are 28 and 14%, respectively, lower than average eggs. The problem of egg size also extends to the practical problem of whether the eggs will fit within the egg trays in the machine.

Fertile eggs which did not hatch showed a significant negative correlation between initial egg mass and percentage mass loss at external pipping time ($r=-0.379$; $P<0.01$, DF=65; Deeming, unpublished observations, 1998). There was no such correlation in eggs which hatched. If an average humidity is used during incubation, and if all eggs would have the same area-specific water vapour conductance, it would cause small eggs to dehydrate and larger eggs to retain too much water. However, this was shown not to be the case, since Ar *et al.* (1996) found no correlation between egg mass and shell conductance. Commercial incubation of ostrich eggs is unlikely to improve unless there is greater uniformity of water loss from the eggs incubated. This can be achieved by utilizing different incubator humidity settings for eggs with different shell conductance or size characteristics (Meir and Ar, 1987, 1991; Ar *et al.*, 1996), or by restricting the range in egg mass and shell water vapour conductance by selection at setting, with eggs at the extremes being discarded.

Eggshell structure

The eggshell not only acts as physical protection for the embryo during development, but is also a mediating barrier in the exchange of water vapour and respiratory gases (Paganelli, 1991). The eggshell in the ostrich is hard and brittle, compared with a tough and more flexible shell found in the fowl (Bond *et al.*, 1986). When placed vertically between two parallel plates, ostrich eggs yield to compression at about 76 kg (Ar *et al.*, 1979) creating concentric (not radial) cracks which advance across the shell at a 45° angle to the surface, indicating shear force action. This eggshell structure is considered to be correlated with the hatching sequence in the ostrich, where the pip hole is very large, the angle of rotation by the embryo is only 90°, and the shell is largely destroyed (Bond *et al.*, 1988; Deeming, 1995b). The shell is, therefore, an important aspect of overall egg quality, and problems with shell thickness, composition, porosity and integrity can greatly influence the outcome of development.

The ultrastructure of the eggshell has been described several times (Tyler and Simkiss, 1959; Sauer *et al.*, 1975; Christensen *et al.*, 1996; Sparks and Deeming, 1996; Mikhailov, 1997; Richards and Richards, 1998a, b) with a fair degree of agreement between the different studies. There are two shell membranes (measuring 30 and 100 μm in thickness for the inner and outer membranes, respectively) consisting of proteinaceous keratin-like fibres measuring 2 μm in diameter (Sparks and Deeming, 1996). The calcitic shell has three distinct zones: cone, palisade and surface crystal layers (34, 64 and 2% of the shell thickness, respectively) with an organic matrix of hollow columns lying within the crystal structure (Sparks and Deeming, 1996), although Richards and Richards (1998a) were

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unable to find such a structure. The pores are complex, branching from a single opening on the inner side to a few openings on the outer side, usually within a shallow groove (Tyler and Simkiss, 1959; Tullett, 1978).

Some authors (Sauer *et al.*, 1975; Christensen *et al.*, 1996; Richards and Richards, 1998b) report that a cuticle is present, but Sparks and Deeming (1996) suggest that it is absent and the outermost structure in the eggshell is the surface crystal layer, measuring approximately 4 μm thick. Careful examination of published scanning electron micrographs (Sauer *et al.*, 1975; Christensen *et al.*, 1996) would support this idea but there is scope for a detailed study to clarify this disagreement.

Abnormal shells described by Sauer *et al.* (1975) were all commonly associated with failure of normal embryonic development, although some shell defects were less serious. Eggs with shells exhibiting linear pore grooves did allow normal development. Failure in the processes of shell formation, producing either excessively thick or thin shells, compromises the ability of the shell to act as an appropriate barrier between the embryo and the incubation environment. In particular, it affects shell gas and water vapour conductance and the efficiency of the shell to act as a physical barrier to microbial contamination (Deeming, 1995a, 1996a).

Button *et al.* (1994) classified the quality of the shells of eggs which failed to hatch in a sample of 408 eggs. Around 20% of the eggs had rough shells, 16% had matt or chalky shells, 22% had thin shells (at the equator <1.47 mm) and 10% had high pore counts at the equator of the egg (>27.6 pores cm^{-2}). Satteneri and Satterlee (1994) also found that high and low pore numbers in ostrich eggshells were associated with reduced hatchability. Unfortunately, it is often the case that almost all ostrich eggs collected are set to incubate irrespective of their quality. Deeming (1997) advocates that selection and management of hatching eggs is very important in determining the overall success of a commercial operation. Selection against and removal of cracked or deformed eggs, together with those having poor quality shells, i.e. chalky, wrinkled, or excessively dimpled, will in the long run increase the success rate of those eggs which are incubated.

Egg production

The success of ostrich farming depends largely on the production of fertile eggs. Nevertheless, there have been few reports of either rates of egg production or fertility of ostriches maintained on farms. Those reports which do describe these aspects of incubation (Table 7.1) show that, compared with poultry (Hodgetts, 1991), ostrich breeding has a long way to go to improve performance.

Egg production per hen in Oudtshoorn, South Africa is only 50 ± 20 eggs during a June–February season of 120 laying days (Smith *et al.*, 1995). The breeding performance of pairs of ostriches was recorded by van Schalkwyk *et al.* (1996) over five breeding seasons (1990–94) in South Africa. The average yearly egg production per hen was 55.5 eggs (SD 26.2) although the length of the breeding season differed from year to year. Egg production performance (EPP), i.e. the

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number of eggs laid expressed as a percentage of the number of days on which eggs could be laid, was used to normalize results. The average EPP was 46.1% (SD 20.8%) with a range of 0–93.2% for individual pairs and shows a strong dependence effect. The EPP of individual pairings during the first breeding season could be used to predict the EPP in subsequent years (average EPP in subsequent years = 7.81±0.763 EPP in first breeding season); EPP was negatively correlated with infertility and positively correlated with hatchability, and had a repeatability coefficient of 0.47.

An EPP of 43.8% (SD 21.9%) was found for the same South African birds recorded from 1990–1996 (Cloete *et al.*, 1998). The EPP of the breeding birds increased from an initial value of 30% at 2 years of age to a peak of 60% at 9 years, but showed a slow decline thereafter to around 45–50% at 17 years of age. EPP had a repeatability coefficient of 0.42.

The bulk of egg production in Israel is between mid-February and September (Ar, 1996). Degen *et al.* (1994) reported that in a small experimental flock in southern Israel, over a 7-month laying season EPP was only 29.2%. Other studies of productivity in commercial flocks in Israel record EPP of mature birds to be 54% (Anon., 1999).

In Queensland, Australia, the bulk of the breeding season was between July and March (More, 1996a). The productivity of farmed ostrich hens in Australia was very low, with over 50% of hens maintained in pairs not laying any eggs during the season studied (July 1993 to June 1994). Only 910 eggs were laid in a year by 61 hens, and 88.8% were laid by birds maintained in pairs. Productivity of the 33 hens never maintained in a trio or a larger group was very low, and 18 of these birds did not lay during the study period. Productivity was higher for older hens. More (1997) recorded egg production of 38 hens and found that the average was only 2.4 eggs laid per hen per month (EPP=16%).

In Britain, hen productivity was reported for the 1995 laying season on one farm with a total of 43 laying birds (Deeming, 1996a). EPP of the flock over the entire season was only 25.2%. The period of highest egg production was between mid-April and mid-September. Mean EPP values for individual breeding enclosures varied from 25.7 to 73.0%, with larger breeding groups producing fewer eggs per hen per week. EPP of individual birds generally ranged from 25.7 to 69.4% and only one hen (in a trio) was laying at close to her potential (EPP was 91.2%). Within trios, the two hens did not usually contribute equal numbers of eggs. Furthermore, increases in productivity were observed for individual birds from the 1994 to the 1995 season, and for individuals after one female was removed from an established trio of birds. Environmental stresses such as sudden rain or sudden heat spells can reduce egg laying temporarily (Anon., 1999).

Such poor results for egg productivity will need to be addressed if ostrich farming is to become more profitable. Factors determining egg production have not been investigated, although the courtship behaviour of the ostriches appears to be important (Deeming and Bubier, Chapter 4), and this is certainly an area for further investigation.

A few reports suggest that the pattern of egg laying may influence hatcha-

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bility. Wilson *et al.* (1997) report that, in the USA, hatchability of ostrich eggs dropped as the breeding season progressed. Deeming (1996a) showed that when egg numbers were low, i.e. at the start and end of the season, then hatchability was very low, although this may reflect low rates of fertility or unfavourable conditions in partially empty incubators.

Fertility

Reports from around the world (Table 7.1) suggest that the fertility of ostrich eggs is highly variable, with average values being low relative to other poultry species. Very few studies have examined the fertility of commercial ostriches and this certainly is affecting development of the ostrich industry. Determination of true fertility is important, because candling at 14 days will show which eggs are not developing but does not indicate which eggs contain young dead embryos. A pilot study in Israel shows that some of the eggs considered infertile are actually fertile eggs in which the embryo died at a very young age (Ar, unpublished results, 1998). There is a need to open eggshells to confirm the absence of any embryonic development.

Fertility of ostriches at the Oudtshoorn Experimental Station, South Africa, averaged 82.9%, but there was a range of 0–100% in those studied by van Schalkwyk *et al.* (1996). Cloete *et al.* (1998) reported that fertility was 81.9% in the same ostriches, recorded over a longer time period. In Australia, fertility for ostriches on 38 farms was an average of 51.3% (More, 1997). A smaller selection of 12 farms had slightly better results (68.1%), but fertility varied considerably between farms (27.4–91.2%; More, 1996b, 1997).

On a British farm, weekly fertility rates during the 1995 season averaged 74.8% (SD=15.3%) for ostriches maintained in a variety of breeding situations (Deeming, 1996a). It started from a low of 50% at the beginning of the season, and rose to a plateau of over 80% by week 10 of laying, which was maintained until around week 26 of lay. Thereafter, fertility was variable, although high fertility was usually associated with high rates of lay. Over the season there was no significant correlation between the number of females in a breeding group and the fertility of the eggs produced in that group, although on average pairs and trios did produce more eggs per hen than birds in larger groups. The average weekly fertility of individual hens ranged from 32–100%.

Factors determining the fertility of these ostriches have yet to be fully investigated but will certainly include behavioural considerations. Deeming (1996a) reports that when in each of two enclosures one of the resident hens in the trios was killed, fertility of the eggs from the enclosure significantly increased. Mate compatibility and freedom from interference in courtship will be important factors in determining whether mating takes place (Deeming, 1997; Deeming and Bubier, Chapter 4). Furthermore, Bubier *et al.* (1998) found that high rates of courtship behaviour of male ostriches towards humans were negatively correlated with fertility of eggs. Despite these studies, the reasons why fertility is generally

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low and variable in ostriches remain unclear, and considerable research is needed in breeder bird management before the fertility of ostriches will approach that observed in poultry.

Embryonic development

Until recently, descriptions of embryonic development of the ostrich were generally photographic representations of changes observed during candling, with pictures of embryos at different stages of development (van Schalkwyk *et al.*, 1994; Buhr *et al.*, 1996). Older studies (Lutz, 1942) simply described development of particular organs in the ostrich embryo. Our understanding of the pattern of development in the ostrich embryo has been strengthened by Ar and Gefen (1998) who removed embryos on alternate days during incubation for morphometric analysis. Equations now exist for relating parameters such as mass, wing, leg and body length to the length of incubation (Fig. 7.2). The curvilinear pattern of embryonic growth reported by Smith *et al.* (1995) and Deeming (1997) is confirmed by Ar and Gefen (1998). These data will be valuable for ageing embryos in studies of the pathology of ostrich eggs.

Embryonic mortality in avian species appears to follow a pattern typified by the fowl embryo (Insko and Martin, 1933), with one mortality peak during the first few days of development and a second, larger peak during the last few days of incubation. This pattern has been described for the ostrich (Deeming, 1995a) although there can be variations on the pattern pathology depending on the

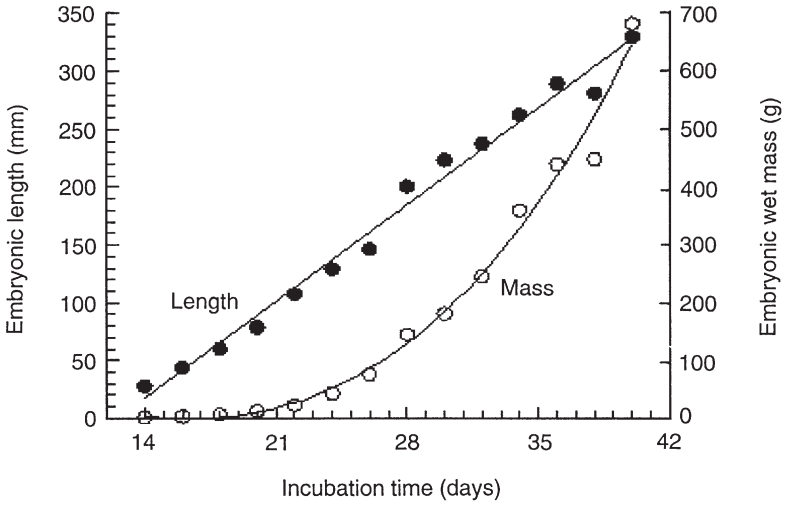

Fig. 7.2. The relationship between embryonic length and wet mass, with incubation time. Mass=134.17−12.14Time−0.02Time^2+0.016Time^3, R^2=0.985; length=–149.35+11.92Time, R^2=0.987. Data from Ar and Gefen (1998).

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causes of mortality, e.g. storage or microbial contamination (Deeming, 1996b). Ar *et al.* (1996) found it difficult to distinguish between early dead embryos and infertile eggs, but showed a definite mortality peak in the last week of incubation.

The incidence and causes of malformations and other developmental abnormalities in the ostrich are poorly documented. Near-term twin embryos are described by Brown *et al.* (1996) and Deeming (1997). Brown *et al.* (1996) reported that only seven embryos, out of a total of 111 studied, showed gross deformities, with four embryos having leg deformities, two having defects of the bill and one being anopthalmic.

Malpositioning is a common problem in dead-in-shell eggs (Deeming, 1995b). Deeming (1997) reported that the incidence of malpositions was 36.9% of the dead-in-shell embryos (Table 7.3). Most of these malpositions were rotational problems, where the embryo was incorrectly positioned relative to the air space, the biggest problem being the head of the embryo positioned at the end of the egg away from the air space. Deeming (1995b), Ley *et al.* (1986) and Button *et al.* (1994) also report that 'head-in-the-small-end' is the commonest malposition. Brown *et al.* (1996) found a high incidence of malpositioning (51 of 93 embryos examined) with rotational problems being commonest. Similar problems were reported by Badley (1996), although the incidence of different malpositions was not described. The reasons for such a high rate of malpositioning are unclear. Certainly, improper turning and errors in positioning the eggs in the incubator because of difficulties in identifying the blunt end can increase the incidence of malpositions in poultry eggs (Deeming, 1991).

Table 7.3. Incidence of malpositions in ostrich embryos which died during the 6th week of incubation. Data from Deeming (1997).

Condition	Frequency	
Died in 6th week	255	
Total malpositions	94	(36.9% of mortality)
Head in small end (180° rotation)	43	(45.7% of all malpositions)
90° rotation	27	(28.7% of all malpositions)
45° rotation	7	
135° rotation	6	
Leg on head	4	
Head between legs	3	
Others	4	

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A common problem with ostrich incubation is the practice by many farmers of assisting chicks to externally pip and hence to hatch (Burger and Bertram, 1981; Jarvis, 1994; Deeming, 1997). Often these chicks are associated with eggs which have lost insufficient or too much moisture during incubation (Ar *et al.*, 1996). Furthermore, Deeming and Ayres (1994) report high mortality of assisted chicks with poor growth rates in the survivors. Although adult ostriches were reported to help crack their eggs after external pipping (Jarvis, 1994), this practice should be discouraged in breeding programmes because there is a danger that weak genetic lines, which are unable to hatch unassisted, are perpetuated in the breeding stock instead of being identified and culled.

FACTORS AFFECTING COMMERCIAL HATCHABILITY

Microbial contamination

In a study of near-term embryonic mortality of ostrich eggs in South Africa, bacterial contamination was observed in 13.4% of the eggs examined and the organisms isolated were typical of soil and faecal environments (Brown *et al.*, 1996). In Australia, 26.5% of dead-in-shell eggs had microbial contamination, most of which were of a faecal origin (Button *et al.*, 1994). Eggs incubated in Zimbabwe showed a high incidence of microbial contamination, with 45% of infertile and 67% of dead-in-shell eggs being infected with a variety of soil and faecal bacteria and fungi (Foggin and Honywill, 1992). Eggs imported into Britain from Zimbabwe also showed a high rate of microbial contamination (Deeming, 1995a); 22.8% of all eggs and 36.3% of fertile eggs were infected with bacteria and/or fungi, although the contamination rate of eggs varied according to which farm supplied the eggs. The organisms isolated were all of soil and faecal origin. Deeming (1996b) found that eggs from a variety of sources (Bophuthatswana (South Africa), the Netherlands and Britain) had rates of microbial contamination of 18–20%. The incidence of fungal contamination was higher in eggs in which the embryo had survived to the end of development. In Britain the contamination rates of eggs laid during the 1995 season were very high, with a third of all eggs incubated being contaminated (Deeming, 1996a). The proportion of eggs contaminated varied between breeding enclosures (2.8–60.7%) and between individual hens (7.0–57.7%). On a weekly setting basis of fertile eggs there was a significant negative correlation ($r=-0.873$, $P<0.001$, $DF=23$) between percentage hatchability and percentage contamination (Deeming, 1996a).

Shell properties are very important in determining the risk of microbial contamination. Shells with high conductance values have a higher risk of contamination. Deeming (1996b) found that in two of three samples, eggs with microbial contamination had average percentage mass loss values which were significantly higher than those observed for uncontaminated eggs. This relationship is confirmed

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by a significant correlation between the percentage of eggs containing microbial growth in different water loss categories (Deeming, unpublished data, 1998).

Sanitation programmes for ostrich eggs are invariably based on procedures employed for poultry eggs, and vary from egg washing through to simply brushing off soil (Deeming, 1997). van Schalkwyk *et al.* (1998) compared hatchability of eggs disinfected using exposure to UV light, or washed with either a peroxide- or quaternary ammonium-based product. The UV light maximized hatchability, but it was not different to that obtained from untreated controls. The washing disinfection procedures appeared to depress hatchability by 6–10% due to increased early mortality (van Schalkwyk *et al.*, 1998). Given their shell characteristics, there is a need for additional research to develop an appropriate sanitation programme for ostrich eggs.

Pre-incubation storage

The importance of storage of ostrich eggs to the ostrich industry cannot be underestimated. The seasonal nature of laying in ostriches requires that eggs be stored in the beginning and at the peak of the laying season to overcome incubator capacity problems (Ar, 1996).

In the wild, a clutch of ostrich eggs often numbers between 10 and 12 eggs (Bertram, 1992). This means that the first egg laid in the clutch has spent 18–22 days exposed to the elements before incubation is started. In a farming environment, regular removal of eggs means that the laying season extends over several months. This is characterized by low egg production by the flock at the beginning and end of the season, with a peak in production during the middle of the season (Ar, 1996; Deeming, 1996a). It is often the case that eggs are stored for up to a week before being artificially incubated. At the start and end of the season, storage may be even longer in order to ensure that sufficient eggs are set.

Research into the effects of pre-incubation storage is limited and most commercial practice in relation to storage is derived from the poultry industry. Although the difference only approached significance, ostrich eggs collected in the evening had lower mortality than eggs collected during the following morning (van Schalkwyk, 1998), confirming the suggestion of Deeming (1995a, 1996a, b, 1997) that ostrich eggs should be collected soon after laying so as to minimize the incidence of microbial contamination and other factors which reduce egg quality. Egg position (i.e. with the air space at the top or bottom, or with eggs held with long axis horizontal) did not affect embryonic mortality of ostrich eggs stored for up to 6 days (van Schalkwyk, 1998).

Swart (1978) showed that ostrich eggs stored at temperatures of 20–23°C for up to 14 days showed little decrease in viability, whereas longer periods of storage caused a significant depression in hatchability. In one batch of ostrich eggs from the Netherlands, Deeming (1996b) showed that as storage period (exact conditions not known because the eggs were supplied by a commercial source) increased, the hatchability of eggs set decreased from around 60% at 9–10 days'

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storage to zero at 17 days. Deeming (1996b) showed that for 12–14 days of storage there was only 50% hatch of fertile eggs, and this was associated with high early mortality (1–7 days) rather than late mortality. Wilson *et al.* (1997) showed a similar decline in hatchability in two sets of eggs stored for varying lengths of time, with increasing storage periods causing an increase in the age of dead embryos.

In Israel, storage of eggs at 15–16°C for periods of 1–7 days showed that hatchability of fertile eggs was depressed by up to 4%, for eggs stored for either 1 day or for 6–7 days (Ar and Gefen, 1998). This depression in hatchability was associated with an increase in early mortality. Ar and Gefen (1998) suggest that ostrich eggs may benefit from a storage period of only 3–4 days. By contrast, the hatchability of eggs stored at room temperature (mean of 20°C) for up to 7 days was not significantly decreased by the length of storage (Deeming, personal observations, 1998). van Schalkwyk (1998) showed that storage temperature was a key factor in determining embryonic viability. Embryonic mortality was lower at a storage temperature of 17°C than at 25°C, although at neither temperature was mortality affected by a 12 h period of incubation before storage. The temperature of storage also affected the size of the blastoderm after 7 days' storage, with the diameter doubling with each degree increase in storage temperature from 25 to 27°C (van Schalkwyk, 1998).

As has been reported by Meir and Ar (1998) for poultry eggs, there appear to be beneficial effects of pre-heating of ostrich eggs prior to storage (Brand *et al.*, 1998). Heating to 36°C for 4 h prior to less than 6 days' storage at 17°C significantly increased hatchability by around 8%, by significantly reducing the percentage of late deaths. By contrast, pre-warming of stored eggs to 25°C for 16 h prior to incubation had no significant effect on hatchability.

Temperature

The incubator temperature adopted for artificial incubation of ostrich eggs has usually been determined in the past with little scientific investigation. Deeming (1993) found that most studies used an incubation temperature of between 36.0 and 36.5°C, although eggs have been successfully incubated at temperatures ranging from 35.0–37.0°C. Incubation of eggs at a variety of temperatures between 36.0 and 36.7°C has shown that incubation at 36.4°C allows 50% of all chicks to hatch at 42 days (Ar *et al.*, 1996). The duration of incubation to 50% hatch (I, days) is primarily a function of incubator temperature (T, °C) in forced draught incubators ($I = 1875.80 - 98.06T + 1.31T^2$; Ar *et al.*, 1996). Ostrich eggs incubated in a home-made room kept at 35°C had an incubation period longer by 2–3 days as compared to incubation at 36°C (Jarvis *et al.*, 1985b). A higher starting temperature (37°C) during single-stage incubation reduced the average incubation period by almost 3 days over a constant temperature of 36.0°C (Deeming *et al.*, 1993).

In nature, the top of the ostrich egg adjacent to the brood patch averages

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37.4°C (Swart *et al.*, 1987; Swart and Rahn, 1988). Therefore, from the start of development the embryo floating on the top of the yolk is close to the temperature experienced by other avian embryos, even though the rest of the egg is at a lower temperature. As development proceeds, heat distribution through the circulatory system (Turner, 1991) and increasing embryonic size and metabolism cause a rise in the average temperature of the egg. Hence the temperature of the centre of the egg approaches that observed at the brood patch (Fig 7.1; Swart and Rahn, 1988).

The normal air temperature adopted during artificial incubation is around 1°C lower than that of 37.0–37.5°C used in artificial incubators for poultry eggs. In free convection incubators, near the end of development the egg content surface temperature under the shell exceeds that of the surrounding air by about 2°C (Meir and Ar, 1990), calling for different temperature control in such incubators. The large size of the ostrich egg means that its relatively low surface-area-to-volume ratio gives it a relatively high thermal inertia: the time constant of an ostrich egg is about 2.75 h which can be compared with that of the fowl, *circa* 0.75 h (Turner, 1985; Meir and Ar, 1990). Thus there is a tendency for metabolic heat to accumulate within the egg which potentially can cause overheating of the embryo. A low incubation temperature is not essential for incubation of ostrich eggs because single-stage temperature profiles, which have started at over 37.0°C with a continuously reducing temperature during the first half of development, have produced viable chicks (Deeming *et al.*, 1993; Deeming and Ayres, 1994; Deeming, 1995a). It is likely that the optimum incubation temperature of 36.4°C, which produces an incubation period of 42 days (Ar, 1996), represents a compromise between the high temperature permitted during early development when metabolic heat production is low and offset by evaporation, and a lower temperature, for egg cooling, during the last third of incubation.

The quality of incubation equipment can be of great significance in the success of artificial incubation. In the Little Karoo in South Africa only 5% of eggs are hatched in modern machines, and older wooden incubators with different temperature settings still prevail despite the problems with cooling of the eggs (Smith *et al.*, 1995). A temperature of 37.3°C was recorded in one old incubator and was associated with hatchability of 44%. Smith *et al.* (1995) make the sensible suggestion that eggs should be moved away from warmer areas as they develop. Problems arise with older equipment because of the systems employed to remove metabolic heat from the eggs and because of poor humidity control: fresh air brought into the machine may be too high in temperature, and/or water cooling systems linked into the control mechanism may cause too high humidity, especially if the surrounding room in which the machine stands is not air-conditioned and/or dehumidified.

The use of single-stage incubation (i.e. only one batch of eggs is incubated in the incubator at any time) has been attempted with ostriches, but the temperature profiles are quite crude (Deeming *et al.*, 1993; Deeming and Ayres, 1994; Deeming, 1995a). Given the potential advantages for matching temperature and humidity to particular batches of eggs at a particular stage of development, this

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type of system is certainly of interest for further research. Theoretical considerations on the requirements for single-stage incubation have been described by Ar (1996).

Exchange of water vapour

In an investigation of the environmental conditions within wooden incubators used in South Africa, Burger and Bertram (1981) found that the humidity within them was much higher than that measured within an ostrich nest (63 versus 41–43% RH, respectively). Not surprisingly, the rate of water loss from eggs incubated in the incubators was lower than that in the nest (2.8 versus 3.8 g day^{-1}, respectively), and this was considered a significant problem contributing to lower hatchability of artificial incubation. Other studies have shown that low mass loss usually results in oedemic hatchlings or dead-in-shell embryos (Ley *et al.*, 1986; Deeming, 1995b).

Gas and water vapour movement across the eggshells occurs by diffusion via the multi-branched pores in the shell and is controlled by Fick's Law (Ar *et al.*, 1974). The total apparent pore area of an ostrich eggshell is 78.9 mm^2, and the average number of pores is 11,196 with a pore radius of 52.5 μm. These values are very different from those predicted from allometric relations of other birds (61,000–128,000 for pore number and 14–20 μm for pore radius; Ar and Rahn, 1978). The air space end of the egg has 20.2 pores cm^{-2} with average values of 18.3 at the equator and 17.7 at the 'sharp end' (Christensen *et al.*, 1996).

Satteneri and Satterlee (1994) showed that relatively high and low pore numbers were associated with reduced hatchability of ostriches, with a dramatic loss of hatchability in eggs which lost too much water during incubation. The importance for hatchability of water loss during incubation has been demonstrated by Deeming (1994, 1995a, 1997). The range of recorded percentage water losses was from 7 to 24%, but embryonic mortality was not uniformly spread across this range. Between 8 and 18% water loss, hatchability was relatively high (at least 50%), but for eggs of both lower and higher water loss, mortality was usually close to 100%. A set of fertile eggs ($N=806$) incubated in a multi-stage system during the 1995 season (Deeming, 1996a) showed a normal distribution for percentage water loss around a mean of 12% to external pipping (Deeming, unpublished observations, 1998). The highest embryonic mortality was in those eggs with the lowest and highest percentage water losses (<7 and >17%, respectively; Deeming, unpublished observations, 1998). Similar results have been reported for a larger number of eggs in South Africa (Blood *et al.*, 1998); between 10 and 18% water loss embryonic mortality was 20% or less. By adjusting water losses of high-conductance eggs, embryonic mortality can be reduced to control values, but this was only partially successful in low-conductance eggs, showing that O_2 supply in such eggs remains a problem (Ar *et al.*, 1996).

Christensen *et al.* (1996) reported that water vapour conductance of seven ostrich eggshells was 795.8 mgH_2O day^{-1} kPa^{-1}, which is lower than that measured

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by Ar *et al.* (1996) who found that the average conductance of almost 10,000 eggs was 1173.8 (SD=347.3) $mgH_2O\ day^{-1}\ kPa^{-1}$. Deeming (1995a) measured water vapour conductance of 250 eggs to be 945.8 (SD=232.5) $mgH_2O\ day^{-1}\ kPa^{-1}$. The water vapour conductance of a 1500 g ostrich egg is predicted to be 1100 $mgH_2O\ day^{-1}\ kPa^{-1}$ (Ar and Rahn, 1978). As was pointed out by Deeming (1995a), mass specific water vapour conductance (G_{sp}) should be calculated so as to take egg mass into account. Average values for G_{sp} are 664.7 (Deeming, 1995a) and 785.3 $mgH_2O\ day^{-1}\ kg^{-1}\ kPa^{-1}$ (Ar *et al.*, 1996). Both low and high values for G_{sp} were associated with high embryonic mortality (Deeming, 1995a; Ar *et al.*, 1996). The duration of incubation is also affected by G_{sp}, with high-conductance shells allowing faster development than average and low-conductance shells (Fig. 7.3).

The loss of water vapour from an egg is dependent on both the water vapour conductance of the eggshell and the partial pressure difference between the inside and outside of the egg (Ar *et al.*, 1974). In practical terms the shell conductance is relatively fixed, although a decrease of around 5% on weeks 3 and 4 of incubation, then rising to 11% above initial values at the end of incubation, was found only in fertile eggs (Ar *et al.*, 1996). Since the water vapour pressure inside the egg is always saturated at egg temperature, the changes in calculated shell conductance (based on incubator temperature) may stem from changes in egg temperature as development proceeds. The loss of water vapour from an egg is controlled by adjusting the humidity of the air in the nest or incubator. In most incubators, there is a single humidity setting, matched to hopefully achieve a 13%

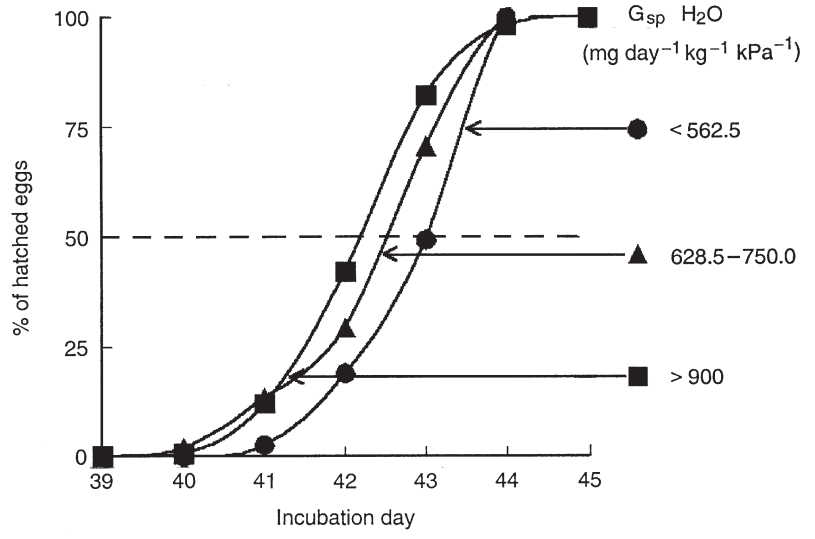

Fig. 7.3. The effect of mass-specific water vapour conductance (G_{sp}) on the length of incubation. Mean $G_{sp(A)}$=100.2±5.90, N=1098; mean $G_{sp(C)}$=130.5±5.96, N=268. Ar and Gefen, unpublished results (1998).

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mass loss up to pipping for the average egg. Hence, eggs with low- and high-conductance eggshells will lose insufficient or excessive amounts of water, respectively. Matching the humidity of the incubator to the shell conductance is a way to optimize weight loss of individual eggs. Ar *et al.* (1996) showed that lowering humidity for low-conductance eggshells increased hatchability by around 5%, whereas around 9% more eggs with high-conductance shells hatched when humidity was increased.

The problem with high-conductance eggshells lies in the excessive mass loss from the egg, leading to dehydration of the contents and mortality of the embryo. High-conductance eggshells are also more prone to microbial contamination (Fig. 7.4), which almost certainly lowers hatchability further. Often eggs with high mass loss have very poor quality eggshells and should not have been set in the first instance (Deeming, 1997). Such eggs can be saved in some cases by partially taping strips over the shell (Ar, unpublished observations, 1998). For normal incubation humidity conditions, better egg selection to remove those eggs with poor quality shells will reduce the problem of egg dehydration.

Low mass loss of ostrich eggs is considered a problem by many authors, because the relatively low humidity required to achieve the appropriate mass loss can be difficult to achieve in artificial incubation (Burger and Bertram, 1981; Ley

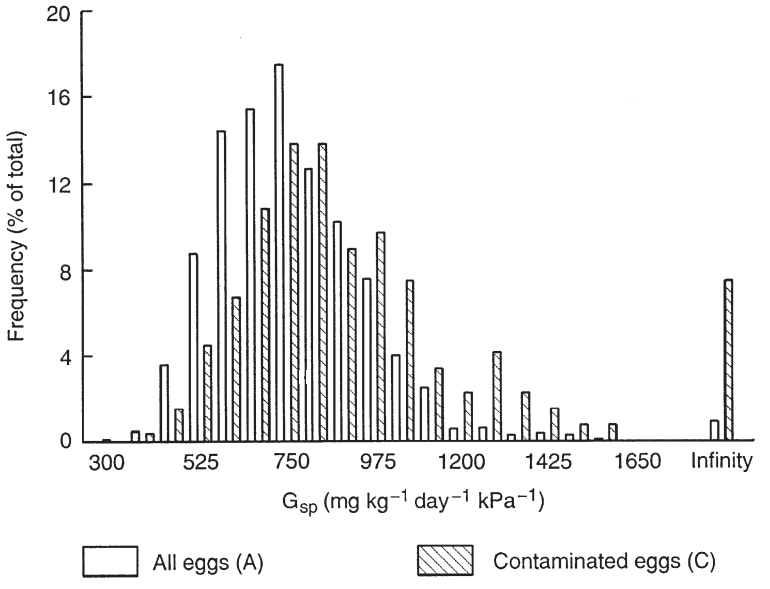

Fig. 7.4. The distribution of mass specific water vapour conductance (G_{sp}) for all eggs and those with microbial contamination. Incubation temperature, 36.0°C; mean=42.8 days; SD=1.0, *N*=1018. Ar and Zemach Ostriches, unpublished observations (1998).

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et al., 1986; Deeming, 1993, 1997; Brown *et al.*, 1996). The consequence of low mass loss is high mortality associated with heavy, oedemic embryos (Philbey *et al.*, 1991; Deeming, 1995a, 1997; Brown *et al.*, 1996). Malpositions, particularly where the embryo is incorrectly orientated towards the air space, are also common in low-mass-loss eggs (Deeming, personal observations, 1994–1996).

Oxygen and carbon dioxide exchange

Insufficient water loss produces, among other things, a small air cell which may bring about difficulties in the hatching process. Such embryos have problems with internal pipping and the embryo makes an external pip hole closer to the air space pole of egg (Deeming, 1995b). Ar (1991) has suggested that a small air cell may prevent complete gas filling of the lungs and airsacs of the hatching embryo. Furthermore, Ley *et al.* (1986) found that most of the oedemic embryos examined had died before internal pipping, and considered suffocation to be the reason for death. Reiner and Dzapo (1995) showed that the rate of oxygen consumption ($\dot{V}O_2$) is associated with the vitality of the embryos in the few days before hatching and could be used to predict whether individual embryos would hatch. Similarly, Tazawa *et al.* (1998) have shown that the heart rate of embryos likely to die is reduced. Low mass loss from eggs certainly causes problems due to the water retention in the embryo but, in addition, the low shell conductance restricts the oxygen uptake of the embryo and CO_2 emission from it.

The oxygen consumption rate of ostrich embryos follows a sigmoidal pattern with time, typical of precocial birds with a dip in $\dot{V}O_2$ a few days before internal pipping (Hoyt *et al.*, 1978; Meir and Ar, 1990; Reiner and Dzapo, 1995; Smith *et al.*, 1995; van Schalkwyk, 1998; Ar and Gefen, 1998). At its peak, $\dot{V}O_2$ averages around 100–120 ml kg^{-1} h^{-1} (Ar, 1996). Reiner and Dzapo (1995) found that embryos with high values for $\dot{V}O_2$ had shorter incubation periods.

The diffusion of both oxygen and carbon dioxide is limited by the conductance of the shell and the pressure difference of the gases between the inside and outside of the egg. Although not investigated in ostrich eggs as yet, it is known that below a certain eggshell conductance, fowl embryos become oxyconformers, i.e. their oxygen uptake is limited by the oxygen flux that can diffuse across the shell (Tullett and Deeming, 1982; Burton and Tullett, 1983; Ar *et al.*, 1991). Higher-conductance shells do not restrict oxygen diffusion and so the embryos appear to regulate their rate of oxygen consumption. In this context it is interesting to note that humidity adjustment during incubation, which is capable of correcting the water problem, had less effect on embryonic mortality in the low-conductance ostrich eggs than in the high-conductance eggs (Ar *et al.*, 1996).

The respiratory quotient (RQ) of ostrich eggs is initially high (1.7 on day 8), probably due to the CO_2 retained within the egg from its time in oviduct, but it gradually drops to 0.65 on days 22–28 and stabilizes at 0.68 during the last third of development (Fig. 7.5; Ar and Gefen, 1998). However, Meir and Ar (1990) reported an RQ in the last week of incubation of 0.79, and there is no plausible reason to explain the difference.

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The total amount of oxygen consumed by ostrich embryos during development is relatively small (Ar and Gefen, 1998). Compared with the fowl embryo, which requires 94.7 l O_2 kg^{-1} egg content, the ostrich embryo requires between 73.7 and 82.81 l O_2 kg^{-1} (Ar and Gefen, 1998). This difference corresponds to the different patterns of growth in the two species, with the relatively slow-growing ostrich embryo having relatively more residual yolk reserves at hatching compared with the fowl.

The heart rate of ostrich embryos has been shown to be influenced by shell conductance (Tazawa *et al.*, 1998). Up to about 60% of incubation, it was 185 beats min^{-1} on average. It then started to decline, but during the period of 33–37 days of incubation, eggs with high values for water vapour G_{sp} (965–1107 mg H_2O day^{-1} kPa^{-1} kg^{-1}) had variable heart rates of around 150 beats min^{-1}, which were significantly higher by about 10 beats min^{-1} than those recorded in eggs with low and medium values for G_{sp} (569–621 and 765–799 mg H_2O day^{-1} kPa^{-1} kg^{-1}, respectively). There were no significant differences between the heart rates of embryos in eggs with low and medium values, or during earlier periods during incubation. Ar *et al.* (1996) found that eggs with higher than average G_{sp} (>900 mg H_2O day^{-1} kPa^{-1} kg^{-1}) also hatched about 1 day earlier than those with values lower than the average (<560 mg H_2O day^{-1} kPa^{-1} kg^{-1}).

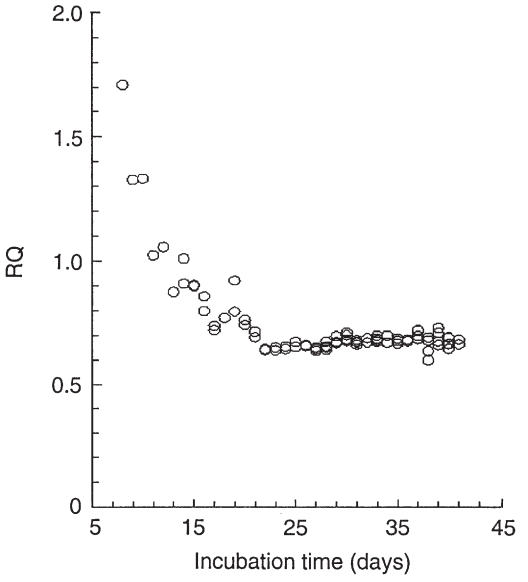

Fig. 7.5. The relationship between incubation length and respiratory quotient (RQ) of ostrich eggs. Data from Ar and Gefen (1998).

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Incubator ventilation

Smith *et al.* (1995) suggest that a concentration of CO_2 in the incubator air of above 0.5% can cause problems with embryonic mortality. For some unstated reason, these authors suggest that the aeration rate of the incubator should be set at only 0.045 $m^3 h^{-1}$ for 1000 ostrich eggs. By contrast, required incubator ventilation rates for an ostrich egg calculated from its $\dot{V}O_2$ on day 36 of incubation suggest that 0.001 $m^3 h^{-1}$ (1 $l h^{-1}$) are required for each egg (Reiner and Dzapo, 1995). However, this is apparently based on a lowered average reduction of up to 1–2% in O_2 content of the incubator (from 21 to 20–19% O_2). An accepted standard for aeration of poultry incubators is at 85 $m^3 h^{-1}$ for 1000 fowl eggs, which is equal to the mass of 40 ostrich eggs. Thus, for an incubator holding 1000 ostrich eggs, the aeration rate should be 2125 $m^3 h^{-1}$ (Deeming, 1997). However, this does not take into account the additional aeration for proper humidity control. According to calculations based on Ar (1996), for a permissible drop in incubator O_2 concentration of 0.4% (and increase in CO_2 of 0.3%), the incubator ventilation for a single stage incubator at peak $\dot{V}O_2$ should be 48 $m^3 h^{-1}$ per 1000 eggs, and for a multistage incubator only 8.8 $m^3 h^{-1}$ per 1000 eggs. Having such the low rate of air exchange would lead to problems of increasing humidity, as suggested by Ar (1996). Thus, for all practical reasons, any incubator ventilation that satisfies water loss and humidity demands in the incubator, will also more than satisfy ventilation requirements for O_2 and CO_2.

Hatcher management

Theoretically, conditions in the hatcher should not be any different from those in the incubators in terms of temperature and humidity (the bird does not change nest at hatching time). However, since eggs produce heat and consume O_2 at maximal rates, hatcher ventilation should suffice to supply enough oxygen and remove enough water; about 25% of the total water loss is lost in the hatcher (Ar, 1996). Nevertheless, the bird probably does react to the warmer eggs at the end of incubation and may have behavioural adaptations which minimize their exposure to the brood patch, and since in commercial incubators the ventilation fan may not be too efficient, lowering the hatcher temperature may help the cooling system. Certainly the number of eggs in the machine is critical, and for full hatchers a lower hatcher set point may be needed in order to reduce overheating. Unfortunately this point has not been investigated thoroughly.

Turning

Failure to turn poultry eggs during incubation causes problems with the formation of the extra-embryonic fluids and in utilization of albumen proteins (Deeming, 1991). Turning, therefore, has an important role during development in promoting normal development of the embryo and is essential during incubation up to

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transfer into the hatcher. The similarities in the relative compositions of fowl and ostrich eggs (Carey *et al.*, 1980; Deeming, 1993) suggest that the effects of not turning during incubation will be similar in both species.

Most modern incubators have automatic mechanisms for turning eggs during incubation, although the angle and frequency of turn can vary considerably (Deeming, 1993). Turning through ±30–45° at hourly intervals almost certainly satisfies normal development, but little research has been carried out on the importance of turning frequency and angle of turning in ostrich eggs. van Schalkwyk (1998) showed that as the angle of hourly rotation increased (from 60° to 90° via 10° increments), the level of both early and late embryonic mortality decreased. The orientation of the egg during incubation also appears to have an influence. Incubating eggs with their long axis horizontal for 2–3 weeks and then re-positioning the eggs with their long axis vertical for the rest of incubation, has beneficial effects on hatchability over positioning the eggs either vertically or horizontally throughout development (Smith *et al.*, 1995; van Schalkwyk, 1998). This pattern of egg positioning during incubation has a significant effect on hatchability if the angle of turn is relatively small (60°) but the advantage is lost when the angle of turn is 90° (van Schalkwyk, 1998).

Ostrich eggs have low hatchability if not turned during incubation (van Schalkwyk, 1998) but do appear to be relatively tolerant of low turning frequency. Wilson and Eldred (1997) showed that hatchability of eggs turned eight times a day was not significantly different from that of eggs turned 24 times a day. Low-frequency turning is particularly effective if the turning angle is large. Hand turning of eggs through 180° only twice daily appears to be sufficient to produce reasonable hatchability, although this is lower than for eggs turned hourly (van Schalkwyk, 1998). The difference in hatchability appears to be related to higher early embryonic mortality in the hand turned eggs (van Schalkwyk, 1998). Hand turning requires that the egg is unrestrained in the incubator and can adopt a natural orientation. In this way, as water loss proceeds during incubation, the air space end of the egg becomes less dense and this end of the egg, which is lighter, tends to rise, and probably aids the embryo to orientate towards the air space (Deeming, 1997).

A characteristic problem associated with lack of egg turning is low hatchability and residual albumen in the fowl egg (Tullett and Deeming, 1987). Badley (1996) showed that the apparent size of the extra-embryonic membranes as assessed by candling at day 35 of incubation of ostrich eggs, correlated with both the amount of residual albumen in dead-in-shell eggs and with hatchability. If the light area at the 'sharp pole' of the egg (i.e. the opposite end from the air space) was 0–10% of the shell area, then hatchability was above 87% of the eggs set. If the area was 20%, then hatchability fell to 75% and none of the eggs with larger clear areas hatched. Although hatchability figures were lower, the same pattern was observed for eggs incubated in Britain (Fig. 7.6; Deeming, personal observations, 1998). The increase in the light area corresponds to which stage of embryonic development individual eggs have achieved; eggs with a light area of 20% or more almost certainly contain an embryo which has slowed in development or

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has already died. Whether the extra-embryonic membrane development failure is the result or the cause of slow development early in incubation is a question that is not yet answered.

IN CONCLUSION

Research into incubation problems in ostrich eggs is still in its infancy and there are many areas of interest which require considerable work. These include: nutritional factors and breeder bird management in order to maximize fertility and hatchability; appropriate egg sanitation and storage protocols; appropriate incubation conditions, particularly temperature and turning; and the relationship between egg mass and embryonic growth. Any research needs to take into account the large variability in mass, shell properties and fertility with ostrich eggs, because these can influence experimental designs and hence the significance of any results. Uniformity of egg quality will not only improve the experimental assessment of incubation problems, but will also reap improvements in hatchability in commercial operations.

The different requirements of the embryo in terms of temperature, ventilation, turning, water loss rate and O_2 and CO_2 pressures during different phases of incubation, which are starting to emerge from present knowledge, may indicate

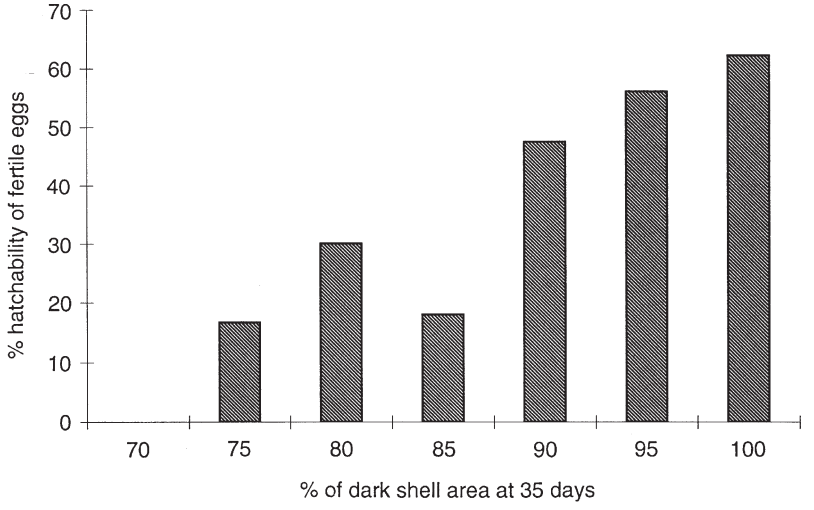

Fig. 7.6. The relationship between the percentage of the shell which is dark (indicating the presence of an embryo) when candled at 35 days and percentage hatchability of fertile eggs. Deeming, unpublished observations (1998).

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that in the future the method of single-stage incubators, where conditions of incubation change to fit embryonic demands at different stages of development, will prevail.

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Rearing Environments Around the World

8

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This chapter reviews the variety of techniques employed around the world for the rearing of ostriches to slaughter. This aspect of husbandry is a critical phase of commercial production and has been, and remains, the cause of significant problems in the majority of countries where ostrich farming is a novel enterprise. It is clear that there are a wide variety of different rearing conditions, all of which are successful to differing extents. This chapter starts with a few particular aspects of ostrich chick biology which have a significant impact on the rearing systems employed. Rearing techniques in major centres of ostrich production (South Africa, Israel and the USA) are described, before briefly describing intensive rearing systems practised elsewhere in the world. The principles behind ostrich rearing irrespective of location are outlined, and a few suggestions are made as to where research is still required in order to improve the success of rearing in general. Descriptions of the behaviour and nutrition of chicks and juveniles are given by Deeming and Bubier (Chapter 4) and by Cilliers and Angel (Chapter 5), respectively.

CHICK CHARACTERISTICS

Chick quality

Ostrich chick rearing is directly influenced by both parental condition and incubation. In common with commercial poultry production, the best results are achieved with the highest quality day-old chicks (Deeming *et al.*, 1996a). How these birds are defined can be rather subjective, but would include the following characteristics.

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An ideal range for chick mass is 780–975 g with little sign of generalized oedema or dehydration. The bird should be alert with clear, round (versus oval) eyes. The navel should be completely closed and dry. The bird should be free from any anatomical defects of the legs, feet and beak and the metatarsal skin fold should not be prominent. At least 80% of any group of chicks should be uniform in mass which persists with growth. The chicks should be free from any residual egg-transmitted diseases. With good chick quality, mortality at 14 days post-hatch should be less than 10%.

When hatchlings are to be transported over long distances it is important that chick quality is maximal. In chickens and turkeys during this period, significant advantages in growth rate, feed conversion and mortality were found when day-olds were dosed with nutritional fluids immediately post-hatch (Noy and Sklan, 1997); these findings support experience with this practice on progressive ostrich farms in South Africa.

The moisture loss from the egg during incubation determines the hydration status of the hatchling (Deeming and Ar, Chapter 7), with excessive moisture loss leading to dehydration. Extensive periods in the hatcher can dehydrate birds. Of more importance to ostriches is the problem of oedema caused by insufficient mass loss. This condition (anasarca) is characterized by gel-like deposits under the skin and within the muscle tissue (Philbey *et al.*, 1991). Afflicted birds have splay legs, preventing them from standing normally (Kocan and Crawford, 1994). The latter problem can be usually resolved by strapping the legs together so that they lie under the abdomen and cannot be displaced laterally (Kocan and Crawford, 1994; Deeming *et al.*, 1996a). After a couple of days the straps can be removed with no apparent ill effect. Alternatively the bird can be suspended in a stretched piece of material (e.g. hessian) with two leg slits, usually for a period of a week. Being kept in a dark hatcher for an extra day or even two can also help to resolve the problem. Deposition of oedemic tissue in the muscles has been shown to lead to myopathy in hatchlings (Philbey *et al.*, 1991).

The quality of chicks is determined by whether they hatch naturally or whether they require assistance, i.e. the shell is broken to aid external pipping. The moisture loss from eggs during incubation is usually critical in determining whether the chick needs to be helped. Data from Israel (Ar *et al.*, 1996) show that at 13% moisture loss (ML), only 19% of fertile eggs needed assistance but at 6% ML the number was 75%, and at 21% ML, 50% of the fertile eggs. Ar *et al.* (1996) report that 73% of the 'very good' quality chicks hatched naturally whereas 83% of the 'poor' and 'very poor' chicks had been assisted to hatch. Deeming and Ayres (1994) found that mortality of assisted chicks was 75% and the growth rate of the remaining birds was extremely poor.

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The residual yolk sac

A critical aspect of the early development of the chick is utilization of the residual yolk sac withdrawn into the abdomen in the last few days of development. In an ostrich of mass 800 g, the yolk sac forms a relatively high proportion of the total body (Deeming and Ar, Chapter 7) and has a mass of around 450 g. It contains yolk lipids and proteins and albumen proteins, and the presence of bile deposited during incubation gives it a bright green colour. Yolk provides nutrition as well as passive immunological protection (as maternally derived antibodies).

The rate at which the residual yolk is utilized has been a matter of great conjecture, with estimates for the time scale of absorption ranging from 7–10 days (Jensen *et al.*, 1992) to 2 weeks (Guittin, 1987) or 2–3 weeks (Smit, 1963). The pattern of yolk utilization has been studied in Britain in chicks which died during the first few days of life (Deeming, 1995). It was shown that the yolk sac constituted around 20% of the initial egg mass, some 30–40% of the body mass at hatching and declined rapidly thereafter until 12 days post-hatch when most chicks had used all of the yolk. In South Africa, the pattern of yolk utilization may be different because many chicks which die from trauma or acute disease during the third week post-hatching have significant amounts of yolk (Verwoerd, personal observations, 1998).

The outdated practice of withholding feed and water from ostrich chicks during the first 3–5 days, so that they can 'dry off properly and absorb the yolk sac faster', certainly compromises their survival. Kocan and Crawford (1994) even recommend that feed and water should be withheld for a period of 6–8 days post-hatching. Ostrich chicks need exposure to feed and water *ad libitum* from the moment they leave the hatcher so as to allow for functional development of the digestive tract as soon as possible. Failure will predispose chicks to be 'non-starters' or 'fading chicks' at the end of the yolk-dependent phase (2nd–3rd week). Absorption of yolk at the optimal rate occurs under a uniform environment and low stress conditions. In domestic fowl (*Gallus gallus*) consumption of feed actually increases the rate of yolk utilization over that observed in fasted chicks (Noy *et al.*, 1996). It is likely that fasting in chicks actually has the opposite effect and retards yolk uptake. Notwithstanding this, prevention of access to food, and particularly water, for extended periods is a serious welfare issue and should be actively discouraged.

Yolk sac infection is a significant cause of early mortality of ostrich chicks, with most birds dying within 14–21 days of hatching (Deeming *et al.*, 1996a). In one year, 75% of all chick mortality recorded by 7 days of age was due to yolk sac infection (Deeming, unpublished observations, 1996). Some instances of persistent yolk sacs have been reported in chicks aged up to 3 months of age (Shivaprasad, 1993; Dick and Deeming, 1996). In Italy, in 38 chicks which died before 20 days of age there were 30 cases of yolk sac infection, with organisms isolated from these yolks including *Escherichia coli*, *Pseudomonas* spp., *Staphylococcus aureus*, *Proteus* spp. and *Streptococcus* spp. (Grilli *et al.*, 1996). Both Shivaprasad (1993) and Deeming (1995) report a similar variety of organisms from infected

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yolk sacs. Yolk sac infection is commonly attributed to poor hatcher hygiene (e.g. Deeming *et al.*, 1996a) or post-hatch navel infections, or even to retrograde infections of the yolk from gastrointestinal pathogens. Yolk is a rich source of nutrients where there are no non-specific immunological defences (compared to the blood or specific organs), which allows excessive microbial growth and so 'infection' can occur (Verwoerd *et al.*, 1997).

The clinical condition of yolk sac 'retention' is supposedly characterized by a large yolk sac which is usually free of infection. Treatment is usually surgery (Kenny and Cambre, 1992; Kocan and Crawford, 1994; Dunn, 1995; Wade, 1995a; Speer, 1996), although success rates are rarely reported. Deeming (1995) questioned the validity of yolk sac retention as a clinical condition, arguing that the presence of a large yolk sac is a symptom of an underlying problem with the rearing environment rather than the initial cause of mortality.

Growth rates

The early rate of growth of ostrich chicks is important in establishing the birds for subsequent growth up to slaughter mass. Hatchling weight is dependent on the initial egg mass from which the bird emerges (Deeming and Ar, Chapter 7), and immediately after hatching chicks lose up to around 20% of their mass within 5–7 days (Guittin, 1987; Degen *et al.*, 1991; Deeming *et al.*, 1993, 1996a; Deeming and Ayres, 1994; Mushi *et al.*, 1998) before beginning a steady climb in mass. The decline in mass is greater and more prolonged in sick birds (Deeming and Ayres, 1994). Thereafter, the birds gain mass at an increasingly faster rate and by 3 months of age they typically should have a mass of 35–40 kg (Degen *et al.*, 1991; Swart *et al.*, 1993; Deeming *et al.*, 1996a). Adult size of around 100 kg is attained only around 12 months of age (Degen *et al.*, 1991).

The growth rate of some birds is far from this typical pattern, leading to considerable variability in chick mass during the first 3 months of age with chicks often not attaining normal rates of growth (Deeming *et al.*, 1993, 1996a; Deeming and Ayres, 1994; Mushi *et al.*, 1998). Factors affecting the size of the bird include: protein content in the diet (Gandini *et al.*, 1986; Deeming *et al.*, 1996a; Angel, personal observations, 1998), social grouping (Deeming and Ayres, 1994; Lambert *et al.*, 1995; Mushi *et al.*, 1998) and disease (Deeming *et al.*, 1993; Deeming and Ayres, 1994). The time of year affects the rate of growth of ostriches. Angel (1996) reared birds in outdoor enclosures in Indiana, USA, during summer and winter months. From 150–180 days of age the birds had a faster rate of mass gain in the summer than birds in the winter (17 kg versus 6 kg, respectively), with feed conversion rates of 3.5 and 10.9 kg kg^{-1}, respectively. Chicks reared in southern Indiana, USA, from hatches occurring from April to September, exhibited body masses of 3.9 kg at 31 days of age, and 29.6 kg at 90 days of age (Angel, 1997). Best growth was obtained in spring-hatched chicks, with a weight of 45 kg at 90 days of age.

Growth rate from hatching to adult size has been described by Degen *et al.*

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(1991). Ten ostriches (six females and four males) were weighed at hatch, and weekly after 35 days of age up to 350 days. The Gompertz equation was used to model growth and showed that maximal rates of growth occurred between 70 and 98 days, and maximal body mass was 104 kg. du Preez *et al.* (1992) studied growth rates in groups of male and female ostriches from three different populations. The Gompertz model was based on repeated weighings ($N=6$ or 10) of relatively small groups of birds (range of 4–24 per group), and for male and female birds from Oudtshoorn the age of maximum mass gain was 163 and 175 days, respectively. By contrast, for birds from Namibia it was 121 and 115 days and for birds from Zimbabwe it was only 92 and 114 days. The maximum mass attained (around 94–104 kg) was no different between the different groups of birds. Cilliers *et al.* (1995) extended this work on a larger group of Oudtshoorn ostriches (26 males and 17 females) and took mass measurements more frequently ($N=19$). The mean mature mass of males was 119.2 kg and of females 122.3 kg, with the maximum gain in mass occurring at 180 and 192 days of age. There were no significant differences between the genders. Mellett and Randall (1994) slaughtered ostriches at 3-month intervals, determined the mass of various body parts and applied the Gompertz model to describe growth, but only growth of the head could be described well by the equation. The age of maximum growth varied, with the head growing fastest (1.62 months) and the legs achieving maximal growth rate around 4 months of age. The wings took well over 5 months to reach their maximum growth rate.

A further aspect of growth is the change in the degree of ossification of the skeleton. Shivaprasad (1995) showed that degree of ossification of the femur, tibiotarsus and tarsometatarsus increased with bird age, with large cartilaginous cores being fully replaced by bone around 60 days of age. The degree of ossification of the pectoral girdle increases with bird age, and at slaughter this characteristic can be used to distinguish between birds of a similar mass but different ages (Sales and Mellett, 1995).

Brinckmann and Haefelfinger (1954), Guittin (1987) and Mushi *et al.* (1998) provide data on the linear dimensions of ostriches at different ages and masses. A method, based on birds measured between 6 and 10 months of age, for estimating the mass and skin area of an ostrich from the size of the front girth (measured around the thorax in cm) has been described by Bezuidenhout and van Schalkwyk (1996). Deeming *et al.* (1996b) took a variety of morphometric measurements for ostriches of a variety of ages, from day-old to adults, so as to develop equations to estimate both body mass and an average mass-for-size which, in combination, allows for body condition to be assessed.

Mortality

The reasons for mortality of ostrich chicks in wild situations are poorly understood because the small birds are easily lost from sight in tall grass (Bertram, 1992) but predation must be key factor. Little is known of the survivability of wild

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chicks but the one report suggests that it is low; in Kenya over 2 study years only 10 and 15% of chicks hatched survived to 1 year of age (Hurxthal, 1979).

By contrast, in a farming environment chick survival to 3 months of age is usually better but is highly variable. Unfortunately, it is usually the case that extreme instances of high mortality (e.g. Button *et al.*, 1996) are reported, rather than data which provide an idea of typical mortality patterns. Some possible examples of the latter follow, but more systematic studies of chick mortality in the field are necessary so as to provide background information about the major causes of death which would be of benefit in development of husbandry systems

In South Africa, typical chick mortality is reported to be 40% (Allwright, 1996) or 50% up to 3 months of age and 10% from 3–6 months of age (Smith *et al.*, 1995). Verwoerd *et al.* (1998) report that typical mortality at 1 week of age is 10–20% and at 3 months it is 10–30%. Mortality from 3 to 12 months of age is typically 5%.

More (1996) compared the mortality of chicks reared on 11 farms in Queensland, Australia over a 4-month period. Average mortality at 4 months was 37.1% of 394 chicks, but each farm showed a different temporal pattern of mortality (Fig. 8.1). Some farms were good at keeping chicks alive up to 30 days but then began to lose them, whereas other farms lost chicks up to 30 days but were able to keep those remaining alive up to 4 months. Only three farms had over 85% survival of chicks at 4 months of age (Fig. 8.1).

Under quarantine conditions in Britain, mortality of two batches of chicks to 3 months of age was 33.3 and 21.7% (Deeming *et al.*, 1993). Under similar conditions Deeming and Ayres (1994) had a mortality rate at 5 weeks of age of

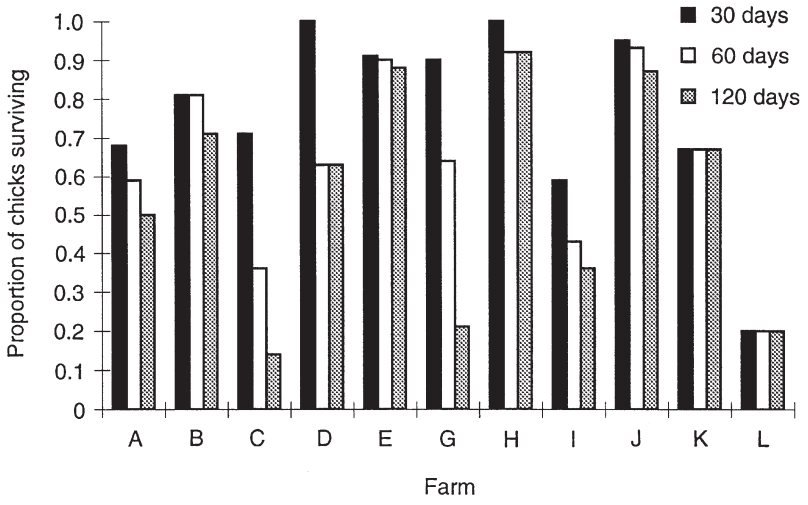

Fig. 8.1. Effect of individual farm in Queensland, Australia, on the survivability of ostrich chicks at 30, 60 and 120 days. Data from More (1996).

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18.6%, although mortality of chicks which required no assistance to hatch was 9.8% compared with 75% for chicks helped to externally pip.

In Israel, mortality rates range from 15–50%. Under intensive conditions, low mortality (<10%) is usually observed at the beginning of the season (March–June) whilst a sharp increase in mortality occurs between June and July when temperatures are high and density in the pens reaches its maximum. During the last months of the season mortality rate is about 50%. One farm experienced 10–15% mortality to 3 months of age (of 6000 birds) using semi-extensive rearing where chicks were reared on lucerne (*Medicago sativa*, alfalfa) and concentrates during the day and put in shelters with heaters at night (Perelman, personal observation, 1998).

Leg problems

Given the lifestyle of ostriches, the health of the legs of chicks is of critical importance. Four key problems exist: tibiotarsal rotation, rolled toes, slipped tendons, and bowed legs, and the frequency of incidence can be critical in determining the survival of any batch of chicks. It is unfortunate that all of these ailments are commonly categorized as 'leg problems' because their aetiologies are quite different.

Tibiotarsal rotation involves a deformation of the distal tibiotarsus bone resulting in the hock joint twisting outwards, with extreme cases leading to birds standing with each leg facing in opposite directions (Bezuidenhout and Burger, 1993; Deeming *et al.*, 1996a; Huchzermeyer, Chapter 12). This condition has been reported to be around 6.3% of a group of birds aged between 2 weeks and 6 months, with the right leg almost always being affected (Bezuidenhout and Burger, 1993). Similarly, Deeming *et al.* (1996a) report that between 5 and 10% of birds can develop tibiotarsal rotation, that the right leg is commonly affected and that most cases occur within 21 days post-hatching. The basis of the condition is a structural twisting of the distal tibiotarsus by up to or beyond 90° (Bezuidenhout and Burger, 1993; Deeming *et al.*, 1996a). Although Bezuidenhout *et al.* (1994) found that bone mineralization was poor in affected bones, the exact cause for the condition is not exactly known; overfeeding, malnutrition, inadequate exercise, trauma, poor flooring and genetics have all been suggested (Black, 1995; Speer, 1996). Deeming *et al.* (1996a) and Dick and Deeming (1996) suggest that it is traumatic damage to the lateral aspect of the distal growth plate of the bone which causes the bone to deform. Young ratites certainly have large cartilaginous growth plates in the long bones of the leg (Reece and Butler, 1984). Physical damage can occur during hatching (Deeming, personal observations, 1994) or when birds fall over during the first few days of life. Indeed a predisposing factor to tibiotarsal rotation is slippery flooring, and this can cause problems in older chicks kept in overcrowded enclosures (Dunn, 1995; Dick and Deeming, 1996).

The incidence of rolled toes is variable, with Dick and Deeming (1996) reporting that 0–25% of birds in any batch were afflicted. This condition is

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characterized by the medial displacement of the pad under the large toe and is common in chicks under 2 weeks of age (Kocan and Crawford, 1994). The aetiology of this condition is unknown although deficiency of B-complex vitamins has been suggested (Dunn, 1995). Although treatments such as splinting the toe are reported to work (Kocan and Crawford, 1994; Black, 1995), Dick and Deeming (1996) report that almost all cases spontaneously revert to normal by 4 weeks of age. The persistence of rolled toes in older chicks appears to be related to rotation of the phalangeal bones (Liswaniso, 1996). Whether the problem is associated with poor muscle tone, which affects the tension of tendons holding the foot pad in place, with lack of exercise or a nutritional deficiency (Deeming *et al.*, 1996a) requires further investigation.

In older chicks, the gastrocnemius tendon can be dislocated from the condyles of the tibio-tarsometatarsal joint (Black, 1995). The damage can be extensive, leading to a compound dislocation as the recumbent bird kicks out, and soft-tissue damage is bilateral (Dick and Deeming, 1996). Causes of slipped tendons are unknown but the role of nutritional deficiencies (e.g. manganese) needs to be investigated further (Black, 1995; Dick and Deeming, 1996). In many of the cases observed, dislocation of the tendon is usually related to some trauma or sharp movement while running or 'waltzing' when abrupt turning occurs. This condition can afflict individuals, and the possibility that this problem may be due to a nutritional deficiency should be considered only if it affects several birds within the flock at the same time (Perelman, 1991).

Bow legs are characterized by a bending of the tarsometatarsal bones (Guittin, 1986). The problem of bow legs is almost certainly due to a nutritional problem. Gandini *et al.* (1986) suggested that it was prevalent in birds on a high-protein (20%) diet, but there are many instances where commercial diets of 22% protein are used without problems being seen (Deeming *et al.*, 1996a). By contrast, Guittin (1986) suggests that it is due to problems with calcium metabolism, and evidence in rheas (*Rhea americana*) suggests that bow legs may be rickets (Angel *et al.*, 1996). Field experience in Israel has shown that levels of 1% calcium in the concentrate ration, similar to those used in turkey or poultry diets, are too low to prevent rickets in ostriches. In Israel most of the diets for ostriches up to 4 months of age have calcium levels around 1.5–1.6%. Rickets is only seldom observed in individual birds, probably due to malabsorption or as a secondary complication in sick chicks (Perelman, personal observations, 1998). Severe rickets has been observed in ostrich chicks fed with breeder diets containing about 3% calcium (Perelman, 1991). The levels of available phosphorus and the calcium:phosphorus ratio may be also important in the prevention of this disorder. The causes of rickets in ostriches is certainly an important field for additional research.

In the early 1990s a high incidence of leg problems (torsion of the proximal tibiotarsus) in the USA was associated with the use of heated floors (Angel, 1992). This was specially true in the spring and autumn when it was cool and wet. Birds were kept indoors on rainy days and birds also tended to stay in when it was cold and windy outside. Given that the main heat inside was being provided in through the floor, the birds did spend a great amount of time sitting.

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OSTRICH CHICK REARING IN SOUTH AFRICA

Ostrich farming was originally developed in South Africa and is practised over an extremely wide range of geographical and climatic seasonal conditions in southern Africa as a whole. These include: semi-desert plains with almost no rainfall in the Northern Cape, Greater Karoo and southern Namibia (dependent on irrigated crops); high winter rainfall with long dry summers in the South-western Cape; semi-desert valleys with very cold, wet winter winds from the surrounding mountains in the Little Karoo; high altitude grassland with medium high summer rainfall in central South Africa; and hot dusty bushveld with sudden high-volume summer thunderstorms in northern South Africa and Zimbabwe. All of these different conditions are experienced in various parts of the Eastern Cape. These conditions dictate to a large extent the techniques which can be successfully used by farmers to rear ostrich chicks.

Furthermore, there are historical considerations. Firstly, traditional techniques have been handed down over two or three generations from father to son with few changes. Secondly, over many years there has been contamination of pastures by pathogens, e.g. the wireworm (*Libostrongylus douglassi*), which has forced the development of 'satellite' chick-rearing arrangements with farmers from non-contaminated areas.

Three phases of rearing between hatch and slaughter are described: immediately post-hatch, rearing to around 4–6 months of age (foster or artificial rearing), and then finishing in feedlots. Techniques primarily employed in South Africa are described, although details are provided for other southern African countries where appropriate.

Post-hatch

Immediately post-hatch, chicks are usually kept inside a building in groups of 20–30 in small areas delimited by a circle of plastic crates or hardboard. The floor can be rough concrete, heated or insulated with carpet or hessian (Hallam, 1992) or, in many instances, a raised, welded metal mesh platform. The temperature of the whole room is controlled above 30°C with little daily variation by heating with domestic asbestos or oil heaters. Ventilation is usually passive, usually through a few openings and with slow vertical mixing fans in the roof space. The chicks usually remain here for 2–7 days. In Zimbabwe, Hallam (1992) recommends that space requirements is 0.16 m^2 per chick which should be extended by 10% per week.

An interesting variation (developed by the Schmidt brothers of Addo, Eastern Cape) involves chicks spending the first 7–10 days in galvanized steel crates (500×900×300 mm, wide×deep×high) stacked in two rows of three on a frame on wheels. Each crate houses three or four ostrich chicks on an expanded metal floor with a sloping piece of sheet metal under each crate to direct droppings and urine to a collecting duct at the rear. Food is provided at the front in

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plastic gutters with water in a shallow plastic tray. Two rows of these frames look towards each other lengthways down the building so that chicks can see their companions. During pleasant weather, the crates are wheeled outside to a concrete slab between adjacent buildings and under shade-cloth. The crates are wheeled back inside during late afternoon. From here chicks spend another 2 weeks in groups of 20–30 inside a building heated to 26°C before being grazed on short lucerne in groups of 50–100 in the usual manner (see below). This system constantly achieves mortality figures of <15% up to 3 months, and chicks grow well.

In all post-hatch rearing situations it is extremely important that chicks should not get chilled, leading to poor yolk sac absorption or secondary infections; nor overheated, which reduces food intake and can lead to dehydration. Very often chicks die from chronic starvation around 2–3 weeks of age (i.e. after all yolk has been resorbed) as a result of environmental, social or nutritional stress experienced during the first week post-hatch (Verwoerd *et al.*, 1997). Typically, temperature variations are measured using only a few minimum/maximum thermometers suspended at chick height. Some progressive farmers calculate skin temperature (taking wind chill into account) and manage heating and ventilation accordingly. The commercial value of intensive management during this critical age has been stressed by Hallam (1992).

Foster rearing

A common practice in traditional ostrich farming areas in South Africa is the use of foster parents for young chicks (de Kock, 1996). The lack of excess breeding stock has precluded the development of this system in other countries around the world. Commonly used where extensive irrigated pastures are available, chicks are cared for by breeder pairs, single or several breeding females, or by yearling females exhibiting early breeding behaviour. After artificial hatching, at 7–14 days of age the birds are given to experienced breeders which act as foster parents. Alternatively, females are allowed to incubate and hatch their own eggs and additional chicks are gradually added to the clutch over a few days up to an average of 15–20 per hen, although experienced females may accommodate 25 chicks. Some farmers with yearling hens move the chicks into shelter at night, returning them to the foster birds in the morning. These shelters can be proper buildings with heating, or field shelters built from straw bales roofed with corrugated iron sheets and over a lucerne pasture. Enclosures used for foster rearing must have low wire netting at the bottom of the fence so as to prevent the small birds getting through the fence (de Kock, 1996).

Areas where there are sudden changes in the weather are not suitable for fostering, and even using experienced breeders can have limited success as every mature bird can shelter only 10–15 chicks. Hence, in colder months only 30–35 chicks can be put with a pair but during warmer months 60 chicks can be fostered (de Kock, 1996). Any excess may succumb to exposure or secondary infections as a result of the cold stress.

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Fostering is followed by several Bushveld farmers towards the end of the breeding season (beginning of winter). At this time the chicks are considered to be second-grade so that any survivors are regarded as a bonus, and it is thought that improved mothering abilities, or 'satisfaction' by the parents, increases egg production and fertility during the following season. To date no scientific study has investigated this interesting possibility.

Problems can arise (de Kock, 1996) when both birds do not show good fostering behaviour or when all of the chicks are attracted to only one bird (often the male) and they are not all covered. Some birds will not accept new additions and kill them by trampling, kicking or throwing them in the air. Some birds may not sit at night thereby preventing brooding and exposing the chicks to hypothermia.

An alternative system common in Namibia and Zimbabwe utilizes a low fence enclosure on lucerne pasture provided with a night shelter, and the role of the foster bird is played by a labourer who alternates between several groups of 20–40 chicks during the day. This system is very often used with chicks older than 8 weeks as it allows the birds to be put in a shelter during inclement weather and at night.

Artificial rearing

Contrary to popular opinion which suggests that ostrich chicks cannot thermoregulate physiologically until their 2nd or 3rd week (e.g. Jensen *et al.*, 1992), Brown and Prior (1998) have shown that even at 2 days of age chicks can maintain near-adult body temperatures even at ambient temperatures around 15°C. Nevertheless the youngest chicks should be raised under artificial heating starting around 30°C with a gradual drop of 0.5°C day^{-1} until a stable temperature of 26°C (±1°C) is reached. Heat sources vary between infrared light, ceramic, oil, or electrical heaters. Underfloor heating is not always used but if chicks are kept on concrete floors at night, or if severe seasonal temperature fluctuations occur, they can be a valuable improvement to the environment. Several maximum/minimum thermometers placed at several heights are used to manage temperature regulation. In many cases, fresh air enters the facilities over a heating element to prevent cold draughts, and slow vertical 'mixing' fans prevent layering of ammonia at chick level. Ideally, extractor fans remove gases from this level and not only heated air from the roof space.

Facilities generally consist of a shelter coupled with an outside run (Hallam, 1992). Shelters are constructed from a variety of buildings: modified shipping containers, wooden shacks, modified corrugated iron agricultural sheds, and modified pig and poultry houses as well as custom-built buildings. Flooring varies from soil or sheep manure, rough concrete or concrete covered with custom-designed interlocking rubber mats, or galvanized welded mesh raised 20–1000 mm above the floor. Insulated roofs (with ceilings) or thatched grass roofs (André Coetzee, personal communication, 1998) assist in achieving optimal temperature conditions. Walls are usually washable to allow for regular disinfection to help

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prevent disease outbreaks. Concrete floors have been used in Botswana for chicks up to 14 weeks of age (Mushi *et al.*, 1998).

Optimal group sizes are 30–50 chicks, with two to three chicks m^{-2} usually available in the shelter. Floor space is largely determined by how long chicks have to be kept inside due to inclement weather. Concrete-floored outside runs are generally used, some extending on to sand/soil or into small lucerne camps. Exposure to new surfaces is gradually managed to prevent sand eating or impaction. Most outside chick runs measure 2–3×10–15 m for this age group (hatch to 4–6 months), and have a portion covered by a shade cloth to provide shelter from the midday sun in summer. Although ostriches of all ages can withstand high environmental temperatures, management within their thermoneutral zone will lead to maximum feed intake and growth. In desert areas where thermoregulation is particularly difficult in summer, feed intake is stimulated by a variety of techniques: feeding denser rations early in the morning; free choice access to mineral licks; provision of very cold drinking water; cooling through misting; and use of shade cloth or desert coolers.

Weekly weighing of a representative sample of chicks from each group allows for early detection and correction of problems as they emerge. Several top farmers plot these data against an expected growth curve for the farm as part of the general management plan, thereby facilitating interactions with veterinary investigations and reports to top management. Weighing is done until 8–10 weeks, and recorded along with all other relevant information including dates, supplements, mortalities plus diagnoses, temperatures, feed batch numbers, etc., on a group basis.

Feed is usually provided in flat-bottomed, shallow plastic containers, and water initially in poultry-type bell drinkers. Both are gradually being changed to hanging wall containers because ostrich chicks typically fall over bowls on the floor, causing minor trauma to the fast-growing growth plates in the legs and thus predisposing them to tibiotarsal rotation.

During mild, predictable weather, chicks are often grazed in groups of 50–200 on short lucerne fields or on very short kikuyu grass (*Pennisetum clandestimum*) lawns. Smaller group sizes allow earlier detection of problems and more uniform growth performance. If grass lawns or longer lucerne are used, chicks should preferably be moved on a daily basis to minimize the risk of ingestion of roots or long stalks which may lead to impaction. Long enclosures with movable fence divisions, as well as those which are rotated, or even small enclosures moved in their entirety, are all variations used during this age.

In desert or semi-desert areas grazing is not available and so sand runs are used. Displacement behaviour, i.e. feather pecking, sand eating and pecking at concrete fence posts, are common problems encountered here. The provision of higher fibre levels in the ration (5–10%) or sterilized crushed bone *ad libitum* have often alleviated such problems. Some groups tend to have more problems than others and in these cases the provision of small areas for grazing has been the most successful approach.

Changing weather patterns usually mean the night shelters need to be

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provided. Temperature regulation is less critical in the older, heavier birds, but care should be taken if environmental temperatures drop below 20°C, as this can predispose birds to respiratory disease. During this period of fast growth rate every effort should be made to provide a balanced, full ration, or a very dense concentrate if supplemental grazing is provided. Floor surfaces should not be slippery and food and water bowls should be located off the floor.

Most farmers have a series of similar camps (3rd to 4th phases) with variable levels of shelter provided, for the period 4–16 weeks before the chicks are moved to the feedlots. During this time there is usually a change from a starter to a grower ration.

Finishing to slaughter

The third phase of rearing is the grow-out phase where the birds spend around 7–8 months grazing on lucerne or natural veld plus a variable amount of supplementation with grower ration. Alternatively, many juvenile ostriches are reared on feedlots denuded of vegetation (zero-grazing) where they are provided with a grower ration and chopped lucerne. Traditionally ostrich chicks of approximately 65 kg (5–6 months) are 'cleaned' (i.e. selective feather plucking) to promote uniform new feather growth for harvesting at slaughter (14 months) as well as maturation of the feather follicles for optimal leather quality (Sales, Chapter 10). Similar patterns of rearing are seen in other southern African countries.

In South Africa, ostriches were historically trucked or driven on foot from extensive, free-range camps to the abattoir immediately prior to slaughter. An outbreak of Crimean–Congo haemorrhagic fever (CCHF) in October 1996 (Swanepoel *et al.*, 1998), and the subsequent ban on ostrich meat exports from South Africa to the European Union, irrevocably changed this situation. The ban was lifted after research findings and specific guidelines on tick and rodent control were enforced during the last 30 days before slaughter. All birds in South Africa are now slaughtered after a preslaughter quarantine period on a zero-grazing feedlot, with rodent control, and after specific acaracide treatments (e.g. flumethrin/deltamethrin) and inspection for ticks. After this period the birds are taken directly to the abattoir.

The design of feedlots in South Africa is now influenced by these statutory requirements. The site should be close to the abattoir in order to minimize transport-related damage to skin and meat. Protection, especially windbreaks, is provided against inclement weather. Slopes and ditches are needed for heavy rain to run off. Feedlots are relatively close to sites of maize and lucerne production because feeding to slaughter relies on a large volume intake and it is almost impossible to run an economic feedlot only on fully commercial rations. Feedlots have to be located as far as possible from commercial poultry.

Fences should be sturdy having single strands with uprights and poles, although woven mesh fencing is commonly used. Uprights are painted white and large, light-coloured objects (e.g. paint tin lids) are often attached to the fence to

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increase its visibility. Floodlighting at night can help to prevent birds running into the fences causing injuries (leading to downgrading of skins) and even death. Stray dogs or jackals can enter the service roads by crawling underneath the gates and then run up and down these lanes between the enclosures in an effort to get out again. This frequently causes mass uncontrolled flight responses in the birds resulting in huge losses, especially if complete darkness enhances the disorientation of the ostriches. All outer perimeter fences as well as gates should be jackal-proof.

The service road to the feedlot is often circular with one-way movement of feed vehicles. A herringbone design is a useful alternative. The handling area has a crush for weighing (monthly) and loading ramp built from poles protected with old car tyres or conveyor belt. The enclosures have no corners less than 90°. For birds over 6 months old, the enclosure is 20×40 m for an optimal group size of 50–60 birds. Some farmers have much bigger feedlot enclosures for larger groups, or provide small camps for younger birds (<6 months) and bigger camps for older birds.

Water pipes and containers should provide cold water (15–20°C) during periods of high ambient temperatures. Small, ball-valve control drinkers are preferred to prevent horizontal disease transmission and allow a continuous supply of fresh water. Feed is supplied once or twice a day, or in the case of self-feeders every few days providing *ad libitum* feeding. Rations are calculated on the basis of dry matter intake and equate to roughly 2 kg bird^{-1} day^{-1}. Truck tyre halves and a variety of designs of self-feeders are used.

Natural hatching and rearing

In Namibia, trials were undertaken to utilize ostriches on 50–100-ha enclosures of natural vegetation in order to produce chicks for intensive rearing (Foggin and van Niekerk, 1995). Survival of naturally incubated chicks was better than for chicks hatched from eggs laid by captive birds.

In Zimbabwe, ostriches living wild on game ranches are being used to produce eggs for artificial incubation, although it is often the case that hatchability is better in nests than in incubators (Foggin and van Niekerk, 1995). This practice has been extended at one site to allow the wild birds to hatch and rear their own chicks, which are then harvested. Both hatchability and chick survival were above 80% and the apparent growth rate of the chicks was better than that observed in captive birds.

Veterinary treatment

There are three basic phases of veterinary management in South Africa. The first is arrival and acclimatization to the feedlot which lasts for around 1–2 months. Birds are given an identification mark (microchips) and are weighed. Various anti-helminthic treatments and vaccinations against, for example, clostridial

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enterotoxaemia, *Mycoplasma gallisepticum*, Newcastle disease (ND) virus and endogenous bacteria, are given according to the health risks based on farm/area of origin – seasonal variables during grow-out – and the disease profile of a specific feedlot. There is a gradual phase-in of new grower ration from that used during rearing. The use of mannanoligosaccharides (2 kg t^{-1}; Biomos-Alltech, Inc.) have been used against bacterial enteric pathogens and as an immunomodulator, with marked improvements in mortality figures and growth rate during this highly stressed period (Verwoerd *et al.*, 1998).

The second phase deals with growth. Mass is recorded on a monthly basis and plotted against an expected growth curve (i.e. a minimum of 10 kg $month^{-1}$ until 10 months old). These data allow early intervention or investigation into problem groups or individuals. The ration is adjusted according to seasonal demand, e.g. high density and metabolizable energy in the winter versus summer months.

The third phase is finishing. All of the compulsory regulations against ND and CCHF as required by veterinary authorities need to be followed. All records are updated per group. The last weighing (80–85 kg) is at 2 months before slaughter so as to minimize the risk of fresh skin damage during the last few weeks. The birds are put on a very high-fibre diet (30–50%) to prevent excess fat deposition. The natural growth curve starts to level off at this age (typically 12 months) and so protein deposition occurs more slowly than fat deposition. Hindgut fermentation is also maximally developed at this stage so that significant savings in the feed bill can be made.

REARING SYSTEMS IN ISRAEL

Two main systems for chick rearing are practised in Israel: semi-intensive and intensive. In the semi-intensive system the chicks are raised on lucerne pastures from the first day out of the hatcher. Groups of 25–50 ostriches are kept together in small enclosures bounded by low fences (450 mm high). Concentrate ration is provided once the birds can feed and walk. In some areas where the diurnal and nocturnal temperature difference is not too great the chicks are left outside without a source of heat. Chicks are usually put into a shelter overnight in order to prevent predation and to provide artificial heating (typically gas heaters) to reduce hypothermia. These shelters may be fixed, but mobile shelters are increasingly being used which allow the area for grazing to be easily moved around the pasture. After around 6 weeks on the lucerne pasture the chicks are moved into enclosures, each holding 150 birds, and fed on chopped lucerne and concentrates.

In the intensive system, birds are raised in enclosures with a fixed shelter, a gas heater, a concrete floor and an area for exercise. All feed is provided as concentrates and chopped lucerne. A 3×3 m enclosure is used for 50–60 birds although better results are obtained at lower bird densities (30–50 birds). The

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exercise area measures 3×10 m for every 50 chicks. The concrete floor is covered with a litter, usually dry hay, covered by shade mesh to prevent excessive ingestion of the litter and isolate the birds from urine. At 1 month of age the birds are moved into larger pens (25×25 m) with heated shelters thermostatically controlled to 22°C. At 2 months of age the heaters are removed.

All the chicks are vaccinated against pox by wing-web puncture and at 2–3 months of age against ND by spray (live vaccine) and injection (inactivated virus). All the chicks are treated against external parasites and mites before they are sent to the feedlot. At around 3 months of age, all birds are sent to feedlots irrespective of rearing system. Here the birds are kept in large enclosures in groups of 150–300 birds. As bird mass increases the ostriches are moved to larger enclosures. In the feedlots, nutrition is initially based on that employed in the rearing systems so that problems with stress, pica and impaction are avoided. After 6 months of age the ration is a concentrate ration supplemented with high-quality hay and in some cases silage. The proportions of each component of the diet are calculated according to the age of the birds and their rate of development. At a body mass of 95 kg, achieved around 10–11 months, the feed conversion ratio (FCR) is 1:4.5. The feedlot enclosure is often denuded of all vegetation (Degen *et al.*, 1989).

At a body mass of 95–100 kg the birds are transported to one of two approved ostrich abattoirs in Israel. The feedlots are in the adjacent area and ostriches are just moved by walking to a quarantine area next to the abattoir. Here they are sprayed with a commercial compound against ticks and kept under quarantine conditions for a minimum of 14 days before being walked into the slaughter facility.

REARING IN THE USA

When the ostrich industry started to grow in the USA, bird management was geared to a breeder market which focused on sales of 3- and 6-month-old birds, although older ostriches (12–24 months) were also sold. At this time chick-rearing principles and appropriate management practices were not well established, and mortality of young chicks was the greatest problem. During the early 1990s, chick mortality was primarily blamed on leg problems, yolk-sac infections, impactions and chicks that failed to start eating, but clear causative agents were not established and the problems continued for the first few years.

Most of the problems encountered by pioneer ostrich farmers in the USA could be blamed in part on poor incubation and hatching, and on inadequate chick-rearing practices. Improper egg weight loss (below 10 and above 17%) was common, and a high proportion of chicks had to be helped out of the shell. The incidence of externalized yolks was relatively high (averaging 10% of chicks). There was a very high incidence of 'wet' chicks with anasarca, as well as a lower incidence of dehydrated chicks. Oedemic chicks were kept in the hatcher until

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they had 'dried out' which led to some birds being kept at 36°C for up to 5 days. Improper substrates in hatcher baskets led to a high incidence of twisted toes and other leg problems.

It was common early on, not to offer feed or water for the first few days (1–9 days) after hatch (Kocan and Crawford, 1994). This practice contributed to the high incidence of poor starters, i.e. chicks that were slow to start eating and drinking. Such birds would often die within the first 2 weeks of life. Once it was introduced to the birds, crumbled feed and water were offered on a free choice basis. Surgical removal of yolk sacs was common, to remove infected yolks but also frequently as a preventative measure.

Preferred rearing quarters were enclosed barns with concrete floors. Lack of attention to wind direction led to facilities being built with access doors facing into the prevailing wind. In northern regions, this led to cold and windy conditions indoors unless doors were closed. This problem was worse in the spring and autumn. Heated floors were common and this led to birds sitting to obtain warmth, which contributed to leg problems. Use of heat pads in brooder areas was common. Floors in indoor facilities were washed and disinfected daily which led to excessive movement of birds and the return of birds to indoor pens that were often still wet. Improper washing after disinfection often led to footpad lesions.

Bedding used on the cement or soil floors in indoor enclosures included: chopped lucerne (mixed with 5% animal fat to minimize dust), thick plastic mesh cover, or shade cloth. Use of lucerne for bedding also led to an increased incidence of leg problems due to preferential consumption of the bedding. There was an imbalance of the calcium-to-phosphorus ratio consumed by the chicks leading to a high incidence of rickets. Chicks were usually brooded for 4 weeks with access to outdoor runs depending on time of the year and latitude. Usually, regardless of latitude or time of the year, birds were not allowed access to outside runs for the first 5 days after they were removed from the hatcher.

Outside pens were constructed with care to minimize any potential presence of objects that could cause gizzard impaction. Generally soil flooring was sifted to remove any rocks. Other substrates varied immensely but the commonest used were: shade cloth cover over either limestone (large size) or soil, very large-size limestone, or concrete. Use of pasture was discouraged based on the idea that the birds would impact on the vegetation. From 2–4 weeks of age, chicks were allowed outside only on sunny and warm days and only for limited times, and were kept indoors overnight. Generally, chick-rearing facilities in the southern regions of the USA, that tend to be warmer all year around, were more open and birds tended to have access to outside pens at an earlier age and more often. Small pasture areas would sometimes be found at the end of pens where birds were allowed access for increasingly longer times as they grew, so as to get them accustomed to the pasture they would be on after 3 months of age.

At 4, more usually 6, months of age, birds were moved to grower enclosures based on pasture. Local pastures were used, and differed greatly throughout the USA. A small shelter with no supplemental heat was provided for the birds although the size of the shelter was dependent on latitude. At northern latitudes

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three-sided shelters were provided. In these areas a large barn was usually available on the farm where the younger birds could be sheltered during severe weather.

Chicks were often weighed daily for the first month and thereafter birds were generally weighed weekly up to 4–6 months of age. There was regular movement of birds between pens so as to keep similar-sized birds together.

Rearing practices in the USA changed drastically in the late 1990s primarily due to a decrease in ostrich prices. Overall survivability improved as producers started to rear chicks more as agricultural animals. As soon as the birds have dried in the hatcher, chicks are moved to outside enclosures equipped with a closed area with a heat lamp. If the weather permits, birds are allowed outside, preferably into an area that has green cover such as grass, small-grain pasture (winter wheat, oats, barley, etc.) or lucerne. Experience has shown that the earlier the birds are allowed access to a natural substrate, the fewer problems with impactions are observed. Birds are reared in large pens (8×40 m) from hatch to 3 months of age in groups of preferably more than 10 birds. Sand or dirt is also used in areas where maintenance of a cultivated substrate is difficult.

Birds are moved to grower–finisher pens at 3 months of age, but preferably once they have reached 35 kg (regardless of age). A grower diet is fed from 35–75 kg. A weight of 75 kg is obtained between 6 and 10 months depending on season, area of the country, feed management and genetic potential of the birds. Management can be semi-intensive or intensive. In semi-intensive systems birds are placed in large pastures. Pastures are typically small-grain pastures with some leguminous plant interseeded. A protected area is available where the birds are housed overnight and where they are fed a dietary supplement formulated based on pasture availability and nutrient quality. Typically the birds receive a daily supplement ration of 1 kg per bird. In intensive systems, 10–25 birds are kept in enclosures typically measuring 8×50 m where they are fed complete diets and supplemented with small quantities of lucerne hay (0.5 kg $bird^{-1}$ day^{-1}).

CHICK REARING IN OTHER PARTS OF THE WORLD

Given the pre-eminence of the USA in promoting ostrich farming in parts of the world other than South Africa and Israel, most rearing systems around the world have tended to be developed using the American system as a model. Local variations exist primarily on the basis of the prevailing climatic conditions. In northern Europe, Scandinavia and Canada, cold and wet winters mean that heated facilities are required for birds up to 3 months of age for much of the year or else growth rates and survival are severely compromised (Kreibich and Sommer, 1995; Deeming *et al.*, 1996; Deeming, personal observations, 1998). During the late 1990s, this has had the effect in Europe of shifting the location of ostrich farms from northern and western countries (the UK, Belgium, the Netherlands and Germany) to southern countries around the Mediterranean Sea (Spain and

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Portugal) where the climate is more amenable to keeping birds outside all year. Other variations usually centre around local foodstuffs and building materials.

The absence of foster-rearing in countries other than South Africa is almost certainly due to the limited number of adult ostriches which would act as foster parents. All adult birds are used as breeders for the entire laying season, rather than losing their production by allowing them to rear their own and other chicks. This reliance on artificial rearing systems may have an adverse effect on production: Bubier *et al.* (1998) found that farmed ostriches showed courtship behaviour towards humans. Such behaviour may be a response to imprinting of chicks to human handlers and is certainly worthy of further investigation.

BASIC PRINCIPLES OF OSTRICH CHICK REARING

In closing, it is appropriate to highlight a few critical principles for rearing ostriches irrespective of geographical location. As has been shown above, there is no single technique for successful ostrich rearing yet there are common threads running through the different techniques described.

Brooding

A common feature of intensive rearing systems is a short period immediately post-hatching when the chicks are brooded. Usually small groups of birds are confined to a small area (e.g. 10–12 chicks in 1.25×1.25 m; Deeming *et al.*, 1996a) and kept at high temperatures which are usually maintained by suspending a heat lamp (gas or electric) over the brooder (Wade, 1995b). Boxes can be placed directly on to heated (25°C) concrete flooring, insulated flooring (Deeming *et al.*, 1996a) or carpet (Kocan and Crawford, 1994), or can have 6 mm metal mesh floors (Jensen *et al.*, 1992). Solid wooden walls help to prevent draughts, although Kocan and Crawford (1994) suggest using stainless steel walls in order to make cleaning easier. Typical temperatures in a brooder box are 32°C (Deeming *et al.*, 1996a), 26.5–32°C (Jensen *et al.*, 1992), 24°C (Kocan and Crawford, 1994). Room temperatures are maintained around 26°C if wire floors are used (Jensen *et al.*, 1992); Deeming *et al.* (1996a) recommend 28°C, although covering the box with a pyramidal tent of plastic sheeting can reduce the need to heat the entire room.

Chicks are restricted to only a small area until they are able to walk easily and have started to peck at food and water which is made available from the start. Deeming *et al.* (1996a) recommend that two or three small (3 mm) stones should be provided within a couple of days of hatching. Small brooder boxes have the advantage that the chicks do not stumble away from the heat source, and they provide a suitable environment within a larger multi-age rearing facility which may contain older, less vulnerable birds.

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Temperature

The temperature at which birds are kept should reflect their body mass rather than their age. Sources of heat should aim to provide an even temperature within the room rather than hot spots in a relatively cool environment. In Britain, Deeming *et al.* (1996a) heated the rearing barn with a gas heater, with the thermostat setting based on the mass of the bird rather than its age (Table 8.1); in addition, each enclosure had a gas brooder lamp (set at 30°C) the height of which was adjusted as the chicks grew. Although young chicks can thermoregulate efficiently, temperatures above 28°C need to be provided so as to ensure that feeding activity is established during the phase when nutrition is also being provided by the yolk. The source of heat can vary on the prevailing conditions, warm sunny weather is almost certainly ideal for chicks but protection against heat loss during cold nights is critical. In colder climates optimal chick survival and growth will only be ensured if there is correct temperature regulation with regard to the size of the bird.

A critical aspect of rearing ostriches in Europe is the prevailing weather conditions when the birds are given access to outside runs. Cold conditions (less than 20°C) reduce rates of growth at the very least and can cause an increase in mortality. Birds reared outdoors without supplemental heating can fare well during summer months, but once autumn arrives the ambient conditions are inappropriate for optimal growth and maximum survival. Planning of a rearing unit in northern Europe needs to take into account the climate in late autumn and winter when birds are going to be 3–6 months of age. Under severe weather conditions in Scandinavia, ostrich chicks are unable to go outside during winter due to the deep snow and so there has to be adequate provision of space in warm shelters.

Table 8.1. Relationship between the age and weight of ostrich chicks and room air temperature at which the rearing facility should be maintained, as suggested by Deeming *et al.* (1996a).

Age (up to)	Weight (kg)	Room temperature (°C)
3 days	< 1 kg	32
7 days	< 1.2 kg	30
14 days	< 1.5 kg	28
21 days	< 2 kg	26
35 days	< 5 kg	24
50 days	< 10 kg	22
3 months	< 35 kg	20

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Ventilation and rearing environment

Ventilation of shelters is very important to ensure that there is efficient removal of noxious gases, mainly ammonia. Failure to properly ventilate buildings predisposes birds to several disease conditions. Ventilation should be provided by wall fans, and air mixed by overhead fans. Lighting should be bright to allow for efficient feeding, and excessive noise should be prevented in order to minimize stress in the birds. The rearing environment should be as stress-free as possible so as to allow chicks to develop normal behaviour patterns. The staff employed to care for the chicks can be critical in determining success (Deeming *et al.*, 1996a).

Flooring

A critical part of rearing the youngest birds is the need to insulate the birds from a cold floor so that nocturnal heat loss is minimized. Other critical aspects of the floor are ease of cleaning and grip for the birds. In Britain, Deeming *et al.* (1996a) opted for a rough concrete floor with an area which is electrically heated to 20°C, although plastic slatted flooring, rubber mats or straw (under a wire mesh) are viable alternatives. The type of flooring used is important in reducing the risk of leg injuries and infections.

Floor area for inside shelters can vary between countries and is primarily dependent upon the prevailing climate. In Germany, rearing is invariably intensive with birds being kept inside enclosures based on an area requirement of 0.25 m^2 per bird at hatching. increasing to 2 m^2 per bird at 3 months of age (Kreibich and Sommer, 1995). In Britain, Deeming *et al.* (1996a) recommend a space requirement of 0.125 m^2 kg^{-1} of bird as a guide for birds up to 3 months of age so that sufficiently large and warm quarters can be provided for exercise during autumn and winter months.

Management practices

Various systems for rearing chicks have been tried, ranging from birds of mixed ages being kept in the same enclosure through to all-in all-out systems where single groups of chicks are kept in the one facility. Most rearing systems are based on maintaining groups of chicks, usually split by age within one large building. Both Wade (1995b) and Deeming *et al.* (1996a) emphasize the value of an all-in all-out operation for rearing birds up to 12 weeks of age. Chicks hatched in one week are kept together within one facility which is designed to house them all until they are moved to another enclosure. Shelter areas are recommended by Wade (1995b) as 0.3–1.4 m^2 $bird^{-1}$ with outside enclosures having 18.5–37 m^2 $bird^{-1}$. By contrast, Deeming *et al.* (1996a) suggest a minimum floor area of 0.125 m^2 kg^{-1} bird mass. The advantages of all-in all-out rearing over multi-age rearing are: rearing environment can be optimized for the age of bird; there is less stress on the birds because they are moved less; and there are improvements in biosecurity

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and disease prevention. Flooring can be sand, rough concrete or rubber matting for younger birds.

Hygiene and biosecurity

The importance of hygienic conditions in intensive rearing units is emphasized by several authors (Wade, 1995b; Deeming *et al.*, 1996a). Rearing units should be run on the basis of high levels of biosecurity (Dunn, 1995; Wade, 1995b) in order to minimize risk of infection from other sites, particularly via visitors. Additional information about biosecurity is provided by Perelman (Chapter 13).

REARING OF JUVENILES

In many parts of Europe, juvenile birds are kept outside in enclosures covered with pasture and with access to a shelter. Fencing is usually based on tensile wires or mesh between posts. In Britain, the quality of fencing is important because farmers are required to have a Dangerous Wild Animal Licence before they can keep the birds. This legislation, originally designed to ensure that members of the public are not keeping dangerous animals without any regulation, requires that fencing should be sufficient to keep the birds within designated enclosures. This legislation is unique to Britain, and elsewhere in Europe and the rest of the world there is no such regulation of ostrich farming.

The use of greenhouses or polythene tunnels as shelters for chicks is considered by Kreibich and Sommer (1995) to be very useful because they can provide sufficient indoor areas for exercise during periods of inclement weather, particularly during winter. Temperature control in the greenhouse is considered very important to ensure that birds do not get overheated. There is usually easy access to outside runs.

AREAS FOR FUTURE RESEARCH

Future research must focus on increasing chick survivability if the ostrich industry is to be competitive in the animal agriculture arena. Early feeding of ostriches, i.e. as soon after hatching as possible, could bring about physical and functional changes in the intestinal tract as well as the immune system. Work with poultry has shown that neonatal nutrition enhances intestinal tract and immune development (Dibner *et al.*, 1998). Understanding the changes brought about by early feeding, particularly with respect to utilization of the residual yolk sac, could be of great benefit in maximizing survival of the young ostrich. Research into stress management can also be fruitful in improving chick survivability. A better understanding of the behaviour of the young ostrich could provide clues as to how bet-

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ter to manage these birds during their first 3 months of life, in order to minimize stress.

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9

Welfare

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Although there are at least 200 species of large terrestrial herbivores in the world, many of which potentially might be employed for commercial meat production, only about 20 have been domesticated for this purpose (Kyle, 1994). Farming of ostriches has a long history, and whilst South Africa still dominates the ostrich industry, there has been increased production in other nations since the mid 1980s (van der Vyer, 1992). Within a decade the attractions to both producer and consumer of this 'new agricultural animal' (Gerlach, 1995) have induced farmers around the world to move into ostrich production (Deeming and Angel, 1996).

It has been suggested in the USA (Duewer *et al*., 1994), Australia (Hastings and Farrell, 1991) and Italy (Endrighi *et al*., 1996) that conditions and circumstances are reasonably favourable for the development of successful and competitive ostrich farming. It is apparent, however, that the climate, terrain and agricultural backgrounds of some of the other countries with embryonic farming operations differ dramatically from those in which ostriches occur naturally. On this basis, and considering the limited experience possessed by farmers in nations new to ostrich production, it may be predicted that a number of difficulties would arise in relation to the husbandry of the birds, nutrition, disease, breeding success and welfare.

Whilst it is possible to establish an economically viable industry with little immediate attention to animal welfare, political and public pressures (particularly in northern Europe) quickly focus attention upon the inadequacies of animal producers whose practices fall short of perceived standards. Questions concerning the welfare consequences of ostrich farming in some nations have been raised. These range from reports of the induction of prominent abnormal behaviours in birds excessively confined indoors during cold winters in Canada (Samson, 1996) to the assertion that current systems of production in Germany may impose

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extreme stress upon growing ostriches and may constitute overt cruelty, thereby contravening national and European legislation (Kosters *et al*., 1996; Hagen and Hagen, 1996). Concern about commercially farmed ostriches has also been expressed in the UK (Moody, 1992; Anon., 1993; Bertram, 1993) resulting in the development of proposals for welfare guidelines and standards (Anon., 1997a). Similar considerations have led to the introduction of regulations governing ostrich farming in Denmark (Petersen, 1996) and stimulated debate of the welfare issues in Sweden (Jansson *et al*., 1996). In the Netherlands, the health and welfare of farmed ostriches are strictly monitored by specialist veterinarians (de Jong, 1994).

ASSESSING WELFARE

There are recognized difficulties associated with objectively assessing the welfare of animals and the necessity of separating this activity from moral and ethical judgements (Broom, 1993). A pragmatic approach has been adopted by the UK Farm Animal Welfare Council (FAWC) who defined an animal's basic welfare 'needs' in 'five freedoms' (Anon., 1992): (i) freedom from hunger and thirst; (ii) freedom from discomfort; (iii) freedom from pain, injury or disease; (iv) freedom to express normal behaviour; and (v) freedom from fear and distress.

Whilst it is self evident that constraints upon these 'freedoms' will compromise the welfare of animals, the freedom to express normal behaviour raises some interesting issues, particularly in the case of farmed animals or species of agricultural importance. The definition of 'normal behaviours' is complex and difficult, and it is proposed that there is a biological requirement or need to perform some of these activities. The concept and underlying mechanisms of behavioural and psychological needs have been extensively debated, but it is generally accepted that expression or performance of highly motivated behaviours are essential to optimal welfare, and frustration or prevention of the expression of such needs is detrimental to an animal's well being (Baxter, 1988; Broom, 1988; Fraser, 1988; Hughes and Duncan, 1988). If a procedure or husbandry regimen compromises one or more of the five freedoms then it can be considered inherently stressful and will reduce the welfare of an animal. It is a major challenge to design animal production systems such that all these freedoms are fully satisfied, and perhaps attempts to minimize stress and maximize welfare are more realistic objectives.

Mitchell and Kettlewell (1998) propose that the concept of the use of integrative, predictive models, which take into account physiological, psychological or behavioural stress, can be useful in the analysis of circumstances which may be considered to threaten the welfare of an animal. This view is supported by the suggestion of Moberg (1985) that 'biological responses to stress may be the key to the assessment of animal well being'. Some confusion still exists, however, due to the complexity and uncertainty surrounding the assessment or quantification of 'stress', animal welfare and 'suffering' (Dantzer and Mormede, 1983; Moberg,

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1985; Barnett and Hemsworth, 1990; Mason and Mendl, 1993; Wiepkema and Koolhaas, 1993; Bekoff, 1994). Whilst stress physiologists and behaviourists may accept the measurement of physiological and behavioural responses as indicative of disturbances in the predictability and controllability of an animal's environment and thus its well being, it is also acknowledged that change *per se* in biological variables need not reflect reduced welfare (Moberg, 1985; Cashman *et al*., 1989; Barnett and Hemsworth, 1990). Highly dynamic patterns of homeostatic response observed during stress make it difficult to deduce any simple relationship between stress and welfare (Wiepkema and Koolhaas, 1993). The concept of a specific cut-off point in a stress response or physiological variable at which welfare is deemed to be at risk has been criticized (Mendl, 1991), and a more integrated approach to stress reactions has been advocated (Dantzer and Mormede, 1983). The use of a spectrum of different stress indices, or the development of stress profiles, may represent a more effective approach which is further strengthened by an understanding of the action and functional significance of the physiological and behavioural responses or welfare parameters to be quantified (Mason and Mendl, 1993).

Cognitive ethology has given rise to the proposal that, in addition to the use of empirical data in making decisions concerning animal welfare, subjectivity and common sense have an important role and subjective assessments should be viewed in the same critical light as ostensibly objective scientific fact (Bekoff, 1994). Anthropocentric claims about the ways in which animals interact in their social and non-social worlds are often used to influence decisions on how animals can or should be used by humans. Acceptance of the cognitive capacities and sentience of animals has led to the argument that if there is uncertainty, even if only slight, about an animal's ability to feel pain or suffer, then the individuals should be given the benefit of the doubt. It was acknowledged that it is still necessary to attempt to answer the following questions: what are positive grounds for imputing suffering or suspecting that they are concealed; what is a significant degree of suffering; can we measure differences in the degree of suffering and are they morally relevant?

In practice it is necessary to have a working definition and understanding of welfare and reductions therein. All encompassing statements, such as: welfare equates with biological fitness and is only reduced if an animal's ability to survive or reproduce is threatened; animal welfare is only impaired if it is experiencing an unpleasant mental state; or the welfare of an individual animal is its state of mental or physical health indicating living in harmony with its environment (Mason and Mendl, 1993; Wiepkema and Koolhaas, 1993), are not indicative of what practical measurements should be made to determine welfare status in commercial production systems. Perhaps the answer to the question of what welfare is should be: 'the state of an animal as regards its attempts to cope with its environment' (Broom, 1988) but qualified by: 'welfare refers to how much an animal has to do to cope, and how well or badly it succeeds in coping'.

In this context simple physiological and behavioural measurements can be made under different conditions and relative judgements made concerning the

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associated welfare effects or risks. It should be emphasized that such measurements must be entirely objective and free from moral or ethical considerations, and that no single physiological or behavioural measure is sufficient (Wiepkema and Koolhaas, 1993). Indeed the construction of physiological stress profiles consisting of multiple biological variables may prove most informative (Mitchell and Kettlewell, 1998).

These concepts are more readily applied to some areas of commercial ostrich farming than to others. Thus whilst it is possible to characterize a range of physiological responses to different types of transportation, the same measures may not easily be used to determine the effectiveness of any given stocking density and paddock construction. Again, a holistic approach must be adopted and behavioural, clinical and production parameters incorporated into the overall model along with physiological stress assessments. The main areas of concern in relation to welfare in commercial ostrich production are outlined below. Many of these topics are described in detail in the rest of this volume, so in some instances only short points are made whereas some categories are dealt with in more detail.

FACTORS AFFECTING OSTRICH WELFARE

Disease

Disease is frequently regarded in many quarters as a separate issue from animal welfare, although veterinarians working in some branches of animal production accept disease as the single biggest threat to welfare. Close attention must be paid to prevention of infection, nutritional imbalance or inadequacies, avoidance of injury through poor management and inappropriate environmental conditions (Huchzermeyer, Chapter 12; Perelman, Chapter 13). Disease and injury may not be amenable to the physiological or behavioural analysis or response modelling recommended above, but it may still constitute important reductions in the well being of animals and must therefore be assessed and strategies for disease prevention, minimization and alleviation developed.

Nutrition

Welfare issues related to nutrition are generally a consequence of a failure to match the diet provided under commercial farming conditions to the specific requirements of the birds, resulting in deficiencies or nutrient imbalance. These problems may be exacerbated by a lack of fundamental knowledge of ostrich nutrition and movement towards production on terrain and in climates which differ markedly from those encountered in nature. This is particularly true for the ostrich in the higher latitudes of northern Europe and North America.

Details of ostrich nutrition are given by Cilliers and Angel (Chapter 5), but

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further research relating to nutrition is essential, with an emphasis on the specific requirements of birds raised in production systems and environments encountered in new-producer nations. A better understanding of the nutrition of young ostriches will reduce the risk of nutritional stress which compromises welfare and productivity.

Behavioural abnormalities

It may be argued that animal production in systems and environments which do not closely resemble those of the natural habitat for that species, particularly for farmed wild animals, may impose constraints which will prevent or frustrate the performance of highly motivated behaviours. Any compromise of the expression of natural behaviours can be regarded as an unacceptable reduction in welfare. In such situations, natural behaviours may be replaced by abnormal and redirected behaviours which may reflect the imposition of psychological stress or be directly detrimental to the animal. In order to optimize conditions in commercial ostrich production and to minimize the disruption of normal behaviours (Deeming and Bubier, Chapter 4), it is first necessary to characterize and understand those normal behaviours and then to analyse the effects of the commercial production environment, e.g. to identify and quantify the incidence of abnormal behaviours.

The spectrum of abnormal behaviours or behavioural problems occurring in commercially produced ostriches, particularly in new-producer nations, represent one of the most important challenges to researchers and the industry. It is essential to fully characterize the natural behaviour of ostriches and to relate their behavioural needs to the demands imposed by production systems. Only by understanding these issues and by matching practices and farming environments to the birds' requirements will it be possible to reduce behavioural stress and to achieve the necessary standards of welfare.

Climate

The ostrich is obviously extremely well adapted to the climatic environments prevailing in Africa, and it tolerates both hot, arid conditions and cooler, wet subtropical zones (Sauer and Sauer, 1966). Stewart (1994) asserts that the birds are very hardy and can be successfully bred and reared in environmental extremes from desert heat to winter snows. Indeed, other authors assured of the hardiness and adaptability of the species suggest that this is an important reason for the global expansion of ostrich farming, that the birds will thrive under extreme conditions (Shanawany, 1996), and that adults can be safely kept outdoors throughout the year in climates such as that encountered in the UK if basic shelter is provided (Moody, 1992). Other studies express concern over the effects of extreme climatic conditions on ostriches of all ages (Hagen and Hagen, 1996; Samson, 1996; Deeming, 1997, 1998). This is perhaps prudent in view of the meteorological differences between some of the regions actively involved in

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ostrich production, e.g. the dry, hot climate of Texas (Duewer *et al.*, 1994) is very different from the cold winters of Canada (Samson, 1996) and Sweden (Jansson *et al.*, 1996). The suitability of the British climate for ostrich farming has been questioned (Bertram, 1993).

Production characters such as growth rate may be affected by the climate (Samson, 1996). Angel (1996) recorded marked depressions (13–24%) in growth rate during the winter season in Indiana where the annual temperature range was −14.4 to +34.4°C. It is not known if the thermal challenges presented to farmed ostriches in the northern hemisphere constitute a threat to the welfare of the birds and surprisingly little research has addressed the problem. In this context Bertram (1993) suggests that in the absence of definitive scientific evidence caution should be exercised, and the colder, wetter climates of Europe and perhaps North America should be regarded as potentially deleterious to the welfare of ostriches unless there is proper management of the birds.

In addition to the physiological and metabolic responses relating to the climatic environment, the behavioural aspects should also be considered. Deeming (1997, 1998) examined the effects of climatic conditions on the behaviour of captive adult ostriches in Britain. The major finding of time–budget analysis was a behavioural response to periods of rain during which birds of both sexes greatly increased the amount of time sitting at the expense of pacing and other behaviours but not feeding or foraging, when compared with dull, bright or sunny conditions (Deeming and Bubier, Chapter 4). These results could have important welfare implications for commercial production in countries such as the United Kingdom. The birds show a propensity to sit out in rainy weather rather than seeking shelter and could thus be adversely affected by wetting during cold weather (Deeming, 1997): as ostriches lack a preen gland and thus may have poor waterproofing of the feather cover, then this may lead to a major disruption of the insulative properties of the plumage during wetting. In other birds this is known to increase heat loss markedly and cause profound hypothermia, especially in conjunction with air movement (Mitchell *et al.*, 1997). It is recommended that ostriches be brought into shelter during prolonged periods of rain, particularly in cold European winters (Deeming, 1997).

The climate and the artificial thermal micro-environments to which ostriches are exposed in commercial systems may affect both welfare and productivity. Whilst the ostrich is physiologically well adapted to survival in a wide range of environments, this is dependent upon the birds being able to exploit their full repertoire of behavioural and physiological responses. These factors should be taken into consideration when housing and transportation designs are implemented. The birds should be able to express behavioural responses to heat and cold, such as seeking shelter, which should therefore be available (Moody, 1992), and have the freedom to use wing spreading and postural changes to increase heat loss when appropriate, e.g. in indoor pens. If heat stress is likely then a fresh water supply is essential. Future improvements in ostrich production systems and environments aimed at increasing welfare standards should be based upon a sound scientific knowledge of the basic physiology and behaviour of the birds.

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Transportation

Despite the obvious importance of transportation of ostriches, for relocation for breeding or rearing, or to sites of slaughter, little published information is available relating to the topic. It has been suggested that transport should not cause mortality in ostriches or compromise their health but does constitute an inevitable source of stress (de Jonge *et al.*, 1997). Public and media attention, however, are focused on the problems when transport mortalities do occur and are reported (Anderson, 1995). The loss of 21 ostriches due to heat exhaustion on a 5 h journey in the UK was described by a representative of the Royal Society for the Prevention of Cruelty to Animals as 'horrific and clearly showing the urgent need for strict guidelines on how ostriches should be transported and humanely killed'.

Ostriches are frequently moved across continents by air and subsequently are transported by road over varying distances. Payne (1993, 1994) reported that on a long flight (6.5 h) birds housed in purpose-built wooden crates and with environmental temperature controlled to 18°C generally travelled well with no obvious ill effects. A degree of agitation and distress was apparent early in the flight in some birds, and there was a risk of trauma as these individuals jumped around in the compartments. Each crate (3.30×2.25×2.13 m) was divided into eight compartments each holding one bird, giving a space allowance of 0.79 m^2×2 m high. The temperature in the hold was regulated by controlled ventilation so that within the crates it was 18–20°C with a relative humidity of below 50%. This is important as high temperature–high humidity combinations are particularly damaging in animals which rely upon evaporative cooling (Mitchell and Kettlewell, 1998). Under these controlled conditions none of the birds exhibited signs of heat stress. General stress in the novel environment was reduced by employing low light levels and this is a good strategy in all forms of ostrich transport.

Road transport of ostriches may be carried out on a number of vehicle types. Often, modified cattle transporters divided into pens may be employed. In one study, when juvenile birds (approximately 10–12 months old) were transported in pens measuring 1.8×2.5 m each containing eight birds, raised respiratory rates and 'gular pumping' were noted accompanied by behavioural signs of distress including neck twisting and inappropriate seeking behaviour (Payne, 1993, 1994). The internal temperature at this time was 18°C with a relative humidity of 89%, and it was proposed that the adverse reactions of the birds were a consequence of the combination of the loading procedures, the novelty of the environment and the imposed thermal load.

In another study, 50 10-month-old ostriches (70–80 kg) were transported on a commercial vehicle, in pen groups of ten individuals, for a period of 4.5 h (Mitchell *et al.*, 1996). Despite a ventilation rate which maintained only a 1.0°C lift over ambient in the transport compartment, physiological and metabolic measurements indicated that the birds experienced substantial stress during the journey (Table 9.1). Thus transportation caused a significant 1.7-fold increase ($P<0.001$) in plasma glucose, suggesting a stress-induced mobilization of

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glycogen reserves and stimulated gluconeogenesis. A 50% reduction in plasma lactate ($P<0.001$) may indicate the substrate for this latter response. Activation of lipolysis and depletion of lipid stores were reflected by a 55% increase in plasma non-esterified fatty acids ($P<0.01$) and a 46% decrease in triglycerides ($P<0.001$). A 2.6-fold increase in plasma uric acid ($P<0.001$), accompanied by a 16% rise in plasma protein ($P<0.05$), is consistent with extracellular fluid shifts or a degree of dehydration which may have been exacerbated by polypnea observed in many birds in transit. A 75% rise in plasma corticosterone ($P<0.05$) and a tendency for heterophil:lymphocyte ratio to increase indicate transport induced stimulation of the hypothalamo-adenohypophyseal-adrenocortical axis. An apparent increase in the efflux of the intracellular enzymes creatine kinase ($\times 2.5$, $P<0.001$) and aspartate aminotransferase ($+18\%$, $P<0.01$) suggest changes in the integrity of the muscle cell membrane, possibly as a consequence of the acceleration forces upon the standing birds and the resulting postural instability observed in transit.

These physiological findings indicate that even in the recommended transport conditions, the birds exhibited glycaemic and lipolytic responses and changes in blood chemistry consistent with the imposition of physiological stress which may include fatigue, dehydration and tissue damage. It is proposed that further studies to identify the particular stressors responsible and to define optimum transport environments and methods for ostriches are essential.

Video recording of the ostriches' behaviour throughout the journey revealed some unusual and aberrant behaviours (Mitchell and Kettlewell, unpublished observations, 1996). Several birds exhibited 'head bobbing' and arching of the neck for long periods during the journey. The motion of the vehicle caused sig-

Table 9.1. Plasma metabolite concentrations, enzyme activities, corticosterone concentrations and whole blood heterophil:lymphocyte ratio (H:L) of ostriches at 10 months of age before and after a 4.5-h period of road transportation. Results are means ($\pm$SD; $N=8$) and are from Mitchell *et al.* (unpublished observations, 1996).

Parameter	Pre-transport	Post-transport
Glucose (mM)	10.6±0.93	18.5±0.81
Lactate (mM)	11.6±0.92	5.8±0.30
Non-esterified fatty acids (mM)	0.47±0.05	0.73±0.05
Triglycerides (mM)	0.81±0.07	0.44±0.02
Uric acid (mg l^{-1})	0.324±0.077	0.853±0.101
Protein (g l^{-1})	0.404±0.007	0.469±0.020
Creatine kinase (IU l^{-1})	560±53	1398±104
Aspartate aminotransferase (IU l^{-1})	115±6.7	137±3.6
Corticosterone (ng ml^{-1})	4.9±2.9	8.6±3.7
H:L ratio	8.5±3.2	24.2±10.3

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nificant postural instability, and sudden braking or accelerations caused disturbances and panic amongst the standing birds. Most birds attempted to stand throughout the journey. Another stimulus which seemed to influence behaviour was visual contact with the outside world, and passing objects and vehicles clearly upset the birds. This was also true of humans approaching the vehicle when it was stationary. These results suggest that more attention should be paid to transport stress in ostriches reared on farms, as even short journeys may severely compromise their welfare.

Pre-emptive measures to improve ostrich welfare during commercial transportation might include ensuring that birds are well nourished and fully hydrated before departure and the provision of a vitamin supplement containing ascorbic acid and α-tocopherol (vitamins C and E) which may offer some benefits in reducing oxidative tissue damage during stress. A clear indicator of inadequate hydration in ostriches is the appearance of a white, thick, concentrated urine (Levy *et al*., 1990). The farmer should check the appearance of the excretions of birds that are to be transported to ensure that birds showing signs of dehydration are not subjected to the further rigours of transport stress without correction of their water balance.

It is proposed that ostriches should be transported on closed vehicles with active ventilation to control the thermal environment. Such vehicles can maintain low light levels which will calm the birds and will insulate them from external noise and visual images. If pens are of the correct size, e.g. 2.5×2.5 m and 2.2 m high with 1.3 m partitions, then at a stocking density of at least 0.75 m^2 per large adult, birds may stand or sit during the journey as they wish. Appropriate bedding such as short (30–50 mm) chopped straw should be provided. The fan ventilation rate should be calculated so as to maintain the internal environment within prescribed limits. If a maximum lift of 5°C was designated for a single deck carrying 50 ostriches, then an absolute minimum ventilation rate of 1.34 $m^3\ s^{-1}$ would be required. For the operational flexibility required in the range of climatic conditions encountered in commercial practice, fans with a capacity of 4–5 $m^3\ s^{-1}$ should be installed. Until vehicles of this design become more readily available and can be fully evaluated, ostriches should be transported in accordance with the general provisions laid down in the UK Welfare of Animals in Transport Order (Anon., 1997c), which implements European Directive 91/628/EEC as amended by Directive 95/29/EC.

Specific guidance for the transport of ostriches is currently in preparation in the UK (Anon., 1998) and a similar document has been produced in South Africa (Anon., 1996). Whilst space precludes description of the entire contents of these guides, specific issues markedly influencing the welfare of the birds merit individual mention. Space allowances should reflect the age and size of the birds, ranging from 0.1 m^2 for 1-month-old birds to 0.75 m^2 for adults. Chicks may be transported in groups of four to six per small crate compartment, and group sizes should be restricted to 12 and eight birds per pen for juvenile and adult birds, respectively. Age groups must not be mixed for transportation. Ostriches should rest, in quiet surroundings, for at least 2 h prior to a journey. Water should be

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available up to departure, but withdrawal of food for periods of up to 4 h (10 h recommended in South Africa) may be desirable to reduce faecal contamination of the vehicle floor (which poses a risk of slipping and injury) and birds in transit. Floor (and ramp) and bedding materials should be non-slip. Loading ramps should have no more than a 25° angle, and loading should preferably be on the level as birds will strongly resist loading when driven up steep ramps (Payne, 1993). Journey durations should be as prescribed for poultry and thus food and water should be provided on journeys lasting more than 12 h. It could be argued that the limits for durations and rest periods pertaining to some of the larger red meat mammals would be more appropriate for adult ostriches. On long journeys a vehicle carrying ostriches should stop for 8 h in any 24-h period, preferably at night, so that the birds may be fed, watered and rested. There are many other areas which impinge directly upon the welfare of ostriches in transit, including vehicle construction and standards, pen sizes, light levels and inspection and access. For further details see Harris (1996) and Anon. (1998).

In common with many areas of commercial ostrich production, progress in transportation and the development of improved procedures, equipment and vehicles are impeded by a lack of basic research. Future studies must assess the induction of physiological stress in ostriches in transit as an indication of welfare problems (Mitchell *et al.*, 1996), in order to identify the main causes and mechanisms of transport stress in this species and to provide soundly based scientific solutions.

Handling

Welfare of ostriches under handling is another area upon which little information is available. Clearly handling and transport are intimately linked and some general recommendations can be made (Anon., 1993, 1997b). Adult ostriches are large animals but can be easily frightened, and if allowed to panic and run at high speed they can suffer serious injury due to collision with fences, vehicles and other agricultural equipment. They also represent a serious hazard to the handlers. All handling should be gentle and considerate, and done by specially trained personnel. Appropriate training should include general biology and behaviour of the ostrich, capture and handling, general management procedures, health controls, signs of disease and signs of stress and distress. Young birds should be handled relatively frequently to become accustomed to human contact. Small birds can be picked up whilst supporting the body, but larger birds can be restrained by standing astride the back (Deeming *et al.*, 1996). Three handlers are required to restrain an adult bird. Care should be taken not to injure the vulnerable neck, and birds should not be held by a single leg or wing. Chemical restraint (e.g. tranquilization) should not be routinely employed but hooding, particularly in fractious birds, is recommended (Perelman, Chapter 13). Whenever possible handling procedures should be undertaken in low light. No objective scientific studies have been undertaken to compare the stress-induced or welfare effects of different handling procedures or

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techniques, and progress is currently dependent on the practical experience of those engaged in the commercial production or veterinary care of ostriches.

A handling (and often pre-slaughter) procedure which will potentially cause significant distress, discomfort and pain to farmed ostriches is the harvesting of feathers by inappropriate means. Traditionally in South Africa the feathers are plucked from live animals (Holtzhausen and Kotzé, 1990). This is regarded as a wholly unacceptable practice in Europe and alternative procedures are required (Bertram, 1993). Clipping of feathers above the blood line in the non-growing zone will be painless. Such clipping of the large wing and tail feathers can be performed without causing distress to the birds (Sales, Chapter 10). It must be ensured, however, that feather removal is not excessive so as not to impair insulation and thermoregulation. New European legislation will specifically ban live plucking and specify clipping protocols (Anon., 1997b). It should be noted, however, that when severe degradation of barbules occurs in the live bird (due to feather pecking or adverse climatic conditions) the resulting bare shafts must be pulled out before a new feather can be induced to grow.

Slaughter

New-producer nations are currently developing their own standards and methods of slaughter of meat ostriches (see Sales, Chapter 10), and at present few slaughter houses are equipped to handle these animals. The absence of facilities and a dearth of knowledge relating to the neurophysiology and cardiovascular physiology of the ostrich represent major obstacles to the provision of humane slaughter methods for these birds. The question of whether ostriches can be slaughtered humanely has been raised (Bertram, 1993) and constitutes a major welfare issue.

Killing must be done without causing undue pain, agitation or distress and be performed by a competent person. Whatever the method employed, it should cause immediate loss of consciousness rapidly rendering the animal insensible to pain and distress, or cause the death of an animal which is anaesthetized or effectively stunned (Anon., 1997b). According to a recently published review, electrocution is the method of choice for the slaughter of ostriches (de Jonge *et al.*, 1997) although precise specification of the type of system to be employed, including stunning voltages and currents, is required in addition to full consideration of the ease of operation of such devices and their safety aspects with regard to humans. Drowning and suffocation are not permitted in Europe.

In the USA, Morris *et al.* (1995) have described a successful technique involving stunning by a captive bolt device. This method may require further development for use in Europe, and the possibility of a gas-stunning technique might also be investigated. The different methods available for the slaughter of ostriches have been reviewed by Paleari *et al.* (1995) and Sales (Chapter 10). It is clear that extensive research in this area is still required before suitably humane procedures, which are practical on a commercial scale, can be readily implemented.

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IN CONCLUSION

It is considered of some significance that the Standing Committee of the European Convention for the Protection of Animals Kept for Farming Purposes has produced a draft recommendation relating to the welfare of ratites in a farming environment (Anon., 1997b). This must reflect the concern felt as commercial production of ostriches expands around the world. The document addresses many of the issues raised in this chapter, and makes numerous recommendations which are in keeping with Articles 3–7 of the convention aimed at improving animal welfare.

This brief review highlights the paucity of information relating to the welfare of ostriches in a farming environment and poses more questions than it answers. Some solutions to problems are offered, but many more wait to be addressed. It is hoped that some insight is provided into the issues pertaining to the welfare and transport of ostriches, and that the reader will be encouraged to explore more deeply the available information as presented in the bibliography and in this book as a whole, and reinterpret and re-evaluate the findings and the proposals. In addition, it is hoped that there will be more fundamental research which will examine the problems of ostrich production in a modern farming setting and thus facilitate and underpin future improvements in commercial practices and systems, and therefore optimize the welfare of the birds.

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10

Slaughter and Products

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The market for feathers for fashion resulted in domestication of the ostrich in South Africa during the middle of the 19th century (Wagner, 1986) and development of an ostrich farming industry (Deeming, Chapter 1) in South Africa. Despite various setbacks in the market the ostrich has remained an agricultural animal and the modern industry in South Africa no longer relies on feathers, but on leather processed from ostrich skins (Wagner, 1986). Ostrich biltong is also popular in South Africa. The export of ostrich meat from the abattoir at Oudtshoorn has steadily increased from 400 tons in 1986 to 500 tons per year in 1992 (Oliver-Lyons, 1997). Ostrich meat is also being exported from Israel, Namibia, Zimbabwe and the USA. This chapter reviews the slaughter process for the ostrich and provides details of the wide variety of products that the bird produces.

SLAUGHTERING

Ostriches are slaughtered in South Africa at approximately 14 months of age to obtain optimal leather quality and a second feather harvest (Swart, 1981). In some other countries where the ostrich is regarded more as a meat animal (Israel, Australia, USA, Europe), and feathers are regarded as a minor by-product, birds are slaughtered at 9 months due to a decline in feed efficiency after this age (Raines, 1995) and because a slaughter mass of 85–90 kg is obtained at a younger age (Jones *et al*., 1994).

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Pre-slaughtering handling

In South Africa a preliminary and partial plucking of feathers (cutting of the remiges and rectrices) is done either on the farm before birds are loaded into open-topped vehicles for sending to the abattoir, or after birds are unloaded at the abattoir (Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996). In South Africa, Canada and the UK, birds are kept overnight in small, fenced areas, with water but without food, before being hooded and brought to the stunning ramp (Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996; Shewring, 1996). In Israel, special attention is paid to the pre-slaughtering phase, with birds being raised in fenced areas that gradually are made smaller and smaller as slaughter age and mass are approached. Birds are moved into a funnel-shaped chute that closes after each bird passes through (Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996).

Stunning

In the Oudtshoorn abattoir in South Africa, an operative guides a single bird into position by pushing and by manipulation of the tail feathers from behind. A second operative 'catches' the bird by the beak and brings the head down into a position accessible to the stunning operative. Birds are electrically stunned using a 90 V and 0.3 A current applied to the head through two electrodes (Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996). A modification to this procedure, used by some abattoirs in South Africa and the UK, involves a shackle being placed on the tips of the wings and raised by an electric hoist only sufficiently to support the mass of the bird upon collapse (Shewring, 1996).

In one study (Wotton, personal communication, 1997), electrical stunning of the head with a current in excess of 400 mA at 50 Hz AC induces an effective stun in at least 90% of ostriches, provided that the stun-to-stick interval does not exceed 60 s. An electrode with a small contact area to the bird's head, although very effective at maintaining contact with the stunned bird as it collapses, results in an exaggerated heating effect at relatively low current levels. This enhances a build-up of carbon deposits which quickly increase the electrode:skin impedance and reduce current flow. An increase in electrode area produces an increase in current flow at a similar voltage and reduces the build-up of carbon on the electrodes. Saline-soaked sponges produce a threefold increase in current amplitude. The stun duration, the degree of post-stun convulsions and the time between stunning and shackling did not significantly affect the resumption of rhythmic breathing movements, which indicate the first stages of recovery, and hence the effectiveness of electrical stunning followed by exsanguination in ostriches. Tong position, when applied vertically to the head, showed a significant improvement over lateral applications.

Whilst electrical stunning is the method used in South Africa and Israel, captive bolt stunning is commonly used in the USA, Canada and Australia (Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996; Shewring, 1996). However, it

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was found that captive bolt stunning causes extremely severe post-stun convulsions that can last for up to 7 min. This could have important implications regarding the welfare of ostriches at slaughter, as it may delay hoisting and neck cutting as well as affecting operator safety (Hewitt, 1996). Pollok *et al.* (1997a) report that the use of carbon dioxide to immobilize and render the bird unconscious eliminates the post-stunning thrashing which normally occurs with most other approved methods. However, this method requires special safety regulations.

Bleeding and skinning

In South Africa, when the bird collapses upon stunning, a leg clamp is applied by an operative so as to secure the legs to the floor and restrain the bird to permit shackling. The bird is then suspended by both legs by chains hanging from the ends of an upturned horizontal bar. The vertical load-bearing axis is connected to the trolley of an overhead guided monorail. The bird is then lifted to an upper floor where it is bled through an incision of the blood vessels just under the head. After bleeding for 10 min, feathers are removed manually. Heads are removed and skinning, initiated by three major incisions through the skin, is performed (Dunster and Scudamore-Smith, 1992; Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996).

In Israel, stunned birds are lifted from the ground and loaded on to a conveyor belt. The head and part of the neck hang down so that blood can be collected after the jugular veins have been cut. In the USA, plucking is done by a mechanical clipper. In the USA, Canada and Australia, skinning is aided by compressed filtered air introduced into the subcutaneous cellular tissues through a nozzle inserted under the skin through a small leg incision (Dunster and Scudamore-Smith, 1992; Paleari *et al.*, 1995; Sales and Oliver-Lyons, 1996).

Evisceration

In South African abattoirs, when skinning is completed the carcass is hooked to the overhead rail system by the wings and the feet are removed by severing the tibial-tarsal joint. At given points along the butchering line the sternum is split, the linea alba cut and the thoracic and abdominal cavity eviscerated. Any parts that are judged unsuitable for human consumption are discarded. Thighs are removed from the carcass, and hung by the distal epiphysis of the tibia, weighed and transferred by another guide rail to the cooling room. After removal of necks and trimming, the rest of the carcass is sent to be processed into bone meal (Fig. 10.1).

The hanging position is by the legs in the USA, Canada and Australia, but the oesophagus, exposed by a transverse cut in the skin at the lower extremity of the neck, is tied in order to prevent microbial contamination of the meat from the gastro-intestinal tract, and evisceration is carried out by removing the breast plate. Whilst in South Africa only thighs are cooled for 24 h at 0°C before

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Fig. 10.1. Simple plan for an ostrich-slaughtering plant (adapted from Sales *et al.,* 1997).

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deboning, in the USA, UK and Australia the whole carcass is cooled (Dunster and Scudamore-Smith, 1992; Paleari *et al*., 1995; Sales and Oliver-Lyons, 1996; Shewring, 1996).

Microbiology of ostrich carcasses

Dunster and Scudamore-Smith (1992) reported that ostriches slaughtered using the Australian method showed low levels of coliforms (less than 1 colony-forming unit cm^{-2}), and the absence of *Salmonella*, thereby indicating a satisfactory microbiological standard. Aerobic plate counts of *Listeria*, *Salmonella* and *Campylobacter* of carcasses slaughtered in the USA immediately post-evisceration were within acceptable ranges (4.0, 3.2 and 3.6 $\log_{10}$ cm^{-2}, respectively). Other predominant bacterial types on carcasses were *Bacillus*, coryneform bacteria, *Flavobacterium*, *Lactobacillus* (homofermentative), *Micrococcus*, *Moraxella*, *Staphylococcus* and the yeast *Trichosporon*, all common in the environment and some native to the skin of animals and humans. The recovery of food-borne pathogens from ostrich carcasses indicates that the same considerations must be taken as with other raw foods of animal origin (Harris *et al*., 1993).

FEATHERS

In contrast to feathers from other birds, the ostrich feather is symmetrical in shape. Furthermore, the absence of tiny barbs (rami), which form an air-resistant unit in flying birds, means that barbules are not interlocking in ostrich feathers (Fig. 10.2).

Under proper care and management an ostrich can provide a feather crop without deterioration in quality for about 35 years (Duerden, 1910), although the best feathers are produced between the ages of 3 and 12 years (Wagner, 1986). An adult ostrich can yield 1–1.2 kg of short feathers and 400–450 g of white plumes (Holtzhausen and Kotzé, 1990), whereas slaughter birds produce around 700 g of body feathers (Swart and Kemm, 1985).

The best tail and wing feathers are made into fashion items such as fans, fringes, feather boas or hats. Ostrich feathers are readily charged with static electricity when stroked, making them extremely suitable for dusters for domestic use and in the auto and computer industries (Holtzhausen and Kotzé, 1990). Ostriches are plucked for feather production only in South Africa. Plucking, when conducted at the correct stage, is the removal of dead material that cannot cause any pain to the bird.

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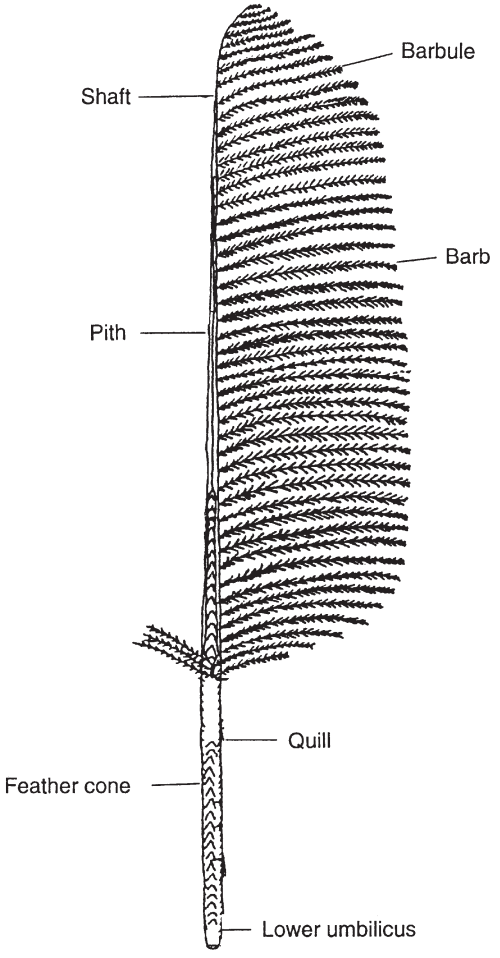

Fig. 10.2. Different parts of the ostrich feather (adapted from Duerden, 1909a). One side of the feather is illustrated and the spaces between the barbs have been exaggerated for clarity.

The plumage

Four different plumages can be recognized in the life cycle of the ostrich (Duerden, 1909a, 1911; Sales, 1995a, 1997). Hatchling plumage consists of small tufts of rather stiff rays or barbs, differing in length, starting from about the same level and lacking a central shaft or quill. Feathers vary in colour from light to dark brown or nearly black, giving a mottled appearance to the chick.

About a week or two after hatching, the natal feathers begin to be pushed

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out of the feather sockets by the chick feathers. The chick plumage is complete at the age of about 8 months. The chick feathers bear the natal down at the tip and are mottled in character because of the light brown upper and dark grey lower parts. Various kinds of feathers (body, neck, head, coverts, wing quills and tail quills) start to differentiate, but both genders are similar.

From 4–5 months of age the body feathers of the chick are pushed out gradually, one at a time, and are replaced by larger juvenile feathers of a uniformly dark grey or slate colour with a rounded tip. From 8–9 months of age the chick begins to lose its mottled appearance. All the juvenile feathers are fully ripe at the age of 16 months, the last to ripen being the wing quills. Body feathers are darker in the male than in the female; ventral feathers are white in the female but change to black in the male. The wing quills of the male are pure white, whilst those of the female are tipped with grey.

Gender differences are most obvious in the adult plumage, acquired when the birds are about 2 years old. The adult male plumage is characterized by black body feathers and coverts, the female's by drab body feathers and coverts. The tail quills of the male are white below and yellowish brown above, whilst those of the female are a mottled light and dark grey.

Kinds of feathers

Feathers are limited to definite feather tracts (pterylae) separated by featherless tracts (apteria) over the lower part of each side of the body and on the entire leg of the adult bird. The first crop of wing quills grown by the chick, tapering towards the tip in a spear-like manner, are known as spadonas (an Italian word for a long, heavy sword). Body feathers, occurring over the body and wings, determine the general shape of the bird, overlap to protect the skin and help in maintaining body temperature.

The largest single row of feathers in the wing are called the quills or remiges. The primaries are attached to the finger bones of the wings and the secondaries are attached to the ulna. These (about 24) feathers on the first row of each wing are called whites in the male and feminas in the female. Bycocks, or fancies, are the four to five partly coloured wing quills towards each end of the first row from the male bird. The upper wing coverts, called blacks in the male and drabs in the female, are arranged in rows of wing coverts above the wing quills. The lower wing coverts, collectively known as floss, are the single row of light and fluffy feathers that cover the wing quills. The tail quills or rectrices cover the stumpy tail. Hair-like filoplumes (hair feathers) are found on the skin around the wing and tail quills (Duerden, 1909a).

Removal of feathers

The feather is a highly specialized part of the skin, comprising the epidermis, a horny or corneous layer (sheath layer) on the outside, and the living, active

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Malpighian layer (feather layer) on the inside. The epidermis is entirely devoid of blood vessels, and only extremely fine nerve branches pass into its lower part. The dermis is richly supplied with both blood vessels and nerves. Each feather is formed from a feather germ, a special group of cells situated in the feather layer. New feathers are always formed below the old ones from a new, unique germ. The surface of the skin in a healthy ostrich is continually shedding the dead cells of the sheath layer. The feather layer continues to divide throughout the bird's lifetime, forming new cells which are gradually pushed outwards to replace those lost.

Growth of the new feather starts when the germ cells at the bottom of the socket increase in number and grow in size, thereby pushing the existing feather further out of the socket. Horny material, which ultimately forms the shaft, barbs, barbules and sheath, is formed from the feather and sheath cells beyond the soft cells of the germ. The emerging feather is surrounded by the horny feather pith for some distance beyond the lip of the socket. As this dries and cracks, the bird preens it away with its beak. The part of the growing feather above the pith is now fully formed feather material which no longer needs to be nourished with blood supply and is ready for clipping. The quill, however, takes about 2 months more to complete its growth. The germ is still active at the bottom of the socket, and the added cells from it push the quill still further out of the socket. As the quill ripens it becomes narrowed and rounded off towards the tip situated at the bottom of the socket. In section the new feather germ, which will give rise to the next plume, can be seen below the ripened quill. The walls of the socket collapse after the quill is drawn. The removal of a quill initiates the new germ.

When ripe plumes are clipped and quills are drawn it is only removal of horny material that would ultimately be cast off by the bird in the natural process of moulting. The ripe quills are dead, horny parts of the skin, and their extraction means no more than the falling out of dead hair (Duerden, 1913; Sales, 1995a).

Feathers that stay on the ostrich after they become 'ripe' lose their lustre and appear dull and worn (Smit, 1963). If plumage is not drawn artificially, quills are not all moulted at the same time, and some will remain in their sockets, which will delay the plumage stage (Duerden, 1908). Plucking (removal of the whole feather from the socket by hand) before the feather is ripe causes bleeding, and successive growth is shorter and the quill is stiffer (Douglass, 1881).

Under the '8-month' system employed in South Africa, spadonas are clipped with pruning shears when the chick is about 6 months old. The quills are drawn 2 months later by pulling with pliers. After quilling, the socket collapses and the hole partly closes. Usually the surface is smeared with petroleum jelly or oil to protect the socket from exposure, to soften the skin and to stimulate the new growth (Smit, 1963). It is not necessary for the juvenile or successive quills to be drawn immediately on attaining ripeness. The germs may all remain dormant for several months beyond 16 months if the quills are left in position (Duerden, 1908). Quilling of the wing quills, plucking of the second and third row of the upper coverts, floss and tails takes place at approximately 8 months of age. Feathers are plucked again at 14 months of age. In order to get an uniform 'plucking' at 14 months of age, long 'green' feathers have to be removed at the 'cleaning' at 8 months.

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If birds are not in good condition or on a poor diet, some feathers of the new crop will appear and may introduce irregularities. The regularity of the 8-month system can be maintained only under the most favourable conditions of weather and food supply. On farms where climatic changes between winter and summer are great and food not plentiful during the winter, a yearly system is conducted. Birds must not be too fat when quilled, as some sockets are likely to stay blank (Duerden, 1908).

Removal of feathers in South Africa is done in a plucking box, triangular in shape, measuring 53 cm wide in the front, 71 cm wide at the rear, 1.2 m high and 1.2 m long. It is usually built of wooden posts or steel piping. The bird is pushed into the box against the front and a movable cross-bar is slipped in behind under the belly to stop it reversing (Smit, 1963).

Sorting

According to De Mosenthal and Harting (1876), breadth, grace and quality were the most important commercial characteristics of ostrich feathers. Duerden (1909a) included the following in his list of commercially important characteristics: length, breadth, flue density, strength and rigidity of flue, quality and lustre, shape, shaft thickness, and absence of bars and other defects. According to Swart *et al.* (1984) size (length and breadth), appearance (evenness and self-support of the flue and feather shape), flue quality (softness and lustre) as well as defects are the dominant factors controlling the price of fashion feathers. A description of the different grades of the South African classification system of ostrich feathers is presented in Tables 10.1 and 10.2.

Bars are the most common defect in feathers, and consist of imperfect development of the barbules. In the region of the defects the barbules are shorter and do not project from the barb to the same degree as elsewhere, making the flue weaker in these places. Bars sometimes occur at regular intervals of 13–25 mm and are rarely wider than 1.5 mm. Bars are present in wing quills and tail feathers, as well as in the shorter feathers. This condition is caused by a wrinkled outer sheath, due to alternations in day and night growth because of differences in blood pressure, which in turn causes the soft, developing feather to be indented. Barring can be prevented by eliminating factors such as insufficient food, ailments and accidents, internal and external parasites, exposure to weather and rapid changes in temperature, that has an influence on the blood supply to the feathers (Duerden, 1909b; Smit, 1963; Osterhoff, 1979). Feathers which stay wrapped in the sheath are another defect of economic importance. This condition is usually associated with a dry, scaly, unhealthy skin, caused by diseases, internal parasites or deficient nutrition (Duerden, 1909b; Smit, 1963).

The various kinds and qualities of feathers are separately sorted and tied in bundles. Loose feathers, for example from the bellies of slaughtered birds, are sold in bags. Feather markets buy the plucking which is further sorted into classes according to colour, quality and length determined by the buyer or manufacturer.

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Table 10.1. Subjective classification of ostrich feathers in commercial grades (Swart, 1979a).

Characteristic	Class				
	1	2	3	4	5
Size					
Length	Very short	Short	Medium	Long	Very long
Breadth	Very narrow	Narrow	Medium	Wide	Very wide
Shape					
Tip	Very narrow	Narrow	Normal	Wide	Very wide
Butt	Very narrow	Narrow	Medium width	Broad	Very broad
Margin	Very tendril-like	Tendril-like	Moderate smooth	Smooth	Very smooth
Flue characteristics					
Strength*	Over weak	Very weak	Weak	Strong	Very strong
Density	Very sparse	Sparse	Moderately dense	Dense	Very dense
Closeness of barbs	Sparse	Moderate	Dense		
Width of plumules	Very narrow	Narrow	Moderately wide	Wide	Very wide
Softness	Hard	Stiff or strong	Normal	Soft-elastic**	Very soft
Lustre	Dull	Medium	Bright		
Oiliness	No oil	Slightly oily	Moderately oily	Oily	Very fatty
Character	Very bad	Bad	Moderate	Good	Very good
Quality	Dry cotton-like	Cotton-like	Silky cotton	Silky	Elastic silky
Flue behaviour	Very bad	Bad	Moderate	Good	Very good
Flue style	Bad	Moderate	Good	Very good	
Damage					
Wear	No wear	Minimal wear	Wear	Much wear	Very much wear
Soiling	No soiling	Minimal	Moderately	Excessively	Extremely soiled
Bars	No bars	Very little bars	Moderate bars	Many bars	Excessive bars
Spiral twist	Bad	Moderate	Good	Very good	
Other					
Plume strength	Very slack	Slack	Moderate	Strong	Very strong
Shaft thickness	Fine	Medium	Thick		
Colour deviations	No colour	Few colour	Moderate colour	Much colour	Excessive colour

*Class 6, too strong; **ideal class.

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Table 10.2. Criteria for classification of ostrich feathers (Swart, 1979a; Mellett, 1995).

Characteristic	Class 1	2	3	4	5
Size					
Length	< 540 mm	*c.* 550 mm	*c.* 600 mm	*c.* 650 mm	> 700 mm
Breadth	< 250 mm	*c.* 280 mm	*c.* 320 mm	*c.* 360 mm	> 400 mm
Shape					
Tip	Sharp pointed	An angle of 90°C or less but not pointed	An angle of more than 90°C but not blunt	Wider point but not round	Broad round point
Butt	Narrow and tapering to a point	Less narrow	Rounded and narrower than the rest of the plume	Rounded or square, but narrower than the rest of the plume	Square and at least as wide as the rest of the plume
Margin	Untidy with lots of streamers	Uneven edge	Uneven plumule length	Ragged edge	Even length of plumules, each with rounded edges
Flue characteristics					
Strength*	Willow-like	Plumules bend at their bases	Plumules bend downwards	Hard, point upwards, plumules still bend	Hard, plumules do bend, but not downwards
Density	Very translucent	Fairly translucent	Even cover and normal density	Even density but slightly translucent	Non-translucent dense flue
Closeness of barbs	Noticeable gaps between barbs	Normal definition of barbs	Barbs closely associated or even double		
Width of plumules	3–4 mm	5–6 mm	7–8 mm	9–10 mm	11–12 mm
Softness	Hard cotton-like and too strong flue	Cotton-like and strong flue	Elastic and cotton like, medium strong flue	Elastic and silky	Very soft and silky
Oiliness	Loose dry barbules without elasticity, mimosa-leaf like flue	Mimosa-leaf like flue	Elastic mimosa-leaf like flue, normal lustre	Elastic willow-like flue	Sticky willow-like flue
Character	Prickly barbules	Clear disruption of barbules	Disrupted symmetry, but no overlapping of barbules	Good symmetry, but not perfect arrangement of barbules	Symmetrical or parallel arrangement of barbules

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Table 10.2 continued

Characteristic	Class				
	1	2	3	4	5
Quality	No elasticity, dull, too strong, very hard and dry	Non-elastic, dull, strong flue, dry and hard	Moderately silky, normal lustre, medium fine to medium strong and of reasonable character	Normal lustre, medium fine, moderate oiliness and good character	Lustrous, noticeable, oiliness, very good character and moderate flue strength
Flue behaviour	No support, lot of disarrangement of barbs	Little support, overlapping of barbs and visual untidiness	Moderate support and overlapping, untidiness not visual	Good support, few or no overlapping	No overlapping, very tidy
Flue style	Very open or broken flue	Noticeable open gaps in flue	Broken flue without open gaps	Unclear broken flue	Uniform and continuous flue
Damage					
Wear	No wear	Minimal wear with no broken tips	Moderate wear with noticeable broken tips	Noticeable wear	Noticeable broken tips, broken plumules and excessive wear
Soiling	White feather flue	Not noticeably soiled	Noticeable diluted soiled	Clearly visible soiling	Red-brown colour
Bars	No or very little bars	Non-noticeable, dull bars	Few bars	Noticeable amount of bars	Lot of bars
Spiral twist	Tip and butt heavily twisted	Noticeable twisted tip	Slightly twisted tip	Traces of twisting	Straight
Other					
Plume strength	One third of plume falls forward	One quarter of plume falls forward	Tip falls slightly forward	Strong spoon-like appearance	No bending
Colour deviations	Pure white plumes	Slight coloured in butt	Slightly coloured in tip or but	Showy colour in tip	Plumes with grey spots

*Class 6, hard, the plumules point upwards and no bending occurs.

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It is recommended to keep the wings, tails, blacks and drabs of males and females apart during plucking (Smit, 1963).

SKINS

Luxury shoes, handbags and purses, popular in Europe, the USA and Japan, are manufactured from ostrich leather. The thinner hides of younger ostriches are used for garments (Holtzhausen and Kotzé, 1990). Recommendations for optimal thickness of the leather are 0.85 mm for clothing, 1.25 mm for handbags and boots, and 1.45 mm for belts (Mellett *et al.*, 1996).

A reptilian type of corium, as found on the volar surface of the feet of birds, is shown in the thigh, and to a lesser extent over all the body, of the ostrich skin. The skin on the legs resembles that of a crocodile.

Whilst the skin of the African Black male ostrich is metallic blue, that of the female varies from light to dark grey. Ostrich skins are characterized by quill sockets ('buds') over large areas of the skin, especially the back and the belly. The buds are larger in older birds and the prepared leather is heavy and hard (Holtzhausen and Kotzé, 1990). If feathers are still 'green' at slaughter, buds will be without form. If too many feathers are removed from the ostrich during plucking or cutting, sunburn can occur which will lower the value of the skin (Swart, 1979b).

Ostriches are slaughtered in South Africa at the age of 14 months, a live mass of at least 75 kg, in order to obtain an optimal skin area of about 1.25 m^2 (Holtzhausen and Kotzé, 1990; Smith *et al.*, 1995). There is considerable debate worldwide as to the effect of age on ostrich hide quality (Angel *et al.*, 1997). According to Mellett (1995), the ideal shape of follicles cannot be achieved before the age of 14 months, although the optimal size can be reached at about 10 months of age. Angel *et al.* (1997) demonstrated that tensile strength (above 75 kg cm^{-2}), as well as the Lastometer test which evaluates resistance to grain tract (above 10 cm whilst the shoe and boot industry required a value of 7 cm), were not influenced by increasing animal age from 7.3 to 16 months. For every day of age, hide thickness increased by 0.0021 mm within this age range.

According to the conventional South African method, the removed hide must include the body, the shin bone up to the joint of the toe, the wing up to the elbow joint and the neck. Only the skin over the head, toes and point of the wings is absent (Smit, 1963; van Jaarsveldt, 1992). After plucking, the skin is removed by a superficial incision along the ventral midline, starting from just below the head and cutting around the sternal and pelvic calluses and the vent. The skin is further cut along the ventral sides of the wings and legs in areas free of follicles, and freed by circular incisions around the limb at the wrist, hock and neck. The incisions along the limbs are continued straight across to the midline incision. The skin is then peeled away from underlying connective tissue and fat, taking care to avoid holes.

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Different 'recipes' are recommended by different manufacturers for the treatment of skins. The traditional South African method, where skins are supplied to the Klein Karoo Agricultural Cooperative, requires that the hide must be free of feathers and washed with water to remove all residual blood, which can provide a medium for bacterial growth. Washing also cools the skin, reducing the possibility of decay. It is important not to damage the membrane at the inside of the hide. The wet skins are treated with 7–9 kg of clean, fine salt, together with naphthalene (1 part naphthalene to 100 parts salt) used to prevent 'pink rotting'. The skin is folded so as to ensure that the brine does not trickle out and it is delivered to the tanner as soon as possible. Drying of the skin will decrease its value (Smit, 1963). van Jaarsveldt (1992) suggests that wet, salted skins can be stored in a pile located on a wooden slatted floor 60 mm above the floor. Each skin is laid flesh side up and covered with a layer of salt.

The varying thickness of the ostrich hide, together with the buds, have necessitated a special tanning process to produce the leather (Holtzhausen and Kotzé, 1990). The basic process of ostrich leather tanning is as follows (Chris van der Merwe and *Exotan*, personal communication). First the skin is soaked to remove salt and to rehydrate the skin after storage. This is followed by liming, which is chemical removal of keratinous protein, usually the feathers and epidermis. During this process the skin swells. Fleshing removes unwanted layers of flesh and fat which are adhering to the inner surface before de-liming to neutralize the skin. Pickling is an acid preparation (necessary for the process of chrome tanning) which precedes chemical bleaching of natural pigments in the skin giving the surface a more even colour. Degreasing, to remove fats from within the skin structure is the last stage before chrome tanning which converts the raw skin into stable, unputrifiable leather. It also improves the thermal stability of the hide. Neutralizing reduces the acidity of the hide in preparation for re-tanning which is designed to impart specific properties (e.g. fullness, lightfastness, colour and softness) to the leather. Fat-liquoring introduces oil emulsions into the leather to lubricate the fibres and soften the hide to improve toggle drying which flattens the leather and reduces its water content. Solvent degreasing removes the remaining natural fats for improved dyeing, i.e. colouring to precise shades. Finishing involves application of protective films for different effects. Most of ostrich leather is given a full aniline finish (pigment free) to maintain its natural appearance. The final process is sorting the tanned hides into different grades. Unfortunately no detailed information has been published about the chemical components used in this process.

Quality of the finished hide is very important. The tanned hide should be free of damage caused by sunburn or lacerations. Follicles must be of average size and must have a rounded shape. Leather should be of sufficient strength to stretch over a boot tree without tearing (Mellett, 1995). van Jaarsveldt (1992) provides a scheme for grading skins. Subjective evaluation of the crown or 'diamond' area is used to grade ostrich skins (Fig. 10.3). An example of a grading scheme in South Africa (Anon., 1998) is as follows. Grade 1: the crown must have good, prominent quills. Only a small, insignificant mark (hole, scratch, scar,

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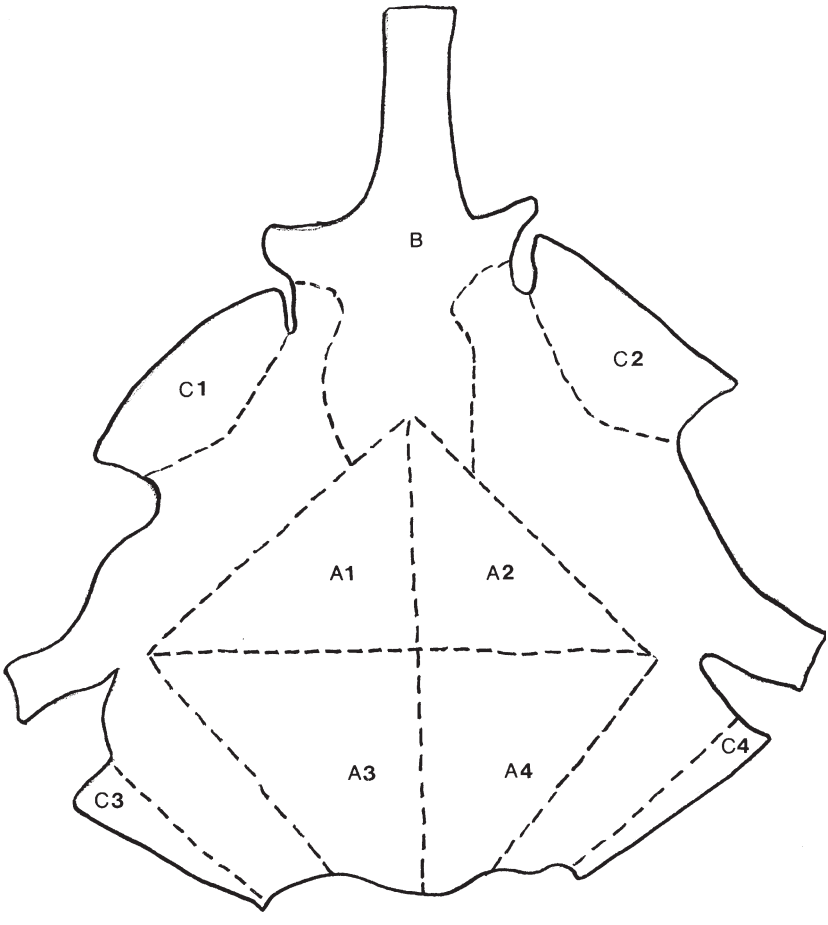

Fig. 10.3. The various quill areas of a tanned ostrich skin viewed from the dorsal aspect, with the neck at the top and tail at bottom. A (1–4), main 'diamond' area of crown; B, neck; C (1–2), upper belly flap; C (3–4), lower belly flap. Redrawn from Anon. (1998).

loose scab or healed wound) will be allowed on one quarter of the crown. Marks on the cutting line of the four quarters, or outside the crown, will not adversely affect quality. Four acceptable panels to be cut from the crown. Grade 2: as grade 1, except that one prominent mark will be allowed in one quarter of the crown and three acceptable panels will be cut from it. Grade 3: two prominent marks will be allowed in two quarters of the crown and two acceptable panels will be cut

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from it. Grade 4: any quill development is acceptable. Prominent marks in all four quarters of the crown are acceptable.

MEAT

Meat yield

Two studies have recorded the average mass of the carcass, the mass and the percentages on a live mass basis of the meat products (Table 10.3). Except for the neck and a pair of muscles from the back (M. obturatorius medialis), all usable meat is situated on the hindquarters (Fig. 2.4). Separable lean meat is 62.5% of the ostrich carcass, which compares with 65% for broiler fowl, 71% for turkeys and 64% for beef (Morris *et al.*, 1995a). Of the lean meat recoverable from an ostrich carcass, about two-thirds consists of the ten major muscles (M. gastrocnemius, M. femorotibialis, M. iliotibialis cranialis, M. obturatorius medialis, M. iliotibialis lateralis, M. iliofibularis, M. iliofemoralis externus, M. fibularis longus, M. iliotibialis cranialis and M. flexor cruris lateralis), with the remaining third as lean trimmings (Morris *et al.*, 1995b). Mean masses of the different major muscles derived from three studies are shown in Table 10.4.

Pollok *et al.* (1997a) found that hot carcasses lost 2.6% of their mass during the chilling process due to moisture evaporation (cooler shrink). In the beef industry carcasses are sprayed with water during the chilling process to minimize cooler shrink, but as yet this is not practised with ostriches.

Although Morris *et al.* (1995a) found no significant differences in slaughter yields due to gender, it was stated that yield differences might be the result of the exhibition of secondary sexual characteristics in mature ostriches. Ostriches fed a complete pellet diet from 4–6 months of age until slaughtering showed a significantly higher amount of fat (5.8 versus 0.8 kg) and bone (10.7 versus 9.8 kg) than ostriches fed a high-forage diet, but showed a similar lean meat yield (38.1 versus 34.2 kg) (Baltmanis *et al.,* 1997). Variations in the time that each ostrich is held off feed and water prior to slaughter affect the amount of ingesta in the digestive tract, and variations in the mass and percentage of the viscera, full gizzard and proventriculus can occur (Morris *et al.*, 1995a). This will have an influence on the dressing percentage (live body mass divided by hot carcass mass).

Although post-transport application therapy appears to have little effect on ostriches, pre-transport use of electrolytes significantly reduces the loss in live mass (17.5 versus 11.3%). Significantly lower total fat and higher lean meat yields of pre-transport-treated ostriches suggests that electrolyte-treated ostriches might have mobilized their fat reserves during the period of *ante mortem* stress (Schaefer *et al.*, 1995).

Slaughter yields will differ between studies due to different carcass standards used in the industry (Baltmanis *et al.,* 1997). In the studies of Pollok *et al.* (1997a–c), warm and cold carcass masses were determined based on a carcass

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Table 10.3. Mean mass (±SE) and percentage of carcass and by-products on a live-weight basis.

Component	Morris *et al.* (1995a, b)[1]		Pollok *et al.* (1997a, b)[2]	
	Mass (kg)	Percentage of live mass	Mass (kg)	Percentage of live mass
Live	95.54±2.55		99.73±1.89	
Hot carcass	55.91±1.64		48.82±1.13	
Cold carcass	54.57±0.42		47.55±1.09	
Dressing percentage		58.6		49.0
Total carcass lean	34.11±0.32	35.7	29.72±0.24	29.8
Total carcass fat	5.03±0.17	5.2	3.45±0.25	3.5
Total carcass bone	14.61±0.09	15.3	9.78±0.14	9.8
10 major muscles	22.59±0.23	23.6	21.91±0.18	22.0
Lean trimming	11.52±0.11	12.1	–	–
Feathers	1.74±0.13	1.85	1.55±0.06	1.6
Blood	2.98±0.37	3.11	3.91±0.10	4.0
Wings	0.74±0.06	0.78	1.82±0.06	1.8
Feet	2.51±0.16	2.64	2.64±0.05	2.7
Tail	0.36±0.03	0.38	0.27±0.01	0.3
Head	0.78±0.03	0.82	0.68±0.02	0.7
Hide	6.71±0.25	7.04	4.77±0.11	4.8
Heart	0.94±0.05	0.99	0.91±0.01	0.9
Lung and trachea	1.29±0.05	1.36	0.95±0.02	1.0
Full gizzard	5.80*±0.52	6.05*	3.14±0.13	3.1
Empty gizzard	2.15*±0.09	2.26*	1.64±0.10	1.5
Back fat	0.87±0.14	0.90	–	–
Liver	1.42±0.08	1.49	1.77±0.10	1.7
Viscera	8.29±0.45	8.68	14.41±0.64	14.7
Abdominal fat	4.11±0.40	4.28	5.55±0.37	5.5
Kidneys	0.39±0.02	0.41	0.45±0.02	0.5
Male reproductive tract	0.08±0.02	0.09	–	–
Female reproductive tract	0.18±0.04	0.18	–	–
Sternum plate	1.22±0.10	1.29	0.95±0.06	0.9

[1]Fourteen ostriches of 10–14 months from Texas, Louisiana, Oklahoma and Indiana.
[2]Twenty-five ostriches of 10–11 months; pure bred and cross-bred animals from Texas.
*With proventriculus.

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Table 10.4. Mean mass (±SE) of the different single muscles from the hindquarters.

Muscle	Sales (1996a)[1]		Morris *et al.* (1995b)[2]		Pollok *et al.* (1997b)[3]	
	Weight (kg)	Percentage of carcass weight	Weight (kg)	Percentage of carcass weight	Weight (kg)	Percentage of carcass weight
M. gastrocnemius pars interna	0.70±0.03	1.72	–	–	1.53±0.08	3.12
M. gastrocnemius pars externa	–	–	–	–	1.50±0.03	3.08
M. femorotibialis medius	0.48±0.03	1.18	–	–	–	–
M. ambiens	0.21±0.01	0.52	–	–	–	–
M. iliotibialis lateralis	0.82±0.04	2.01	3.49±0.16	6.43	1.71±0.05	3.51
M. iliofibularis	1.16±0.04	2.85	3.49±0.12	6.38	1.69±0.05	3.46
M. iliofemoralis	0.30±0.01	0.74	0.95±0.04	1.71	0.54±0.02	1.10
M. iliofemoralis externus			1.45±0.06	2.69	0.72±0.02	1.47
M. fibularis longus	0.33±0.02	0.81	2.59±0.20	4.71	–	–
M. iliotibialis cranialis	0.39±0.02	0.96	1.41±0.05	2.56	0.69±0.02	1.42
M. flexor cruris lateralis	0.27±0.02	0.66	1.04±0.05	1.92	0.52±0.02	1.06
M. obturatorius medialis	–	–	1.68±0.08	3.12	0.83±0.03	1.69
FFF	0.37±0.01	0.91	–	–	–	–
II	0.35±0.02	0.86	–	–	–	–

[1]Thirty-nine African Blacks aged 8–14 months from Oudtshoorn district; trimmed of all external fat and epimysial connective tissue.
[2]Fourteen ostriches of 10–14 months; Texas, Louisiana, Oklahoma and Indiana; trimmed of all external fat and epimysial connective tissue.
[3]Twenty-five ostriches of 10–11 months; pure bred and crossbred animals from Texas; trimmed of all external fat but not epimysial connective tissue. FFF, M. femorotibialis externus; M. femorotibialis internus; M. femorotibialis accessorius; II: M. iliofemorotibialis externus; M. iliofemorotibialis internus.

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with the neck, abdominal fat, wings, breast plate and legs 6 inches above the hocks removed. Unfortunately Morris *et al.* (1995a, b) did not describe in detail how warm and cold carcass masses were determined. Differences in the components included in determination of these parameters could account for the differences in dressing percentages found in the two studies (Table 10.3). Apart from differences between strains, cutting method and amount of trimming have a definite influence on the mass of different muscles (Table 10.4).

Meat quality

In contrast to other species where meat is sold as cuts or portions, ostrich meat is usually sold as individual muscles. The nomenclature of the muscles of the proximal part of the pelvic limb of the ostrich was first described by Haughton (1865), although more recently Mellett (1994) has applied avian musculature nomenclature (van den Berg, 1979) to the different muscles. Trade names for the various muscles as used by different countries are summarized in Table 10.5.

Due to differences between individuals, regions and countries, the establishment of standards for the different components of eating quality is complicated (Amerine *et al.*, 1965). Meat quality is determined by the consumer according to a combination of characteristics that define the level of acceptability (Kramer and Twigg, 1962). These include: sensory evaluation according to visual appearance when meat is bought; flavour when meat is cooked; and juiciness, taste and tenderness which are evaluated over a short period of chewing (Smith *et al.*, 1970). Some histological, physical and chemical characteristics of meat are correlated with quality. Histological, biophysical and physical characteristics of different ostrich muscles are shown in Table 10.6. Observed variations mean that no single muscle is suitable as a representative of all individual muscles of the carcass. Different muscles have to be evaluated for a variety of characteristics (Sales, 1996a).

pH

A striking characteristic of ostrich meat is the relatively high hydrogen ion concentration measured 24 h after the animal is bled (pH_f). The pH of living muscles is around 7.2, but when the animal dies glycogen is broken down by anaerobic glycolysis, producing lactic acid which causes a drop in pH. Normally glycolysis takes place slowly and proceeds to a pH_f value of approximately 5.5. If glycolysis takes place very quickly, such meat has a light appearance and poor water-holding properties. By contrast, if only a slight drop in pH occurs over time, meat will have a dark colour, high water-holding capacity and limited shelf life. This dark, firm, dry (DFD) condition is associated with depletion of glycogen in the muscles and it is common in animals that are stressed before slaughter (Hofmann, 1988). The glycogen levels in one unidentified muscle of ten ostrich carcasses ranged

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Table 10.5. Trade names of different muscles from the ostrich carcass in different countries.

Muscle	South Africa[1]	Australia[2]	USA[3]	Canada[4]	Belgium/Zimbabwe[1]	Israel[1]
Leg						
M. gastrocnemius, pars interna	Drum steak	Inside leg	Inside leg	Inside leg	Flat drum*	Inside drum
M. gastrocnemius, pars externa	Drum steak	Outside leg	Outside leg	Outside leg	Big drum*	Outside drum
M. gastrocnemius, pars media	–	Leg fillet	–	–		
M. fibularis longus	Drum steak	Heel	Mid leg	Inside leg	Small drum*	Outside drum
Thigh						
M. pubo-ischio femoralis	–	Fillet middle	–	–	–	–
M. flexor cruris medialis	–	Fillet flat	–	–	–	–
M. iliofemoralis	Bergie filet	Fillet outside	Inside strip	Inside strip	Eye filet	Filet
M. flexor cruris lateralis	Triangle steak	Fillet long	Outside strip	Outside strip	Triangle steak	Flat filet
M. iliofibularis	Fan fillet	Fan filet	Fan	Fan	Triangle filet	Fan filet
M. iliotibialis lateralis	Rump steak	Rump outside	Round	Outside thigh	Rump steak	Full rump
M. ambiens	Tournedos	Rump eye	–	Pearl	Small filet	–
M. iliotibialis cranialis	Oyster filet	Rump point	Top loin	Top strip	Tenderloin	Inside filet
M. iliofemoralis externus	Goulash	Rump round**	Oyster**	Oyster**	Oyster fillet	Oyster fillet
M. femorotibialis medius	Moon steak***	Rump inside***	Tip***	Tip***	Moon steak***	Round
Back						
M. obturatorius medialis	Small leg	Loin	Tenderloin	Back tender	–	–

[1]Oliver-Lyons (1997).
[2]Anon. (1995).
[3]Anon. (1996a).
[4]Anon. (1996b).
*Confusion due to not mentioning of scientific muscle names on meat charts.
**Together with M. iliofemoralis internus, M. iliotrochantercicus caudalis, M. iliotrochantercicus cranialis.
***Together with M. femorotibialis accessorius, M. femorotibialis externus, M. femorotibialis internus.

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Table 10.6. Values (mean±SD) for histological, biophysical and physical characteristics of different ostrich muscles from 39 South African Black ostrich carcasses (Sales, 1996a).

Muscle	Fibre diameter (μm)	Sarcomere length (μm)	pH_f	Cooking loss (%)	Warner-Bratzler shear force (kg)	Pigment content (mg g^{-1} haem)
M. gastrocnemius pars interna	57.5^{a} ±7.54	2.34^{a} ±0.14	5.92^{b} ±0.08	35.8^{bc} ±03.62	2.97^{c} ±0.53	5.79^{d} ±0.85
M. femorotibialis medius	56.5^{a} ±8 .79	2.11^{c} ±0.13	5.90^{c} ±0.12	37.7^{a} ±2.83	2.94^{c} ±0.62	5.70^{d} ±0.92
M. ambiens	58.2^{a} ±8.78	1.88^{d} ±0.17	5.88^{c} ±0.06	35.1^{c} ±3.05	3.67±1.20	7.90^{b} ±1.14
M. iliotibialis lateralis	56.0^{a} ±6.41	1.89^{d} ±0.13	5.84^{d} ±0.08	36.4^{b} ±2.91	3.46^{b} ±0.94	6.12^{c} ±0.91
M. iliofibularis	49.5^{b} ±6.06	2.22^{b} ±0.16	6.04^{a} ±0.16	36.0^{b} ±2.83	4.44^{a} ±0.99	5.10^{e} ±0.84
M. iliofemoralis	51.5^{b} ±5.85	1.80^{e} ±0.14	5.79^{e} ±0.06	31.9^{d} ±3.11	2.64^{c} ±0.99	9.09^{a} ±1.33
Mean	54.9±7.96	2.04±0.24	5.91±0.12	35.5 ±3.68	3.35±1.08	6.62 ±1.73

Values in columns with different superscripts differ significantly ($P < 0.05$).

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from 2 to 301 mg 100 g^{-1} wet meat (Dunster and Scudamore-Smith, 1992).

Post-mortem glycolysis, as described by the decline in muscle pH, has been investigated in several ostrich muscles (Sales and Mellett, 1996). Whilst the M. gastrocnemius pars interna, M. femorotibialis medius, M. iliotibialis lateralis and M. iliofemoralis showed the typical pattern of descending pH decline, the M. ambiens and M. iliofibularis showed a very rapid decline in pH until 2 h post mortem, and thereafter pH increased (Table 10.7). In the case of the M. iliofibularis and the M. ambiens, unrealistic values of 9.01 and 9.80, respectively, for the estimated pH at time 0 h, and 3.918 and 3.035 units h^{-1}, respectively, for the rate of pH decline, illustrate the unusual pattern of these two muscles over time. In comparison to beef, ostrich meat can be classified as an intermediate meat type between normal ($pH_f = 5.5$) and extreme DFD ($pH_f > 6.2$) types.

Electrical stimulation of carcasses is primarily applied to accelerate the reduction in *post mortem* pH decrease (Carse, 1973). If muscles are deboned and cooled to an internal temperature of below 10°C before a pH of 6.0 is reached, the phenomenon of cold shortening, responsible for the toughening of meat, occurs (Locker and Hagyard, 1963). Both beef and sheep carcasses with a high pH_f do not respond favourably to electrical stimulation, which can even cause toughening of meat (Chrystall *et al.*, 1982). Standard South African slaughtering procedures of ostriches involve the removal of legs from the carcass by 30 min *post mortem*, and then subjecting carcasses to cooling temperatures of 0°C. Under these conditions, relatively long sarcomere lengths (a measurement of the extent of contraction in muscles) and the absence of a significant linear relationship between sarcomere length and Warner–Bratzler shear force (WBS) values showed that no cold shortening occurs in the different muscles (Dunster and Scudamore-Smith, 1992; Sales, 1994, 1996a). Only two muscles (M. iliotibialis lateralis and M. iliofemoralis) showed a high frequency of shortened (20–40%) sarcomeres. However, these muscles had relatively low WBS values (i.e. tender) compared with other muscles (Table 10.6). Morris *et al.* (1995a) showed that electrical stimulation (400–500 V, 1.5 A, 60 Hz, 20 pulses per min for 2 min within 45 min *post-mortem*) had no significant effect on *post-mortem* pH or temperature decline in ostrich muscles.

Cooling rates of six muscles from different regions when the whole ostrich carcass was cooled at 0–3°C for 24 h are shown in Table 10.8. Dunster and Scudamore-Smith (1992) found that carcasses took 10 h to reach 10°C when the chiller temperature ranged between 4 and 6°C. With chillers operating at an air temperature of 1°C and with an air velocity of 0.5–0.75 m s^{-1}, carcass temperature is reduced to 4°C over a period of 14 h (Shewring, 1996).

Different pre-slaughtering and stunning techniques led Sales (1995c) to conclude that genetic adaption of muscle fibres for glycogenolysis, and not only pre-slaughter stress, might be responsible for the high pH_f. By contrast, Berge et al. (1997) found that emus rested for 2 weeks near the abattoir and then transported and stunned within 15 min had a pH_f value of 5.6 within 2–4 h of bleeding. Meat of ostriches treated pre-transport with electrolytes tended to have a lower pH_f than the control (Schaefer *et al.*, 1995). The pH of the M. iliotibialis cranialis and

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Table 10.7. Mean pH values (mean±SE) at fixed times after death, of different muscles from five South African Black ostrich cooling thighs (Sales and Mellett, 1996).

Time (h)	M. gastrocnemius pars interna	M. femorotibialis medius	M. ambiens	M. iliotibialis lateralis	M. iliofibularis	M. iliofemoralis
0.5	7.13^{a}±0.11	6.73^{a}±0.19	6.32^{a}±0.11	6.59^{a}±0.23	6.31^{a}±0.15	6.51^{a}±0.25
2.0	6.51^{b}±0.19	6.46^{b}±0.17	5.85^{b}±0.12	6.27^{b}±0.18	6.00^{c}±0.09	6.17^{b}±0.15
4.0	6.26^{c}±0.09	6.18^{c}±0.08	5.87^{b}±0.05	5.97^{c}±0.18	6.07^{bC}±0.06	5.91^{c}±0.08
6.0	6.12^{d}±0.06	6.02^{cd}±0.07	5.94^{b}±0.01	5.99^{c}±0.07	6.08^{bc}±0.04	5.88^{c}±0.03
8.0	6.07^{d}±0.06	6.03^{cd}±0.08	5.94^{b}±0.03	5.96^{c}±0.02	6.09^{bc}±0.04	5.94^{c}±0.04
24.0	6.05^{d}±0.09	5.99^{d}±0.06	5.92^{b}±0.05	5.94^{c}±0.06	6.13^{b}±0.10	5.84^{c}±0.11

Values in columns with different superscripts differ significantly ($P < 0.05$).

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Table 10.8. Cooling rate (mean ± SD) described by $y = a.e^{-bt}$ of different ostrich muscles when the thigh (5 South African Black ostriches) is cooled at 0–3°C (Sales, 1994).

Muscle	Temperature at time 0 h (a) (°C)	Cooling rate (b) (°C h^{-1})
M. gastrocnemius pars interna	$39.1^{c} \pm 1.26$	$0.18^{b} \pm 0.01$
M. femorotibialis medius	$35.9^{de} \pm 1.81$	$0.15^{c} \pm 0.01$
M. ambiens	$40.9^{bc} \pm 1.67$	$0.20^{ab} \pm 0.01$
M. iliotibialis lateralis	$37.6^{cd} \pm 2.24$	$0.18^{ab} \pm 0.02$
M. iliofibularis	$42.6^{ab} \pm 1.19$	$0.19^{ab} \pm 0.02$
M. iliofemoralis	$42.2^{ab} \pm 0.06$	$0.21^{a} \pm 0.01$

Values in columns with different superscripts differ significantly ($P < 0.05$).

M. flexor cruris lateralis ranged from 6.1 to 6.3 during storage at refrigerator (2°C for 14 days) or freezer (–20°C for 4 months) temperatures (Chin and Keeton, 1997).

Tenderness

Tenderness is currently the most important characteristic of quality sought by the average consumer in meat. Tenderness usually refers to the ease of shearing or cutting during mastication, whilst texture is related to the mealiness, greasiness, softness and structural fineness of the meat before and after mastication. Various instrumental methods, based on shearing, penetrating, biting, mincing or compressing actions, have been adopted to assess the tenderness of meat objectively because of the difficulty in using consumers with different regional preferences. The WBS device is used to record meat tenderness objectively. This machine works on the principle that as meat becomes tougher, more force is required to cut a core of meat in half (Lawrie, 1991). The ultimate evaluation of tenderness is subjectively determined by the consumer.

According to taste panellists in South Africa, there are no significant differences between tenderness of the M. iliofibularis, M. iliotibialis lateralis and M. femorotibialis medius (Mellett and Sales, 1997). In the USA, taste panel ratings indicate that consumers have the same perception of overall acceptability and tenderness acceptability for M. iliofibularis, M. obturatorius medialis, M. iliotibialis lateralis and M. gastrocnemius steaks, compared with choice beef top loin

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steak. The M. obturatorius medialis is rated by consumers as being tougher than the M. iliofibularis (Harris *et al.*, 1993).

WBS values indicated no significant differences in tenderness of meat derived from birds of either 8, 10, 12 and 14 months (Sales, 1994; Mellett and Sales, 1997). By contrast, taste panellists found meat from 8-month-old birds significantly more tender than meat from 10-, 12- and 14-month-old birds, and meat from 10-month-old birds more tender than that from 12- and 14-month-old birds (Mellett and Sales, 1997). Objective and subjective measurements of tenderness were found to be similar between bird genders (Jones *et al.*, 1994; Sales, 1994). According to Pollok *et al.* (1997d), feeding regimen (complete pelleted diet versus high-forage diet) had no significant influence on WBS measurements of three different ostrich muscles.

Connective tissue has an effect on tenderness, which is correlated with animal age. The total collagen content decreases with increasing animal age, but the solubility of collagen decreases (Smith and Carpenter, 1970). Ostrich meat is characterized by a low connective tissue content with a collagen content of 0.41% (Sales, 1996a), compared with 0.61% reported for beef (Lawrie *et al.*, 1964). The solubility of collagen in ostrich meat was 12.96% compared with 40.14% for beef (Heinze *et al.*, 1986; Goossens, 1995). This low connective tissue content makes ostrich meat suitable for dry heat cookery (a relative short heating period and high temperature), e.g. roasting (Sales, 1997). Jones *et al.* (1994) found that ostrich roasts (M. iliotrochantericus caudalis) took significantly less time to reach an internal temperature of 70°C than beef M. semitendinosus muscles (7.76 versus 9.92 min 100 g^{-1}). There were no significant differences in WBS measurements of the M. iliotibialis lateralis if broiled in a forced-air convection oven to internal temperatures of 60 (rare), 70 (medium) or 80°C (well done). The M. iliofemoralis, however, was significantly more tender at 60°C than at either 70 or 80°C (Sales, 1998a).

Colour

Colour is usually the first attribute of meat detected by the consumer. The dark colour of ostrich meat can be partly explained by the high pH_f that might be responsible for muscle fibres being tightly packed together, presenting a barrier to diffusion by light (Lawrie, 1991).

Ostrich muscles are slightly dark red to slightly cherry red, in comparison to slightly cherry red to moderately cherry red for beef (Morris *et al.*, 1995b). The darker intensity of ostrich meat (compared with beef) was also measured as colour coordinates with a Minolta Chroma Meter II reflectance meter (Jones *et al.*, 1994). Neither gender (Jones *et al.*, 1994; Schaefer *et al.*, 1995), nor pre-transport electrolyte treatment (Schaefer *et al.*, 1995), had any influence on either subjective (Morris *et al.*, 1995b) or objective colour measurements. Pigment content (Table 10.6) also contributes to the dark colour of ostrich meat. Naudé *et al.* (1979) reported the pigment content of ostrich meat as from 104–153 mg Fe g^{-1} compared with 69 mg Fe g^{-1} in beef muscle from animals of comparable age. As

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there are significant subjective colour differences between muscles from the same ostrich carcass (Morris *et al.*, 1995b), separation of ostrich muscles in comparable colour groups is recommended, not only in the marketing of whole raw muscles, but also to reduce variation in the visual appearance of final processed products (Sales, 1996b).

Flavour and odour

Flavour and odour are complex characteristics influenced by texture, temperature and pH. The ultimate evaluation of flavour and odour, which develop during the cooking process, needs subjective evaluation (Fenaroli, 1975). USA consumers preferred the less intense flavour of choice beef top loin steak when compared to the M. gastrocnemius, but the M. iliofibularis, M. obturatorius medialis and M. iliotibialis lateralis had similar ratings for flavour acceptability. Consumers tended to indicate that ostrich steaks were bland more frequently than choice beef top loin steak. Whilst the M. gastrocnemius was identified as bland more frequently than the M. iliofibularis, M. obturatorius medialis and M. iliotibialis lateralis, the M. obturatorius medialis was described as strong or intense in flavour more frequently than the other three steaks (Harris *et al.*, 1993). Soured and salt flavour scores were higher in cooked steaks from forage-fed ostriches than in cooked steaks from complete pellet-fed ostriches (Table 10.9).

Water-holding capacity

Water-holding capacity is the ability of meat to keep water during the presence of external forces, for example cutting, mincing and heating. Pre-cooking appearance, cooking ability, juiciness during chewing and the total amount of saleable meat are influenced by water-holding capacity (Trout, 1988; Barge *et al.*, 1991). The water-holding capacities of ostrich meat cooked to temperatures of 60 and 80°C were 54.97 and 41.51%, respectively. This is in agreement with values of 54.72 and 45.14% for beef cooked to similar temperatures (Heinze *et al.*, 1986). A value of 23.7% for water-holding capacity for ostrich meat, determined using the method of Grau and Hamm (1953), was lower than values of 27 and 30% reported for fowl and beef, respectively (Goossens, 1995).

Over time, ostrich muscles gradually lose moisture in a vacuum package whether refrigerated (2°C for 14 days) or frozen (−20°C for 4 months). This could affect juiciness of the cut when cooked or reduce the capacity to hold moisture when processed into a product. Water-soluble protein decreased and salt-soluble protein increased over time. However, after 4 months of frozen storage the salt-soluble protein concentration decreased, possibly due to freezer denaturation. Loss of water- and salt-soluble protein could decrease the water-holding capacity and binding ability of muscles when used in processed products (Chin and Keeton, 1997).

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Table 10.9. Sensory flavour (0 = none; 8 = extremely intense) and objective tenderness evaluation of three muscles for two feeding regimes (Pollok *et al.*, 1997d).

	Concentrate			Forage		
	M. gastrocnemius pars interna	M. iliotibialis cranialis	M. obturatorius medialis	M. gastrocnemius pars interna	M. iliotibialis cranialis	M. obturatorius medialis
Aromatics						
Cooked ostrich flavour	5.93	6.29	6.01	6.04	6.00	5.75
Cooked ostrich fat	0.13	0.21	0.31	0.07	0.33	0.41
Serum/bloody	1.36	1.71	1.72	1.68	1.78	1.69
Grainy/grassy	2.21	2.43	2.43	2.49	2.44	2.38
Gamey	2.20	2.38	2.46	2.35	2.49	2.31
Soured	0.03[b]	0.06[b]	0.18[b]	0.27[a]	0.43[a]	0.62[a]
Cardboard	0.03	0.00	0.00	0.00	0.10	0.00
Painty	0.00	0.00	0.00	0.00	0.00	0.10
Fishy	0.00	0.00	0.00	0.09	0.00	0.05
Livery	1.49	2.30	2.35	1.52	2.01	2.03
Feeling factors						
Metallic	2.08	2.25	2.19	2.21	2.35	2.26
Astringent	1.44	1.61	1.45	1.59	1.63	1.85
Tastes						
Salt	1.99[b]	2.04[b]	2.03[b]	2.05[a]	2.10[a]	2.13[a]
Sour	1.70	1.96	2.03	1.93	2.35	2.63
Bitter	1.99	2.34	2.36	2.11	2.43	2.46
Sweet	2.35	2.26	2.36	2.46	2.08	2.06
Warner–Bratzler shear force (kg)	3.40	2.60	2.36	3.27	3.04	2.63

Values in columns with different superscripts differ significantly ($P < 0.05$).

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Ageing and shelf life of ostrich meat

The high pH_f will put a restriction on the shelf life of ostrich meat. Meat of pH_f near 6.0 is considered as unsuitable for holding because of microbial spoilage and undesirable odours. Even in evacuated gas-impermeable packs, bacteria will produce H_2S which leads to the formation of green sulphmyoglobin and thus undesirable discoloration. The storage of meat at low temperatures for 10–14 days will, however, increase the tenderness of meat (Lawrie, 1991). The toughening effect during the beginning of rigor mortis is gradually reversed during an increase in the time *post rigor* (Davey and Winger, 1988).

Vacuum-packed ageing, at 3°C for 7 days additional to the 3.5 days' storage before distribution used for ostrich muscle in South Africa, would only be beneficial in improving the tenderness of M. iliofibularis and M. iliofemoralis. Minor changes in the ultrastructural appearance of the M. iliofibularis showed that tenderization during *post-mortem* storage is due to factors other than Z-line degradation (Sales *et al.*, 1996a).

Proteolysis of myofibrillar proteins, including lysosomal as well as non-lysosomal proteins, appears to be a major contributor to meat tenderization during *post-mortem* storage (Dutson and Lawrie, 1974; Koohmaraie *et al.*, 1984). The different myofibrillar proteins of ostrich in comparison with beef are presented in Table 10.10.

Ostrich M. iliofibularis muscle samples stored at 2–4°C for various periods up to 12 days showed a decrease in Ca^{2+}-dependent protease (CDP) activity with increasing storage time. Only 45% activity remained after 12 days of storage. The same activity was found for cathepsin H. Cathepsins B, B+L and D were all very stable with storage and showed no decrease in activity after 12 days of storage. Calpain and cathepsin H activities, however, did not correlate with WBS data in ostrich meat. Close similarities between electrophoretic patterns of calcium and CDP-incubated myofibrils and myofibrils stored at 2–4°C for 12 days clearly implicated CDPs as the causative factor, producing changes in myofibrillar proteins in *post-mortem* ostrich muscle; however, this did not lead to any tenderization as measured by WBS values (van Jaarsveld *et al.*, 1997).

The improvement in tenderness with ageing is out-massed by the potential increase in microbial growth and a subsequent decrease in storage life (Pollok *et al.*, 1997d). According to microbiological criteria, where a total aerobic plate count of >6 log cm^{-2} is unacceptable, vacuum-packaged ostrich steaks are of marginal quality after 14 days' refrigerated storage and unacceptable after 21 days (Table 10.11).

Colour and flavour were not drastically effected by vacuum-packaged refrigerated storage of ostrich meat up to 21 days. The effect of 'cowy' and soured odour, however, increased over time. Vacuum-packaged steaks became lighter and brighter in colour with increased storage time at less than 7°C, whilst retail over-wrapped steaks became darker brown and less red. Based on microbial counts, ostrich meat was unacceptable after 3 days' vacuum-packaged storage (7.35 log cm^{-2}) and 1 day in retail over-wrapped packages (5.99 log cm^{-2}). Soured

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Table 10.10. Myofibrillar protein (μg of bovine serum albumin equivalents per μg of myofibrillar protein; mean±SD) in ostrich muscle in comparison with beef (Goossens, 1995).

Protein	Ostrich	Beef
Titin	48.35±7.49	48.89±9.84
Nebuline	19.05±5.20	23.25±7.09
Filamin	3.12±0.86	1.62±0.57
Creatine phosphokinase	13.01±0.51	29.36±9.57
M-protein	35.79±3.43	35.93±6.46
C-protein	23.97±1.64	18.60±3.29
Actin	127.75±6.08	147.93±12.95
α-Actin	24.76±1.03	28.43±3.48
Tropomyosin	7.76±1.25	17.99±5.86
Troponin C	8.97±0.82	5.02±1.16
Troponin I	19.70±1.05	20.00±2.40
Troponin T	0.90±0.20	4.35±2.72
Troponin T2	2.15±0.22	3.45±2.59
34 kDa	4.47±1.07	12.88±8.26
30 kDa	4.23±1.13	10.30±5.84
Myosin heavy chain	248.35±12.28	248.77±21.65
Myosin light chain 1	14.08±0.74	21.49±2.49
Myosin light chain 2	30.08±0.85	30.71±2.46
Myosin light chain 3	5.93±1.36	2.94±1.04

and rancid odours increased significantly with display time in both packaging systems (Pollok *et al.*, 1997d).

Nutrient composition

The modern consumer wants to be aware of the nutritive value, and especially the health aspects, of food consumed. Thus correct marketing strategies based on nutrient composition are of utmost importance when ostrich meat is introduced to the developed world. Water, protein, fat, ash and collagen contents differ between muscles from the same ostrich carcass (Table 10.12).

Ostrich meat has an exceptionally low intramuscular fat content relative to other species (Sales, 1995c). This low intramuscular fat content is one of the most promising characteristics of ostrich meat in marketing strategies of this

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Table 10.11. Physical and microbial values for meat at four storage treatments (Pollok *et al.,* 1997d).

Parameter	Days' storage			
	2	7	14	21
Purge (%)	0.10[a]	0.49[b]	0.61[b]	0.65[b]
Hunter colour[1]				
L*	39.2	36.9	37.8	37.9
a*	15.3	14.5	15.1	14.5
b*	1.5	2.2	2.4	2.2
Warner–Bratzler shear force (kg)	3.1[a]	3.0[ab]	2.7[bc]	2.6[c]
Total aerobic plate counts (log cm^{-2})	2.2[a]	2.8[b]	5.5[c]	6.9[d]

[1]Colour mathematically measured and defined using a reflectance meter: L* = brightness; a* = red to green axis; b* = yellow to blue axis.
Values in rows with different superscripts differ significantly ($P < 0.05$).

product. However, the absence of fat causes a loss of sustained juiciness during chewing, largely due to the stimulatory effect of fat on salivation (Lawrie, 1991). Ostrich meat might thus give an impression of a dry sensation in the mouth, especially if the cooking time is too long. Ostrich meat should not be cooked to the well-done (80°C) stage. Although a high pH_f may be favourable regarding a high water-holding capacity, this benefit effect may be contradicted by the low intramuscular fat content of ostrich meat (Sales, 1995b). Muscles having a high intramuscular fat content tend to have a high water-holding capacity, possibly because the intramuscular fat loosens up the microstructure and more water is retained (Lawrie, 1991). By using the ether-extractable fat and protein content, the caloric content of raw ostrich meat is 391 kJ 100 g^{-1} (Sales *et al.*, 1996b) compared with 517 kJ 100 g^{-1} for beef (Holland *et al.*, 1993) and 508 kJ 100 g^{-1} for fowl (Paul and Southgate, 1978).

Cholesterol content does not differ largely between species (Sales, 1995d). It is possible that the commonly held belief that ostrich meat is low in cholesterol arose because of the low intramuscular fat content of ostrich meat. Intramuscular fat content, however, is poorly correlated to cholesterol content. Cholesterol is mainly a structural component of cell membranes. Due to differences in the subcellular distribution of cholesterol in muscle tissue, its content does not increase as intramuscular fat content increases (Hoelscher *et al.*, 1988).

Since it was discovered that cholesterol is stored in blood vessels of people suffering from arteriosclerosis and thus contributes to heart infarct, cholesterol has been perceived as a problem. However, cholesterol also has functions that are important to life, e.g. it is built into cell membranes and the nervous tissue (Kühne, 1977). The daily intake of cholesterol in the average US diet is approximately 450 mg, whilst the human body synthesizes 800–1500 mg day^{-1} (Anon.,

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Table 10.12. Chemical characteristics (percentage of wet weight; mean±SD) of different ostrich muscles from 39 South African Black ostrich carcasses (Sales, 1996a).

Muscle	Moisture	Ash	Protein	Fat	Collagen
M. gastrocnemius pars interna	$77.7^{a}\pm0.9$	$1.16^{abc}\pm0.13$	$20.6^{de}\pm1.41$	$0.27^{f}\pm0.17$	$0.61^{ab}\pm0.15$
M. femorotibialis medius	$77.3^{cb}\pm1.1$	$1.11^{c}\pm0.14$	$20.6^{de}\pm1.24$	$0.31^{ef}\pm0.14$	$0.45^{d}\pm0.15$
M. ambiens	$76.0^{d}\pm1.0$	$1.12^{c}\pm0.15$	$21.5^{b}\pm0.76$	$0.42^{cd}\pm0.25$	$0.34^{e}\pm0.09$
M. iliotibialis lateralis	$76.2^{d}\pm0.4$	$1.21^{a}\pm0.14$	$21.2^{bc}\pm1.07$	$0.40^{de}\pm0.21$	$0.48^{cd}\pm0.18$
M. iliofibularis	$77.6^{ab}\pm1.0$	$1.10^{c}\pm0.12$	$20.9^{cd}\pm1.35$	$0.42^{d}\pm0.24$	$0.30^{e}\pm0.08$
M. iliofemoralis	$75.1^{e}\pm1.5$	$1.18^{ab}\pm0.12$	$21.9^{a}\pm0.92$	$0.69^{b}\pm0.30$	$0.29^{e}\pm0.35$
M. fibularis longus	$77.2^{c}\pm1.1$	$1.13^{bc}\pm0.13$	$21.0^{c}\pm0.05$	$0.24^{f}\pm0.17$	$0.64^{a}\pm0.27$
M. iliotibialis cranialis	$77.3^{abc}\pm0.9$	$1.15^{bc}\pm0.10$	$20.0^{f}\pm0.93$	$0.52^{c}\pm0.31$	$0.29^{e}\pm0.13$
M. flexor cruris lateralis	$75.3^{e}\pm1.3$	$1.11^{c}\pm0.17$	$21.0^{c}\pm0.91$	$0.82^{a}\pm0.37$	$0.36^{e}\pm0.17$
FFF	$77.2^{c}\pm0.8$	$1.14^{bc}\pm0.12$	$20.4^{e}\pm0.82$	$0.52^{c}\pm0.27$	$0.51^{cd}\pm0.26$
II	$76.2^{d}\pm0.9$	$1.16^{abc}\pm0.15$	$20.6^{de}\pm0.93$	$0.69^{b}\pm0.38$	$0.55^{bc}\pm0.28$
Mean	76.6±1.4	1.14±0.14	20.9±0.16	0.48±0.32	0.44±0.24

Values in rows with different superscripts differ significantly ($P < 0.05$).
FFF: M. femorotibialis externus; M. femorotibialis internus; M. femorotibialis accessorius; II: M. iliofemorotibialis externus; M. iliofemorotibialis internus.

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1980). A high level of cholesterol in blood does not necessarily lead to arteriosclerosis if there is exchange of cholesterol with the tissues. The exchange is mediated by lipoproteins which are important in the development of coronary heart diseases. Low-density lipoproteins are the carriers of more than two-thirds of the blood cholesterol between tissues. Any factor that affects the low-density lipoprotein levels in blood also tends to affect total blood cholesterol levels. High-density lipoprotein is believed to be the carrier of cholesterol from the body cells to the liver where it is transformed into bile acids and excreted into the intestine. An increase in high-density lipoprotein levels is associated with a reduction of the risk of arteriosclerosis and coronary heart disease.

Sales (1998b) showed that cholesterol content differed significantly between muscles from African Black ostriches (Table 10.13). According to Horbanczuk *et al.* (1998), cholesterol content does not differ significantly between meat from red-neck (64.27 mg 100 g^{-1}) and blue-neck (67.01 mg 100 g^{-1}) ostriches.

Over many years the concept of reducing saturated and increasing polyunsaturated fatty acid intake in an attempt to reduce the risk of coronary heart diseases was preached to the world. Current knowledge is that intake of saturated fatty acids increases plasma levels of low-density lipoprotein, whilst it is decreased by intake of polyunsaturated fatty acids. Intake of polyunsaturated fatty acids, however, also decreases plasma levels of high-density lipoprotein (Grundy, 1986). Monounsaturated fatty acids in the diet decrease low-density lipoprotein levels with no influence on high-density lipoprotein levels (Mattson and Grundy, 1985).

Ostrich meat is higher in polyunsaturated fatty acids than either beef or fowl (Sales *et al.*, 1996b). However, it must be emphasized that the fatty acid composition of tissues in ostriches and fowl could be altered by inclusion of fatty acids in their diet (Sales, 1996b).

Although the percentage of individual fatty acids differed significantly between ostrich muscles and variations were found within muscles, the percentage of total saturated, monounsaturated and polyunsaturated fatty acids were relatively constant between muscles (Table 10.13). Although the total percentage of saturated fatty acids and total monounsaturated fatty acids were similar in two muscles between red- and blue-neck ostriches, the total percentage of polyunsaturated fatty acids was significantly higher in blue-necks (23.78%) than in red-necks (23.65%) in the M. gastrocnemius, but not in the M. iliofibularis (Horbanczuk *et al.*, 1998).

Feeding regimen has no significant influence on intermuscular fat or on saturated or monounsaturated fatty acid content of ostrich muscles, but the polyunsaturated fatty acid content was significantly higher in meat from birds on a complete pellet diet (24.75%) than from birds on a forage diet (21.25%) (Pollok *et al.*, 1997c). As with any nutrient component, individual fatty acid content will be concentrated and increased with cooking (Sales *et al.*, 1996b; Pollok *et al.*, 1997c), depending on cooking temperature.

Except for a few amino acids, the consistency of the amino-acid pattern

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Table 10.13. Cholesterol values (mg 100 g^{-1} edible portion) and mean fatty acid (%) determined in different ostrich muscles from 19 South African Black ostrich carcasses (mean±SD; Sales, 1998b).

	M. gastrocnemius pars interna	M. femorotibialis medius	M. ambiens	M. iliotibialis lateralis	M. iliofibularis	M. iliofemoralis
Cholesterol	58.71^{de}±4.98	56.61^{e}±3.12	66.52^{b}±5.91	59.99^{cd}±4.17	61.53^{c}±4.85	71.12^{a}±4.47
Fatty acids						
Saturated						
16:0	19.21^{bc}±3.56	20.96^{ab}±4.93	19.95^{abc}±2.44	21.55^{a}±2.83	18.59^{c}±2.74	21.06^{ab}±3.95
18:0	16.10^{a}±2.61	16.07^{a}±3.26	15.47^{ab}±2.59	16.17^{a}±3.06	14.07^{c}±2.27	14.68^{bc}±2.30
Monounsaturated						
16:1	3.85±1.19	3.72±1.32	4.02±1.21	3.76±1.29	3.87±1.35	4.17±1.13
18:1	29.13^{bc}±2.83	27.10^{e}±3.09	30.52^{a}±3.37	27.74^{de}±3.27	28.33^{cd}±2.75	29.69^{ab}±2.73
Polyunsaturated						
18:2*w*6	15.18^{c}±3.12	15.52^{c}±2.57	15.55^{c}±2.57	16.42^{bc}±3.10	18.50^{a}±2.49	17.81^{ab}±3.73
18:3*w*3	2.43^{abc}±1.02	2.21^{c}±0.82	2.61^{ab}±0.94	2.26^{bc}±0.91	2.81^{a}±1.08	2.82^{a}±0.96
20:3*w*6	0.58^{ab}±0.41	0.68^{a}±0.36	0.46^{b}±0.40	0.72^{a}±0.29	0.69^{a}±0.45	0.44^{b}±0.31
20:4*w*6	8.51^{a}±2.28	8.48^{a}±2.37	7.91^{ab}±2.14	7.08^{b}±1.82	8.24^{a}±1.44	7.18^{b}±1.92
20:5*w*3	1.78^{a}±1.01	1.59^{ab}±0.99	1.41^{b}±0.89	1.64^{ab}±0.81	1.80^{a}±1.05	1.56^{ab}±0.95
22:5*w*3	1.44^{a}±0.57	1.39^{ab}±0.40	1.08^{c}±0.39	1.20^{bc}±0.37	1.33^{ab}±0.46	0.44^{d}±0.26
22:6*w*3	1.79^{a}±1.34	1.98^{a}±1.21	1.01^{c}±0.69	1.42^{b}±0.96	1.77^{ab}±1.27	0.52^{d}±0.60

Values in rows with different superscripts differ significantly ($P < 0.05$).

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Table 10.14. Amino-acid and mineral composition (g 100 g^{-1} edible portion) of ostrich meat compared to beef and chicken.

	Ostrich[1]	Beef[2]	Chicken[3]
Amino acids			
Threonine	0.757	0.915	0.904
Isoleucine	0.915	0.947	1.130
Leucine	1.704	1.555	1.605
Lysine	1.647	1.742	1.818
Methionine	0.548	0.536	0.592
Phenylalanine	0.939	0.817	0.849
Tyrosine	0.608	0.704	0.722
Valine	0.972	1.018	1.061
Arginine	1.358	1.323	1.290
Histidine	0.394	0.717	0.664
Alanine	1.059	1.263	1.167
Aspartic acid	1.897	1.913	1.907
Glutamic acid	2.507	3.146	3.204
Glycine	0.820	1.142	1.051
Serine	0.586	0.801	0.736
Minerals			
Calcium	8	6	12
Iron	2.3	2.2	0.9
Magnesium	22	23	25
Phosphorus	213	201	173
Potassium	269	358	229
Sodium	43	63	77
Zinc	2.0	4.4	1.5
Copper	0.10	0.08	0.05
Manganese	0.06	0.01	0.02

[1]Sales and Hayes (1996); mean for M. iliofibularis, M. femorotibialis medius and M. gastrocnemius pars interna from seven South African Black ostriches aged 12–14 months.
[2]Paul and Southgate (1978); Holland *et al.* (1993); lean only.
[3]Paul and Southgate (1978); Anon. (1979); flesh without skin.

between species showed that the amino-acid composition of meat protein remains markedly consistent (Table 10.14). The low sodium content of ostrich meat has a distinct advantage for people who have to maintain a low-sodium diet.

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Ostrich meat products

Ostrich meat may be used as a substitute for beef in almost any product (Shewring, 1996). Due to the low fat content it is often necessary to increase the pork fat content in recipes when used as a replacement for beef. Biltong is made by cutting meat in slices, after which it is marinated in spiced brine for 12 h, then dried and smoked at 85°C for 72 h (Basson and Visser, 1972).

Cured ostrich products have excellent colour and appear to have good binding properties, acceptable flavour and texture (Harris *et al.*, 1993). Ostrich meat, with its high pH_f value, cannot be recommended for raw hams but it will be suitable for cooked hams. Furthermore, if such meat alone is used for the production of dry and frankfurter-type sausages, it will not keep well (Hofmann, 1988) and so processing of ostrich meat together with meat from other species with a pH_f of 5.5 is recommended. Starter cultures of *Lactobacillus sake* and *Lactobacillus curvatus* proved effective in lowering the pH of ostrich salami from around 7.0 to below 5.0 within 6 days of fermentation (Böhme *et al.*, 1996).

OTHER PRODUCTS

Eggs

Eggs from females not mated, those which are slightly damaged, or those with poor shell quality are unacceptable for hatching and can be available for human consumption. On average, 25% of 1 million eggs laid yearly in the Little Karoo of South Africa are infertile (van Schalkwyk, 1994). The nutrient compositions of ostrich and fowl eggs are shown in Table 10.15. Fat content of ostrich eggs is somewhat lower than that of fowl eggs. Furthermore, the total amount of essential amino acids determined in ostrich eggs (6.585 g 100 g^{-1} liquid edible portion) is higher than that of the fowl egg (5.837 g 100 g^{-1}) (Sales *et al.*, 1996c). However, the cholesterol content of ostrich yolk is in the upper range described for fowl yolk and the levels of saturated fatty acids were 7% higher in ostrich than in fowl yolk (Reiner *et al.*, 1995).

Eggshells, empty or broken, are processed (painted and decorated) into curious items such as lamp holders and jewellery boxes.

Oil

Fat in the ostrich carcass is situated in specific depots, for example in the abdomen, overlying the sternum and between muscles, but intramuscular fat is limited. In a study where ostrich oil was refined by heating for 17 h at 80°C in a closed vessel in an air-convection oven (dry rendering), it was found that 67 and 41% oil can be recovered from abdominal and breast fat, respectively (Sales and Franken, 1996). Oil from the breast is darker than oil from the abdominal depot. Some physical and chemical characteristics of ostrich abdominal fat are com-

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Table 10.15. Nutrient composition of non-fertile ostrich eggs in comparison to fowl eggs (per 100 g liquid edible portion).

Nutrient	Ostrich	Fowl
Proximate (g)[1,2]		
Water	75.1	74.7
Ether-extractable fat	11.7	12.3
Protein (N×6.25)	12.2	12.0
Amino acids (g)[3,2]		
Essential		
Arginine	0.527	0.771
Histidine	0.284	0.279
Isoleucine	0.672	0.600
Leucine	1.336	0.998
Lysine	0.947	0.851
Methionine	0.395	0.388
Phenylalanine	0.600	0.572
Threonine	1.013	0.597
Valine	0.811	0.781
Non-essential		
Alanine	0.316	0.644
Serine	0.832	0.921
Tyrosine	0.547	0.528
Vitamins[2,4,a]		
Vitamin A (µg retinol equivalents)	5.79	6.15
Vitamin E (mg D-α-tocopherol equivalents)	0.04	0.01
Folic acid (µg)	48	30
Pantothenic acid (mg)	0.75	0.38
Riboflavin (mg)	0.24	0.32
Thiamine (mg)	0.15	0.09
Minerals (mg)[2,4,a]		
Calcium	64.7	58.5
Iodine (µg)	80	72
Iron	2.51	2.25
Magnesium	13.92	12.41
Manganese	0.16	0.39
Phosphorus	196.71	237.9
Zinc	1.34	1.50

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Table 10.15 continued

Nutrient	Ostrich	Fowl
Cholesterol (%)[5,b]	1.98	1.5-1.9
Fatty acids (%)[5,b]		
C14:0	1.9	0.3-0.5
C16:0	35.7	23.4-29.9
C18:0	6.1	8.2-10.5
C16:1	8.1	3.4-5.3
C18:1	30.6	41.4-48.8
C18:2	11.1	0.3-13.4
C18:3	2.4	0.3-3.5
Other	4.1	1.0-7.4

[1]Romanoff and Romanoff (1949).
[2]Cotterill *et al.* (1977).
[3]Du Preez (1991).
[4]Angel (1993).
[5]Reiner *et al.* (1995).
[a]Values were corrected for moisture loss during incubation, ostrich eggs were obtained after 14 days of incubation; [b]only in the yolk.

pared with emu oil in Table 10.16.

Oil from the emu and rhea is used in cosmetics (skin creams, lotions, lip balm, shampoo, massage oil) and first-aid products (burn creams, arthritis rubs, sports rubs). The reason for the effectiveness and uniqueness of emu and rhea oil in these products is unknown and is under investigation. The Australian and British ostrich industries claim that ostrich oil is superior in cosmetics products (Sales and Franken, 1996).

CONCLUSIONS

Although the ostrich was originally domesticated more than 130 years ago for the production of feathers, for the latter half of this century leather has been the main product. Since 1990, as the ostrich industry has expanded outside South Africa, there has been a shift towards meat production. There has been less emphasis on the skin and feathers by non-South African ostrich industries because of the introduction of subspecies other than *Struthio camelus* var. *domesticus*. These subspecies still have a high proportion of wild genes, with inferior skin and feather quality. Furthermore, it is claimed by the South African industry that optimal leather quality can be achieved only at a slaughter age of 14 months, whilst the

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Table 10.16. Comparison of some physical and chemical characteristics between ostrich and emu oil.

Characteristic	Ostrich oil[1]	Emu oil[2]
Refractive index[3]	1.466 (25°C)	1.464 –
Iodine value[4]	72.6	71.0
Saponification value[5] (mg KOH g^{-1})	205	187
Fatty acids (% of total)		
C14:0	0.81	0.9
C16:0	28.44	17.5
C18:0	6.26	10.1
C16:1	8.44	2.1
C18:1	36.94	62.2
C18:2	13.29	5.2
C18:3	4.85	–

[1]Sales and Franken (1996).
[2]Gunstone and Russell (1954).
[3]The refraction index is described as the degree of deflection of a ray of light passing from one transparent medium into another, and is being used for the qualitative identification of unknown compounds by comparing the index of the unknown with literature values of various known substances.
[4]The iodine value is a measurement of the unsaturation of fat.
[5]The saponification value is a measurement of the amount of alkali required to saponify a definite weight of fat (Kirschenbauer, 1960; Williams, 1966).

acceptable meat yield is already attained at 10 months of age and feed conversion efficiency declines drastically thereafter.

The importance of meat is also illustrated by the amount of research conducted on it relative to that on skins and feathers. Although in South Africa 70% of the income from an adult ostrich is still from the skin, to date only one scientific study has been conducted on skin quality. Despite this interest in the ostrich as a meat producer, it is a very small industry. If ostrich meat were to replace 0.0001% of the US beef market, as many as 750,000 ostriches would have to be slaughtered annually. In 1996 approximately 270,000 ostriches were slaughtered in South Africa, and 70,000 elsewhere. This means that ostrich meat will remain as a speciality in restaurants and a few households in only a few countries in the world. Marketing, advertising and development of different products from the ostrich are of utmost importance.

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11

Breeding and Genetics

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Most people are familiar with the old 'nature versus nurture' argument, in which the former stresses that genes determine everything whilst the latter insists that the environment is more important. In reality, the appearance/performance of an individual is determined by both its genetic make-up and the environment. In the case of the ostrich, the environment means all the components that go into the management of the bird such as nutrition, disease prevention, proper housing, etc. No-one would argue that good basic management practices are not important for success in raising ostriches. However, stock which has not been selected for a specific purpose, so that each generation is improved over the preceding generation, will never see its performance increase. As the ostrich industry grows and matures, genetic improvement will have to play a greater part in producing and developing birds to meet future markets, particularly for meat and leather production.

This chapter provides a brief history of ostrich breeding and genetics, followed by a short guide to basic genetics. The practical application of genetics in ostrich breeding, including molecular techniques, is then described.

THE GENETIC BASIS OF FARMED OSTRICHES

At the turn of the 20th century, the ostrich was viewed as an example of evolutionary 'degeneration' because of the absence of feather barbules, a reduced wing size compared with other birds, the lack of a sternal keel, and the reduction in the number of toes (Duerden, 1920a, b). Unfortunately, Duerden concluded that such 'degenerative' changes had no relationship to adaptation, and therefore

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were not due to natural selection but to something 'wholly intrinsic and independent of any external modifying cause'. Nevertheless, he believed that artificial selection could improve the stock.

The ostrich used in South African farming was based upon the capture of wild chicks. Only chicks were obtained at the time because wild-caught adults were impossible to handle and did not adapt well to captivity. In the early days of the industry, little attention was paid to a breeding programme, and any bird reaching sexual maturity in 3–4 years was kept as breeding stock (Duerden, 1919a). As the industry grew with the demand for feathers, attention began to focus on the characteristics of the plumage and only birds exhibiting the best plumage for market were retained for breeding. However, birds were selected only in terms of feather quality (e.g. length, width, strength, shape, density and lustre), and other characteristics such as rate of gain and egg production were not taken into account. Duerden (1919a) noted that the quality of plumage varied greatly and few birds ever obtained all the ideal traits in one feather. In general, he believed that progress in nutrition and management helped to improve feather quality, and that the results of selection were to combine the best features found among various wild South African birds into one bird. Furthermore, attempts to change plumage characteristics beyond the range found in the population were unsuccessful. This observation, coupled with the general opinion that North African ostriches had better quality plumage (Martin, 1891), led to the idea that the crossing of North African wild ostrich with South African stock might improve commercial feather production.

In 1912 about 132 ostriches obtained from wild nests in Nigeria were imported to the Union of South Africa (Duerden 1919b). Most of the surviving chicks were about 6 months old, but very few imported adult birds could adapt to the new environment and subsequently succumbed to parasitic diseases not present in northern Africa. Duerden was in charge of the cross-breeding project with the goal of determining if the northern birds could be used to improve the plumage of the southern bird (Duerden, 1919b). From the surviving birds, those producing the most desirable plumage were retained and any other birds were culled. It took about 4 years to obtain approximately 100 crossbred birds of breeding age. In his detailed evaluation, Duerden (1919b) compared the general characteristics of 'pure' North African and South African stock to the resulting crossbred birds. In comparison with the South African birds, the Nigerian stock tended to be larger, with a longer neck and weighing about 125 kg, with the number of remiges averaging 36 (range 33–39). Only northern birds had a bald patch on the head. The skin colour of sexually mature males was bright red on the legs, head and neck, while this was less pronounced in the southern birds. The egg shape of northern birds was much rounder, and the number of obvious pits in the shell was considerably less than observed in eggs from southern stock. In most cases, the northern/southern crossbred birds exhibited an intermediate phenotype between the two populations in the first generation (F_1) for all traits measured. Limited data from the F_2 (second generation) indicated that offspring from the crossbred birds exhibited a large amount of variation for most traits. The only

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exception to this was the bald head patch. All crossbreds had the bald patch, while some of the F_2 birds obtained did not show baldness. Hence, Duerden (1919b) concluded that the trait was homozygous dominant in the Nigerian stock and that its expression was due to simple Mendelian inheritance.

Mating systems for ostriches at the turn of the century were composed of pairs and trios of a male and two females, and eggs were often removed from the nest to increase production (Martin, 1891). The pairing of birds reflected a belief in 'blending inheritance', and Duerden (1919a) described the basic approach of the farmer: 'He starts with a bird which produces plumes the most nearly approaching his ideal, and mates it with another most closely resembling it, but perhaps lacking for surpassing in one or more points; another season he may resort to a different mating to secure other features. From different breeding sets he may rear two or three hundred chicks in a season'. The progeny of this system showed much variation, with the offspring usually being intermediate between the parents. When the birds matured, the most desirable were chosen as breeders. If the stock had a weak point, birds were purchased that were strong in that particular characteristic. Duerden (1919b) concluded that this method simply resulted in a mixture of germplasm and that the frequency of any single hereditary factor would not change. Interestingly, farmers at the time were afraid to 'fix' lines through the use of inbreeding, for fear that the competition would get ahead. This sentiment is often voiced even today.

Nevertheless, South Africa was successful in its effort to produce better feather quality through crossbreeding with wild northern stock coupled with effective culling. Strains were often named and an ostrich section was included in the South African Studbook (Drenowatz *et al.,* 1995). Such progress was remarkable because knowledge about genetics, particularly the principles of quantitative genetics as a direct application to animal agriculture, did not emerge until the 1940s to 1950s.

Around the end of the 19th century, the booming industry in South Africa caused American, Australian and European investors to seriously begin ostrich 'ranching'. In the USA, birds were initially imported into California in 1883, with other imports following soon after to form the basis of the North American stock (Doughty, 1973). Many birds did not survive the long journeys, which often were routed through South America to avoid tariffs. For most American farms, mortality meant that flocks were established from single breeding pairs. By 1910, the number of birds in the USA exceeded 6000, with 80% of the farms in Arizona and 17% in California, the rest being scattered through other states. Problems with feather quality meant that farms which started with South African stock imported 'Nubian' ostriches which were most probably the north African birds. With the onset of World War I, general austerity and limited access to world markets caused a severe slump in demand for feathers, which meant that interest in ostrich farming faltered in the USA and elsewhere. However, ostrich farming remained an important industry for South Africa where birds are now raised for leather, meat and feathers (Sales, Chapter 10).

From the mid 1980s interest in farming ostriches and other ratites re-

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emerged in the USA, Australia, Europe and elsewhere, with much of the stock being descended from wild birds. Today, advances in animal breeding that have been applied to the major animal agricultural industries during the second half of the 20th century offer considerable tools to assist in the genetic improvement of ostriches for commercial production.

BASIC GENETICS

A trait is any characteristic that can be visually identified or measured in a bird, such as feather colour, number of eggs, rate of gain, fertility, etc. All traits can be divided into two categories: qualitative and quantitative. Characteristics which are usually determined by a few specific genes are known as qualitative traits, and include feather and skin colour, plumage mutations and lethal genes. These traits can be readily selected for (or against), as the visual appearance of the birds (the phenotype) is an indication of the presence of a particular gene (the genotype). However, most (if not all) traits of economic importance are quantitative traits that result from the interactions of many genes in a complex manner. For example, growth rate is dependent upon many different physiological systems which have thousands of genes influencing the phenotype. Whatever the trait, the underlying basis for both qualitative and quantitative traits is the gene.

Genes and chromosomes

All genes are made of DNA and are found on the chromosomes in the nucleus of the cell. All genes occur in pairs because every animal has two of each chromosome. Each parent contributes only one copy of the gene to any given offspring, because only one of the two parental chromosomes is passed on. Like all birds, the ostrich contains both macrochromosomes, a series of large chromosomes easily differentiated by size and shape, and microchromosomes, which are very small and nondescript. The paired (diploid) chromosome number of the ostrich is reported to be 80 (Sasaki *et al.,* 1968; Itoh *et al.,* 1969; Takagi *et al.* 1972), only about six pairs of which are distinguishable as macrochromosomes (Fig. 11.1).

Included in the chromosomal make-up is a pair of sex chromosomes, which in birds are designated ZZ for the male and ZW for the female. It is significant that the sex chromosomes of ratites in general, and the ostrich in particular, are monomorphic, i.e. the two chromosomes in the pair are indistinguishable in appearance. Hence it has been impossible to identify ostrich Z and W chromosomes in a karyotype using traditional identification techniques such as chromosome banding. Recently, using a series of Z and W marker genes of the fowl, Ogawa *et al.* (1998) were able to isolate equivalent markers in the ostrich and show that the fourth largest pair of macrochromosomes are the sex chromosomes.

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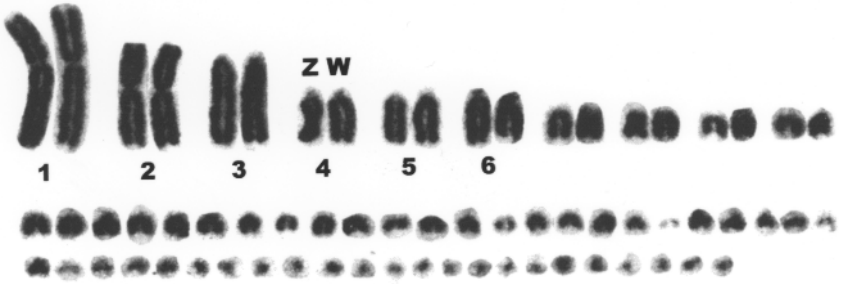

Fig. 11.1. Karyotype of a female ostrich illustrating the pairs of macrochromosomes (numbered 1–6) and the many microchromosomes arranged according to size. The fourth largest pair is the sex chromosomes, ZW. Redrawn after Takagi *et al.* (1972) with modifications.

None of the markers were W-specific and only one was Z-specific, and so it would seem that there are only minor differences between the Z and W chromosomes. Such a feature has implications for the development of rapid methods to sex ostriches using DNA technology.

'Simple' quantitative genetics

Although all genes occur in pairs within an individual animal, many forms of the gene can exist in a population. Different forms of a gene are known as alleles ('alternatives') and the position of a gene on a chromosome is called a locus. An animal with two copies of one form of an allele is a homozygote, whereas if an animal has two different alleles of the same gene it is a heterozygote. Alleles are not equivalent and the expression of one may be favoured over another. Hence there are dominant alleles which are expressed in preference to recessive ones. Dominant and recessive alleles are usually designated in shorthand by capital and lower case letters, respectively.

The connection between qualitative genetics (often called Mendelian genetics after Gregor Mendel who first demonstrated inheritance) and quantitative genetics (also called population genetics) can be a difficult concept to grasp. Mendelian genetics remains the basis for population genetics, the difference being the number of genes involved. The transition between the two can be illustrated by considering a hypothetical animal in which body mass is controlled by two pairs of genes, *Aa* and *Bb*. Each of the dominant genes, *A* and *B*, adds 10 kg to the base value of 200 kg for the *aabb* recessive genotype. This illustration is reliant on the assumption that the environment has no effect on gene expression.

Therefore, an *AABB* male (240 kg) crossed with an *aabb* female (200 kg) will produce identical F_1 offspring of *AaBb* [(240+200)/2=220 kg]. When the F_1 generation is crossed (i.e. *AaBb*×*AaBb*) the proportions of the nine possible F_2 genotypes are shown in Table 11.1. Notice that without selection, the average of

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the population remains close to the preceding generation and no improvement is obtained. However, the performance of individuals in the F_2 population ranges from 200–240 kg. Duerden (1919b) encountered this phenomenon in individual crossings of northern and southern African ostriches. A southern male with 42 first-row plumes was crossed with a northern hen with 36 first-row plumes (42+36/2=39). The 24 offspring from the mating had an average of 39.5 plumes. The population had a range of 37–42 plumes. He concluded that the parents were heterozygous for the genetic factors responsible for plumage number, and speculated that the average number of first-row plumes could be increased only by selection.

In breeding programmes, the task of selecting replacement stock involves choosing the superior genotypes from the population based upon the phenotypic variation observed, so that the average performance of the population increases. Variation is the raw material for genetic improvement because it describes that which is visible (the phenotype) and invisible (the genotype). In developing a selection programme, the challenge is to improve the mean performance of the flock for a trait (or a few traits) and to reduce some of the variation. However, sometimes flock averages and the variation in a flock are ignored when describing the success of a breeding programme. Notoriety appears to be gained more by highlighting the 'outstanding' performance of a single individual. This is

Table 11.1. Hypothetical example showing that without selection the average of the population does not improve.

Generation	Genotype	Mass (kg)
Parents	*AABB*×*aabb*	240×200
F_1 offspring	*AaBb*	220
F_2 offspring		
1	*AABB*	240
2	*AABb*	230
1	*Aabb*	210
2	*AaBB*	230
4	*AaBa*	220
2	*Aabb*	210
1	*aaBB*	220
2	*aaBb*	210
1	*aabb*	200
	Mean	219

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unfortunate because when the flock average increases due to selection, the performance of all individuals will have improved.

Factors controlling genetic progress

Any progress in genetic improvement is dependent upon the heritability (h^2) of the traits, the selection differential (S) and the generation interval (G). The concept of heritability is important because it is an indication of the role that genes (rather than the environment) play in the expression of a particular trait. The heritability of a trait in general represents that portion of the phenotypic variation that is due to differences in genes and gene combinations. Therefore, $h^2=V_g/V_p$ and $V_p=V_g+V_e+V_{eg}$, where V_p is the total variation or variation of the phenotype; V_g is the variation due to genotype; V_e is the variation due to the environment; and V_{eg} is the variation due to the interaction between genotype and the environment.

Heritability is expressed on a scale of 0–1 (or 0–100%) and can be classified as low, medium or high. A trait with a low heritability has a value from 0–0.1, medium from 0.1–0.3 and high above 0.3. While this division may appear arbitrary and can be debated, in general only traits with a medium-to-high heritability will respond to selection at an acceptable rate. Although Table 11.2 lists the heritabilities of some economically important traits in the domestic fowl (*Gallus gallus*), the range of estimates is fairly uniform in a variety of commercial species. Parameters such as fertility, hatchability and chick viability have low heritability

Table 11.2. Heritability estimates in domestic fowl for several traits of economic importance (Crawford, 1990).

Trait	Heritability (%)
Fertility	5–10
Livability	1–15
Hatchability	10–15
Age of first egg	15–30
Aggressiveness	20–40
Egg shape	25–50
Body weight	25–65
Feed efficiency	35–50
Rate of gain	40–60
Egg size	40–50

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and are influenced more by management practices than by the overall genetics of the stock. However, several important traits such as body weight, rate of gain and egg size have higher heritabilities. These traits would respond to genetic selection better than traits with low heritabilities. Smith *et al.* (1995) noted that egg weight appears to respond positively to selection in the ostrich, although specific data were not given. Louw and Swart (1982) estimated the heritability of ostrich wing quill scores to be about 0.16–0.18. Often selection for one trait can improve other traits that respond to better management practices. For example, egg size is moderately heritable and there is considerable variation in egg size in ostrich stocks (Deeming *et al.,* 1993; Stewart, 1996; Badley, 1997). Selection for a more uniform egg size would help in attempts to standardize incubation conditions for optimal hatchability, which is another major problem in ostrich production (Ley *et al.,* 1986; Deeming *et al.,* 1993; Deeming, 1996). In general, variability in reproductive traits is a problem in ostrich farming worldwide (Badley, 1997; Deeming and Ar, Chapter 7).

Recently, van Schalkwyk *et al.* (1996) and Cloete *et al.* (1998) estimated the repeatability and phenotypic correlations among reproductive traits in the ostrich. Correlations of egg production with hatchability and infertility were favourable. Hence, selection for increased egg production should lead to improvements in overall reproductive performance. However, a negative correlation was noted between body weight and hatchability in females, but not for males. In other species of poultry, increased body weight often results in declining reproductive efficiency (Chambers, 1990). The repeatability of adult body weight in ostriches was moderately high in both sexes, indicating that past performance would be a good indicator of future performance. However, all reproductive traits measured were moderately repeatable. The reproductive performance of the birds in the first breeding season was a good indicator of subsequent performance. These results suggest that selection decisions based upon the first year's performance would be sufficient, thereby decreasing the need to maintain breeding stock for more than one season to evaluate performance. Although the reports of van Schalkwyk *et al.* (1996) and Cloete *et al.* (1998) represent the first known attempts to actually characterize some important quantitative traits in ostriches, their results suggest that the ostrich is not dramatically different from other species of commercial poultry.

In addition to heritability, the selection differential (S) also influences the rate of genetic improvement. The selection differential refers to the average difference between the current breeding stock and those selected to produce the next generation. For example, if all the females in the flock lay an average of 50 eggs and the top 10% of the females average 80 eggs, the selection differential would be 30 eggs. When this is coupled to the generation interval, i.e. the average age of the parents when the first offspring are hatched, the rate of genetic progress per year (ΔG) can be calculated as follows: $\Delta G = (h^2 \times S)/G$.

For example, given a heritability for egg production of about 0.25, a selection differential of 30 eggs and a generation interval of 3 years, the amount of genetic progress that can be expected is $(0.25 \times 30)/3 = 2.5$ eggs year^{-1} on average. Genetic

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improvement of the ostrich will take a considerable time but no genetic gains will be made without selection.

Given the long generation interval of about 2–3 years, progress in genetic selection will be slower than that for commercial poultry. Furthermore, with the exception of South Africa, the ostrich industry is relatively young in most parts of the world and few efforts have been made to develop long-term selection programmes or even specific lines of birds in response to consumer markets for meat and leather.

OSTRICH SELECTION PROGRAMMES

Any attempt to improve the genetics of ostrich populations must include: (i) goals for the breeding programme; (ii) genetic evaluation of performance; and (iii) a mating system that includes the number of females and males, the amount of selection to be applied and the period of time that the parents are to be used in the flock.

Breeding objectives

For any animal industry the breeding objective depends on economic considerations. For example, will improvements in meat, leather or feathers provide the most economic gain? Of the three products, which one is of most importance? Are there any indications that one commodity will become a major commodity that will surpass the others in the future? The ratite industry should take heed from the history of the early poultry industry, where attempts to develop a dual purpose bird, i.e. a bird for meat and egg production, were very difficult and unsustainable in the long run. Hence it would be wise to develop stock for specific commodities. Once a major commodity is chosen, the next step is to ask which traits influence the product the most. No matter what the product, improvements in reproductive efficiency would be beneficial. For meat production, however, rate of gain and body weight at slaughter must be taken into account.

A lack of clear goals for the breeding programme is also counter-productive. Often this results in an attempt to improve too many traits at once, or traits that are negatively correlated, i.e. where positive selection of one trait results in negative selection of another. However, a better understanding of genetics in general can go a long way towards understanding the goals and the pitfalls of developing a breeding programme.

Genetic evaluation

Once the breeding objectives are in place and the traits chosen for improvement, the next step is to evaluate the genetic performance of individuals. As indicated

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above, this requires excellent record keeping of all the traits placed under selection, as well as those traits that might be important should economic circumstances change. Given the long generation interval of the ostrich, selection decisions taken now will have an impact on performance after 3–5 years. Producers must keep accurate records of egg production and quality, fertility and hatchability, chick quality and livability, rate of gain, and feed consumption, among others. Without such information, it is impossible to identify individuals for the next generation that could lead to genetic improvement of the stock.

Information can be stored on paper or computer, the latter being a more powerful tool. Whatever the record system, it should be simple yet contain all relevant information necessary to make these decisions. In addition to performance data, the record system should contain pedigree details, as these two types of information are closely interrelated.

Poor record keeping can be caused by a variety of misconceptions or causes. Some operators may fear loss of income or status due to the poor performance of specific birds or to the low output of a flock during a particular year. Some producers may develop a distrust of records for a few traits and feel more confident in a visual assessment of the birds. While the latter is essential for an assessment of current health status, judging an animal only by eye ignores the genetic merit demonstrated by the performance record.

Breeding systems

In contrast to breeding in the wild (Deeming and Bubier, Chapter 4), captive birds are kept either as pairs or trios in a paddock or, if the numbers of birds warrants, birds are kept in large groups up to the hundreds in large enclosures. In South Africa, the combination of pair breeding and group breeding has been a common practice. In other countries, particularly those where ostrich farming is a recent development, pairs and trios are most commonly used. Natural incubation is inefficient with group breeding, as several females will lay eggs in a given nest: the eggs are removed at least daily and incubated artificially. Even with pair breeding it is common to remove the eggs for artificial incubation so that the productivity of a hen increases. As with other species of birds, hens will lay more if eggs are removed from the nest. Interestingly, Deeming (1996) examined the productivity of females in pair matings versus trios and colony breeding, and found a higher level of productivity from females in pairs. However, for operations with vast numbers of birds, pair and trio matings should be reserved for the best breeding stock. It is not uncommon for the best birds to be kept for breeding for up to 30 years (Bertram, 1984). However, the value of this practice is questionable if the flock is to improve at an acceptable rate. Furthermore, the productivity of females in South Africa has been reported to peak at 9 years of age and decline thereafter (Cloete *et al.*, 1998).

A breeding system that will lead to genetic improvement depends on the breed structure. At this time, many producers in the USA classify birds simply as

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'reds', 'blues', or 'blacks'. During the past 20 years or so, many of these producers have been crossbreeding these 'varieties' in the hope that an improvement in performance will be observed. The belief is that these birds are distinctive enough to provide superior performing crosses, much like that used at the turn of the century for feather production in South Africa. However, the development of specific lines based on performance goals rather than these designations is more desirable.

Unfortunately, very few goal-oriented, long-term programmes have been implemented. Part of the problem is that the industry has to change from a system where all farms are viewed as breeder farms and only the culls and old birds are slaughtered for meat, to a system where breeder birds supply stock specifically for meat production (Figs 11.2 and 11.3). In the latter model, most of the birds are slaughtered and selection of the breeder stock is not based upon having blues, reds or blacks, but upon specific lines selected for traits of economic importance. If the target product is meat, an issue that must be considered in a breeding programme is the negative correlation between body weight and reproductive efficiency.

There are variety of selection processes depending on the basis of the stock. These include crossbreeding, inbreeding and linebreeding. No matter which breeding programme is chosen a general rule is to breed with the best birds and

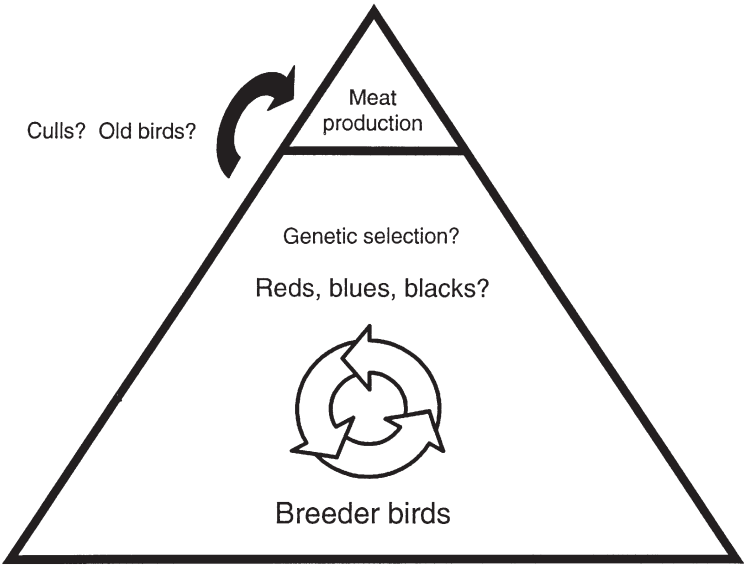

Fig. 11.2. An illustration of the current breed structure of commercial ostriches, where most producers interbreed various birds known as reds, blues and blacks. The extent of genetic selection is unknown. Few birds are raised and slaughtered specifically for meat.

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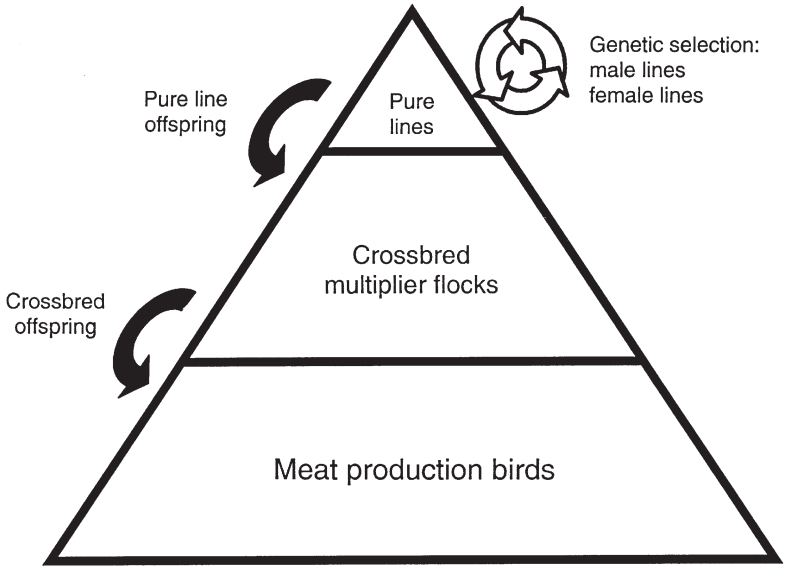

Fig. 11.3. Possible breed and breeding structure for meat production. Primary breeders would be the smallest component, while growers will be the largest. Genetic selection in this model takes place only at the pure line level, with crossbred flocks providing the offspring grown specifically for meat production.

cull the rest. Culling removes an individual from the population, preferably by slaughter, thereby preventing any chance of the bird passing on poor genes in the population. Despite what has happened in the past, cull birds should never be sold as breeder stock.

One method of crossbreeding would be to select a male line specifically for meat, and select a separate female line specifically for egg production with less emphasis on meat. The offspring of a cross between the males from the meat line and the females from the egg line should exhibit considerable hybrid vigour and produce offspring that would exhibit all the desired traits (Fig. 11.3). Traits that should be given high priority in developing a male Line A are shown in Table 11.3. Both males and females would be selected for these traits, but only the males would be used for crossbreeding. Any depression in egg production due to selection for growth rate and body size would be alleviated by crossing the Line A males with females from the female Line B. Traits of importance for the female line are also shown in Table 11.3. The emphasis in the female line is on reproduction, particularly for age at sexual maturity (to shorten the generation interval), egg production and uniform egg weight. The desirable traits of the crossbred birds (AB) are good livability, high body weight at slaughter age, high feed efficiency, and high percentage carcass dressing. It is these crossbred birds that would be sold and their offspring grown and marketed. None of the crossbreds would be used in the parental breeding stock.

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Table 11.3. Useful traits for development of a 'male' line A and a 'female' line B.

Male line A	Female line B
Body weight	Sexual maturity
Feed efficiency	Feed efficiency
Aggressiveness	Egg production
Livability	Livability
Fertility	Hatchability

It should be noted that for Lines A and B, some amount of inbreeding is to be expected as the population of these 'pure' lines will be much smaller than those of the crossbred birds. In developing pure lines for breeding stock, a complete pedigree with accurate performance information is essential so that the rate of inbreeding can be monitored. Inbreeding is the best method for producing lines of birds that are distinct from each other and suitable for crossbreeding. When coupled with selective culling, it can uncover and eliminate detrimental genes. However, the only reason to inbreed is to use the inbred lines for crossbreeding purposes. Inbreeding on its own will not improve performance. One method to slow the inbreeding would be to rotate males among the females rather than to use full-sibling and half-sibling matings exclusively.

Obviously in order for the above crossbreeding system to work, large numbers of birds are required and ideally several male and female lines should be available. Only the largest operations could implement a programme of this magnitude. For smaller operations linebreeding, a mild form of inbreeding, may be more suitable. Here the emphasis is placed on the superior performance of an individual animal. For example, if a superior male was identified, the proportion of the next generation contributed by this male could be emphasized by keeping him and his high-performing offspring for the next generation, thereby concentrating his genotype in the population. As before, excellent pedigree information and performance records are required.

MOLECULAR GENETICS

In addition to the traditional tools for selection of replacement stock, advances in molecular genetics offer new tools that can assist in ostrich breeding. Techniques such as DNA typing (DNA fingerprinting) offer the opportunity to examine genetic diversity and relatedness between individuals, populations or species. In practice, DNA typing has been used to identify individuals and to make decisions on pairing birds for the next breeding season and for gender identification of young

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birds. So far, essentially three methods of DNA typing have been applied to ratites. These include multilocus DNA typing in which a DNA probe marks many loci on the chromosomes; single-locus markers detected using the polymerase chain reaction (PCR); and restriction fragment length polymorphisms (RFLP) for sexing.

The ostrich genome appears to have many repetitive sequences in common with the fowl, but with less frequency of repetition (Eden *et al*., 1978). Despite this observation, Petitte *et al.* (1996) used multilocus DNA typing for individual identification and in pedigree analysis of ostrich, emu (*Dromaius novaehollandiae*) and rhea (*Rhea americana*). In this case a conserved minisatellite sequence was used to probe restriction enzyme-digested ratite DNA. A typical multilocus DNA fingerprint is shown in Fig. 11.4. In general, the results suggest that a considerable amount of genetic variability was present in the population examined. Most

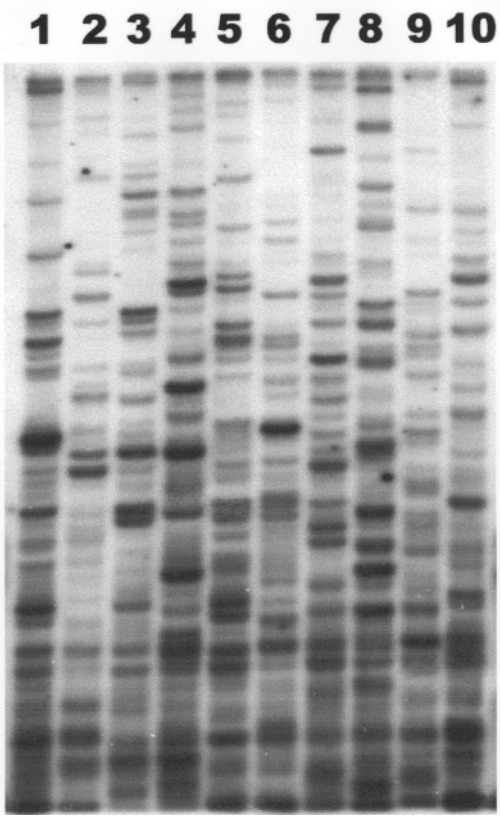

Fig. 11.4. An example of a multilocus DNA fingerprint of ten individual ostriches. Each dark band can represent a locus on a chromosome. If the pattern of banding is distinct enough (polymorphic), the DNA fingerprint can be useful in estimating genetic diversity, individual identification, pedigree analysis, and similarities or differences between individuals or selected lines. Note that the pattern is distinctive for each bird, which indicates considerable variation between birds.

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commercial services for DNA typing of ratites use a multilocus probe system for individual identification and to evaluate genetic diversity.

Polymorphic, single-locus microsatellite markers in ostrich have been isolated and can be used for identification, parentage typing and an examination of relatedness between subspecies (Ward *et al.,* 1994; Kimwele *et al.,* 1998; Kumari and Kemp, 1998). Ward *et al.* (1994) reported a single microsatellite sequence (VIAS-OS2) that identified four codominant alleles. Kumari and Kemp (1998) used 14 microsatellites and noted remarkably different allele distributions between East African subspecies (*Struthio camelus molybdophanes* from Kenya and *S. c. massaicus* from Zimbabwe). Freitag and Robinson (1993), using mitochondrial DNA, also support a distinct separation of *S. c. molybdophanes* from other subspecies of ostrich. Kimwele *et al.* (1998) characterized an additional seven microsatellites with a range of four to nine alleles. The heterozygosity of the seven markers in 14 unrelated individuals ranged from 0.40 to 0.79. In the emu, Gallaway *et al.* (1995) used ten microsatellite loci and the performance records of 36 pairs to calculate a breeding coefficient based on the number of shared alleles, and examined its relationship to embryonic death, fertility and saleable chicks. A positive correlation between embryonic death and an increase in relatedness was observed, and negative correlations were observed between relatedness, percentage hatchability and percentage saleable chicks. In addition, when birds with poor production histories were mated based upon genetically determined pairings, increases in productivity were observed. Similar work with microsatellites is needed for the ostrich.

How the information gathered from DNA typing is used depends upon the goals of the breeding programme and the mating system. Usually, the goal of small operations is simply to improve the performance of the next generation without the use of inbreeding and specific crossbreeding. In such cases, DNA typing can assist in making decisions on individual pairings, particularly if the genetic base of the stock is unknown (Petitte *et al.,* 1996). However, if the goal is to produce specific inbred lines for use in crossbreeding, then DNA typing can be used to monitor the rate of inbreeding in each line and provide information on which inbred lines would yield the best crossbred birds. Hence, how the information will be used in DNA typing depends on the breeding strategies employed.

A few words of caution should be noted regarding the use of DNA typing and the determination of relatedness. In the absence of pedigree information and DNA samples of the parents and other offspring, it is impossible to determine the specific relationship between any two individuals, i.e. brother/sister or parent/offspring. That two individuals have a similar fingerprint does not mean that they are, in fact, first-order relatives. The more a population becomes inbred, the more similar all of the DNA profiles become. In theory, with 100% inbreeding the DNA fingerprints of all individuals will look the same. Indeed, DNA fingerprints of individuals from highly inbred lines of fowl are indistinguishable from one another (Petitte *et al.,* 1990). Therefore, without comparisons with the parents and other offspring, DNA typing results can indicate only that the individuals have a similar genetic make-up. In addition, because of differences in the procedures used

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the results of some DNA fingerprints from different laboratories often cannot be compared, so it is better to have all DNA typing work done at one location.

The third method of DNA typing provides a simple yes-or-no answer to a question regarding the presence or absence of a specific DNA sequence in any particular bird. The most common use of this method is the identification of gender. Until the advent of DNA sexing, ostriches were sexed by examination of the cloaca (Samour *et al.* 1984; Gandini and Keffen, 1985). Today several DNA-typing services can sex birds using the same procedures as for DNA typing. Unfortunately, this procedure is time-consuming and can take up to 2 weeks depending on the methods used. No W chromosome-specific DNA sequences have been identified in the ostrich which would allow for a faster method of DNA sexing.

FUTURE CONSIDERATIONS

The ostrich industry is reaching the point at which genetic information will become invaluable, both for developing stock for specific markets and for improving the overall genetic merit. As with other animal industries, this necessitates pooling of performance records to obtain large amounts of reliable data, for use in mathematical models for calculating breed values that can help compare the genetic merit of individual birds despite the different environments. Should the industry have national registries for breeding stock that include performance information? The first task would be the standardization of records. What traits should be measured and when? How will the industry be structured? While the trend is to raise birds for meat, not every operation can be a breeder farm. Whatever specific form the industry takes in the future, record collections and management at local and national levels would go a long way towards building a sound basis for the genetic improvement of ostriches in a commercial setting.

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12

Veterinary Problems

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There are no infectious or contagious diseases exclusive to ostriches, with the exception of a few host-specific parasites; but ostriches can contract infections from other species of birds and mammals. Often they are less sensitive than the original hosts to these infectious agents, and need additional factors and circumstances to manifest clinical disease. Most ostrich diseases are multifactorial, a point essential for veterinary treatment of these birds.

Under commercial production, ostriches must be managed in a similar way to other production stock. In most cases the value of an individual bird is too little to warrant specific treatment or, in particular, expensive surgery. When there is a disease problem in a flock the veterinarian has to establish a diagnosis in cooperation with a laboratory, and supplement this with a thorough investigation of circumstances on the farm. Only when a complete picture is available can a course of remedial treatment be charted.

Transmission of infectious agents from other species to ostriches has to be prevented or minimized. The most important sources of infectious agents are domestic and wild birds. Whenever possible ostrich farming should not be undertaken in the vicinity of a poultry farm, and no poultry or pet birds should be kept on an ostrich farm. Wild birds are attracted to the feed troughs of ostriches in open enclosures and camps. This threat can be reduced by feeding concentrates for short, limited periods and feeding only roughage (silage or hammer-milled hay) *ad libitum* for the rest of the day.

Rats and flies are other important sources of infectious agents, particularly of the bacteria causing enteritis. Protective clothing and footbaths at the entrance of a rearing unit make little sense if it is frequented by swarms of flies. Such measures only lead to a false feeling of security. Rather, the utmost should be done to get rid of flies and other insect pests.

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Once an infectious disease has broken out on a farm it can easily spread from one age group to another. This can be prevented only by the adoption of all-in all-out rearing systems as practised on poultry farms. At present, most ostrich farms follow multi-age-group rearing systems, thereby increasing the risk of infectious diseases.

Some of the disease agents affecting ostriches also can cause disease in people, either when in contact with live or dead birds or, potentially, when consuming meat from infected ostriches, although for the latter the risk is minimal (Huchzermeyer, 1997a). Zoonotic aspects of ostrich health are discussed below under the individual disease headings where appropriate.

MULTI-FACTORIAL DISEASES

Yolk-sac retention and infection

The factors involved in this condition include poor hygiene during egg handling and incubation which allows bacteria to penetrate the eggshell (Deeming, 1997). Another problem is infection of the navel during or soon after hatching, and there can be problems with initial gut colonization by pathogenic bacteria. In the rearing barn, incorrect brooding temperature (too cold or too hot), brooding under heaters on a cold concrete floor, restricted water intake and a delayed start to feeding can all predispose chicks to yolk-sac infection.

Clinically affected chicks are poor starters and fail to gain weight towards the end of the first week (Verwoerd *et al.*, Chapter 8). This is because they are not receiving the nutrients and antibodies from the yolk sac, and its decomposition may lead to the absorption of bacterial toxins. A persistent yolk sac can be palpated or visualized by the use of ultrasound (Blue-McLendon and Homco, 1995). If the infection has taken place via the navel, a pea-sized abscess at the navel can be palpated. Deaths may start within a few days after hatching and usually continue for 2 weeks, although putrid yolk sacs can be found encapsulated on the wall of the peritoneum of older birds (Deeming *et al.*, 1996).

On *post-mortem* examination the yolk sac is too large for the age of the chick, it may show signs of inflammation, and its contents may be inspissated or putrescent. Dull or dirty green discoloration of the yolk is due to bile pigments which have entered the yolk sac via the vitello-intestinal duct due to abnormal peristalsis in chicks with delayed feed intake, while a bright green colour is due to the storage of bile pigments during incubation (Deeming *et al.*, 1996).

Yolk-sac infection does not respond to treatment with antibiotics. In confirmed cases the infected yolk sac can be removed through a crescentic incision of the abdominal wall close to the sac and after ligation of the vitello-intestinal duct with its blood vessels (Kenny and Cambre, 1992). Alternatively, a large needle attached to a syringe is inserted into the yolk sac through or close to the navel, through which the contents of the yolk sac are sucked out and replaced

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with a small quantity of an antibiotic solution. Given the value of the birds at this age, the suitability of these treatments is questionable.

Prevention of infection is a better course of action. Nests should be kept dry and covered with clean sand from time to time. Eggs should be collected before they have time to cool down, as during cooling the contents shrink and bacteria from a wet nesting site then can be pulled into the shell. Incorrect egg washing can also facilitate the penetration of the shell by bacteria and microbial spores (Deeming, 1995, 1997; Huchzermeyer, 1996a). Incompletely healed navels of hatchlings should be routinely disinfected using a topical disinfectant or antibiotic.

Enteritis

Failure to establish and maintain a normal gut flora, or destruction of the gut flora by use of antibiotics, can lead to the problem of enteritis. Other factors include malnutrition, insufficient fibre in the diet or a sudden change in the feed which reduces ingestion (Huchzermeyer, 1998). Environmental conditions, particularly cold, can predispose chicks to enteritis. Behavioural problems, such as desertion stress (Huchzermeyer, 1997b), and excessive coprophagy due to delayed feed recognition, are also implicated. Unhygienic conditions, particularly involving flies, can cause problems. Lastly, there can be primary infection with bacterial agents (salmonellae, pathogenic strains of *Escherichia coli*, *Klebsiella*, *Pseudomonas aerogenes* and certain strains of *Campylobacter jejuni* and of *Clostridium perfringens*), viruses (avian influenza and coronavirus) or protozoa (Cryptosporidia and *Histomonas meleagridis*) (Shivaprasad, 1993; Verwoerd *et al.*, 1998; Huchzermeyer, 1998).

Clinically, affected chicks are very depressed, and the condition can spread rapidly through the whole group. There may be no visible diarrhoea if only the small intestine is affected. *Post-mortem* examination reveals a variety of forms of inflammation, including serous, sero-mucoid, serofibrinous, ulcerative or haemorrhagic, which may affect part or all of the intestine. Ostriches lack mesenteric lymph nodes and often are unable to limit the spread of infection; hepatitis and septicaemia are then found in conjunction with enteritis. A specific diagnosis should be based on direct-smear microscopy, bacteriological examination and transmission electron microscopy of the intestinal contents as well as on histopathology.

Treatment depends on the specific diagnosis. Antibacterial treatment alone may be contra-indicated, as it further inhibits the intestinal flora. Alternating between antibiotics (in the morning) and probiotics (in the evening) limits the damage, as it temporarily restores a working flora and thereby gives better results (Verwoerd, personal communication, 1998).

Prevention of enteritis is based on detailed attention to all predisposing and triggering factors. The most important of these is the early establishment of a normal intestinal flora and its maintenance (Huchzermeyer, 1998). This can be

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achieved by dosing the chicks as early as possible after hatch with a commercial probiotic containing live bacteria; plain, live yoghurt can also be used (Deeming *et al.*, 1996). After a few days of such treatment the chicks should be exposed to a wider range of bacteria, by placing them on pasture even if only for a few hours, by scattering a handful of fresh garden soil in the concrete run or by exposing them to faeces of other herbivores such as rabbit, horse, goat or sheep but not poultry manure. These measures, where practised on South African ostrich farms, have led to a drastic reduction in cases of enteritis (Huchzermeyer, unpublished observations, 1998). Furthermore any antibacterial treatment should be followed up with a similar procedure to re-establish a normal gut flora.

Fibre in the ration stimulates intestinal development and enhances the development of a normal flora, while its undigested components bind and eliminate bacterial toxins. Fibre should be an essential part of all ostrich rations, particularly for chicks. For this reason all ostrich rations should contain a minimum of 10% fibre irrespective of nutritional requirements or recommendations (Huchzermeyer, 1998).

Gastric stasis

In this disease gizzard contractions stop, no food is processed and transported into the intestines, and consequently the affected bird starves despite having a full proventriculus (Huchzermeyer, 1994). The factors involved in the development of this condition include suboptimal temperatures, injury to the gastric mucosa by foreign bodies, any disease process depressing normal functions, and behavioural problems (Huchzermeyer, 1998).

Clinically, birds stop growing and start losing weight despite apparently moving and behaving normally. Auscultation reveals the absence of gastric contractions. In the end the bird becomes too weak to stand up and it usually dies after a short period of recumbency.

Post-mortem examination shows the bird to be emaciated, without fat in the coronary groove of the heart. The inner lining of the gizzard is soft with folds (koilin hypertrophy) and may be ulcerated (Figs 12.1 and 12.2). The proventriculus may be empty or filled with normal feed, but not impacted. The small intestine is usually empty and may have a congested mucosa; there will be some faecal pellets in the lower colon. Some of the birds may also have lesions of secondary hepatitis and/or airsacculitis, but the results of bacterial isolation will be inconsistent.

Treatment of gastric stasis consists of eliminating the triggering factors, dosing with a high-energy liquid (vegetable oil or equal parts of milk, sugar, egg yolk and vegetable oil), and restarting the gizzard contractions by intravenous injection with metaclopramide HCl at 0.1 mg kg^{-1} live mass (Shakespeare, 1996).

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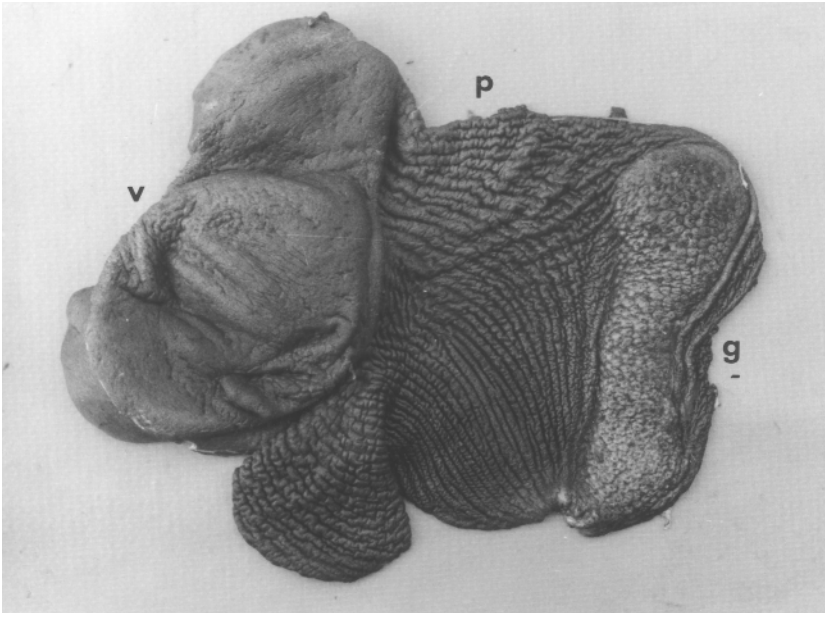

Fig. 12.1. Normal proventriculus and gizzard of an ostrich chick. Note the parallel folds of the proventricular mucosa and the smooth surface of the koilin layer of the gizzard. v, Gizzard; p, proventriculus; g, glandular patch.

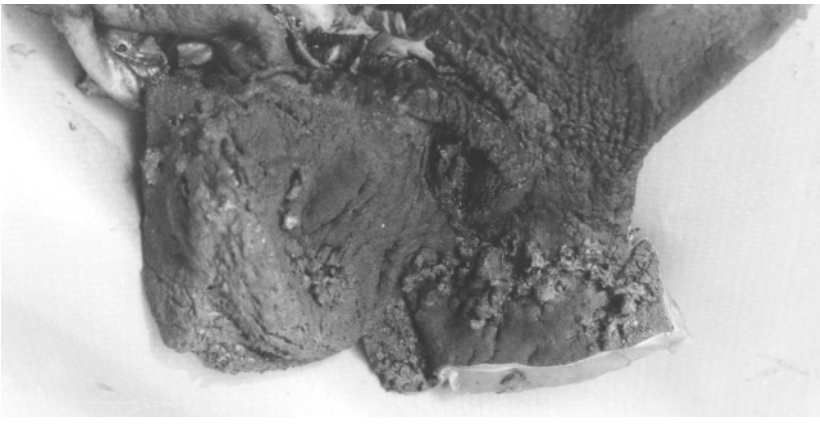

Fig. 12.2. Gizzard of an ostrich chick that died from gastric stasis. Note the uneven surface of the koilin layer in the gizzard (koilin hypertrophy).

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Impaction

Impaction is an accumulation of food or non-food items (sticks, metal, glass, etc.) in the proventriculus, with the subsequent blockage of the opening into the gizzard causing a failure of food to move along the gastro-intestinal tract (Huchzermeyer, 1994, 1998). Impaction should be regarded more as a symptom of behavioural problems such as disorientation stress, desertion stress or frustration with regard to finding food (Huchzermeyer, 1997b). Access to substrate or foreign bodies can cause problems, but only if the environment is poor.

Disorientation takes place when ostrich chicks or juveniles are moved from one place to another, from one pen to another or even from the night accommodation to the outside run, and particularly from farm to farm. In such a situation the birds also need to be comforted by the presence of a parent figure. Frustration can be caused by non-recognition of feed after a change to a different feed, or in adult birds by being unable to reach a coveted sexual mate (Huchzermeyer, 1997b).

Stressed birds compensate by abnormal pecking or feeding behaviour (Huchzermeyer, 1997b). Frequently this leads to the ingestion of long grass, litter, foreign bodies, sand or gravel (Huchzermeyer, 1994, 1998; Deeming and Dick, 1995). The accumulated matter leads to an occlusion of the passage between proventriculus and gizzard or of the intestines (sand impaction). Sharp foreign bodies may pierce the wall of the proventriculus or gizzard and cause a localized infection or peritonitis and septicaemia (Deeming and Dick, 1995). In all cases the result is a secondary gastric stasis leading to starvation and death. This can be a problem associated with whole groups of birds but it can also affect single birds.

The clinical signs are those of gastric stasis, but in impacted birds the distended proventriculus or the sand-filled intestines can be palpated (Huchzermeyer, 1994, 1998). *Post-mortem* examination will show an emaciated bird with depletion of coronary fat and koilin hypertrophy, but foreign bodies, the rolled-up fibrous matter in the proventriculus or the sand-filled small intestine and caeca, readily point to impaction (Huchzermeyer, 1994, 1998).

Many cases of impaction can be treated successfully by gastric lavage (Putter, 1996). For this a small bird is held hanging by its legs, or larger birds are held in lateral recumbency on a table or a trailer with the head hanging down. Then a tube of appropriate size and with water running (not jetting) is introduced through the open beak into the oesophagus and gently pushed up into the proventriculus, where the running water loosens the impacted matter. After 60 s the tube is withdrawn, the water allowed to run out and the bird allowed to regain its breath, before the treatment is repeated. Three to four washings suffice to remove all impacted matter from the proventriculus. Alternatively an oesophagostomy (Burger, 1976) or a gastrotomy (Honnas *et al.*, 1991) could be performed for the removal of the impacted matter.

Sand can be neither washed nor removed surgically from the intestines. Dosing orally with emulcents (psyllium muciloid, 0.5–1.0 g kg^{-1} live mass, and/or

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vegetable oil, 1–2 ml kg^{-1} live mass) may help to remove the blockage (Huchzermeyer, 1994; Shakespeare, 1996). All impacted birds are in danger of running out of energy reserves and should be kept warm until fully recovered.

Such treatments are only of value if the original stressor has been removed. Prevention of impaction, based on minimizing behavioural stress and limiting access to substrate and/or foreign matter, is a much more appropriate course of action.

Leg deformation

Young chicks are most commonly afflicted by leg problems (Verwoerd *et al.*, Chapter 8). Splayed legs are due to slippery surfaces and excessive yolk-sac size. If attended to early, splayed legs can be treated by tying the legs of the chick together with a piece of string or tape (hobbling) in a way that allows the chick to walk with small steps (Deeming *et al.*, 1996).

Twisted toes are possibly caused by unsuitable surfaces and certain vitamin deficiencies (Deeming *et al.*, 1996). They can be corrected by the use of L-shaped splints, with the short arm of the L pointing in the opposite direction to the rotation (Huchzermeyer, 1998). In some cases exercise alone leads to correction.

In tibiotarsal rotation the bone rotates outward along its longitudinal axis usually at its distal end (Deeming *et al.*, 1996), with the foot then pointing sideways and the bird unable to walk properly or at all (Bezuidenhout and Burger, 1993). Genetic factors, excessive growth rate, lack of exercise and nutritional imbalances (calcium, phosphorus, vitamin D_3, certain microminerals), as well as stumbling and falling over feed and water troughs, are suspected to predispose to and precipitate cases of this condition (Bezuidenhout *et al.*, 1994; Huchzermeyer, 1994, 1998). There are no reports of successful surgical correction.

Slipping of the gastrocnemius tendon from the condyles of the hock joint often causes compound dislocation of the joint with an open wound. The causes are unknown. Severely affected birds have to be culled, while strapping of both hock joints of less severely affected birds might lead to improvement (Dick and Deeming, 1996). A link to perosis in poultry and manganese deficiency has not yet been proven.

Respiratory disease

Factors involved in respiratory disease include keeping birds in cold conditions. High dust levels and insufficient ventilation leading to high levels of ammonia can also be important. These and other stressors can depress the immune system, making the birds more susceptible to moulds or bacterial and viral agents.

Respiratory disease most frequently affects the nasal passages, the infraorbital sinuses, the conjunctivae, larynx, trachea and air sacs, but less frequently the lungs. The avian lungs are constructed in such a way that the inhaled air bypasses the gas exchange tissue thus avoiding contamination, allowing inhaled

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bacteria and spores to move through and settle in the air sacs (Schmidt-Nielsen *et al.*, 1969). Avian pneumonias rather are localizations of septicaemic conditions, rarely related to or extensions of the other respiratory diseases. Air-sac lesions are silent and cannot be detected by auscultation. Bacteria isolated from respiratory disease in ostriches include *Pasteurella haemolytica*, *Pseudomonas aeruginosa*, *Bordetella* spp., *Haemophilus* spp., *Staphylococcus* spp., *Streptococcus viridans*, *Corynebacterium pyogenes*, *Mycoplasma* spp. and *Chlamydia psittaci* (Pericard *et al.*, 1991; Kolb *et al.*, 1993; Shivaprasad, 1993; Huchzermeyer, 1994).

Most avian inflammation processes are accompanied by the exudation of fibrin, forming cheesy deposits in passages and cavities. This is a primitive defence mechanism intended to immobilize the infectious agents. However, these fibrin deposits tend to occlude the passages and interfere with their function. Even after a successful antimicrobial treatment of the disease, these fibrin deposits remain and may permanently incapacitate the bird (Huchzermeyer, 1998).

The treatment of respiratory disease depends on the outcome of the laboratory investigation, including sensitivity testing of isolated bacteria, and on the results of the investigation on the farm with the elimination of damaging environmental factors. With any antibacterial treatment the effect on the intestinal flora should be considered.

BACTERIAL INFECTIONS

Gram-negative bacteria

Important Gram-negative bacteria in ostrich disease situations include the salmonellae, pathogenic serotypes of *E. coli*, *P. aeruginosa* and *Klebsiella* spp. (Huchzermeyer, 1994; Henton, 1998; Verwoerd *et al.*, 1998). These bacteria are acquired from the environment (flies, rats, even unwashed human hands) and can colonize an intestine not protected by a normal flora. Depending on other factors they may then cause an inflammation of the intestine. Furthermore, bacteria can penetrate the blood circulation and cause septicaemia via two separate routes. Firstly, birds lack lymph nodes to filter bacteria from the lymph, so they are carried into the blood stream. Secondly, under severe stress bacteria can directly enter the blood stream in the intestinal mucosa and cause stress septicaemia, while wound infections normally are localized by fibrin exudation. Predisposing and contributing factors as well as diagnosis, treatment and prevention have all been discussed previously. Salmonellae can cause disease in people.

Clostridia

Clostridium perfringens is a normal inhabitant of the intestines of many species of herbivore, including ostriches (Odendaal, 1994). A disturbance of the intestinal flora brought about by a sudden change in the ration such as going on to lush

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pasture, by anti-helminthic treatment, or by other stresses and disease processes, allows these organisms to multiply out of control and produce toxins which accumulate to pathogenic levels. Toxins A, B and D are most commonly involved in clostridial infections (Huchzermeyer, 1994). Other clostridia reported to have caused disease in ostriches are *C. chauvoei* (Lublin *et al.*, 1993), *C. difficile* (Frazier *et al.*, 1993), *C. sordellii* (Poonacha and Donahue, 1997) and *C. colinum* (Perelman quoted by Jensen *et al.*, 1992).

Clinically, affected birds are very severely depressed and death occurs rapidly. *Post-mortem* examination reveals a severe serous or haemorrhagic enteritis of the jejunum, ileum, caeca and upper rectum. This enteritis is often diagnosed as coccidiosis although no coccidia are found. Moreover, no reports of confirmed cases of coccidiosis in farmed ostriches have ever been published. In chronic cases there may be small ulcers in the mucosa of the duodenum and jejunum. Diagnosis should be confirmed by isolation of the bacteria in anaerobic cultures and the determination of their toxin type.

Clostridiosis is treated by dosing with tetracyclines or synthetic penicillins, after which the normal intestinal flora has to be restored. The treatment must be accompanied by the elimination of the extraneous triggering factors. For prevention it is important to maintain a protective intestinal flora, and to avoid sudden feed changes and other stresses. In addition the vaccination against *C. perfringens* toxin types B and D at 3 and 6 weeks of age is recommended where this disease is a problem (Huchzermeyer, 1994).

Mycobacteriosis

Mycobacteriosis, or avian tuberculosis, is caused by *Mycobacterium avium* through contact with infected faeces of poultry or other birds. This disease is common in zoos and bird collections but very rare on ostrich farms (Hobday, 1896; Nouvel and Leclerc-Cassan, 1972; Burger, 1976; Korbel, 1991; Huchzermeyer, 1994, 1998). *M. avium* can also infect humans.

Affected ostriches develop either localized lesions (eye, phallus) or general infections in which they slowly waste away, and on *post-mortem* examination small, hard, white nodules are found in the liver and spleen and sometimes in other organs. However, similar nodules are also produced by other bacteria (*P. aeruginosa*) and by fungi (*Aspergillus* spp.). Diagnosis has to be confirmed by microscopical detection of the acid-fast bacteria on stained smears, by histopathological preparations and by culture of the organism. Several serological tests are also available (Phalen *et al.*, 1995). There is no treatment: infected ostriches should be culled from the flock, and measures should be taken to eliminate all contact with birds of other species.

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Megabacteriosis

Megabacteriosis is an infection of the koilin layer of proventriculus and gizzard by megabacteria. These very large fungus-like bacteria (Fig. 12.3) do not yet have a scientific name. For some time the disease has been known as 'going light' in show budgerigars and other cage birds, and it is believed that the infection spreads into ostriches from these birds although wild birds may also have been involved. Other factors are probably needed to trigger outbreaks of megabacteriosis, but once in a rearing unit the disease becomes established and causes high mortality. Initial outbreaks in South Africa were devastating, with more than 90% mortality (Huchzermeyer *et al.*, 1993), but subsequently the megabacteria appear to have lost some of their virulence.

Clinically, and *post mortem*, affected chicks show typical signs and lesions of gastric stasis. Diagnosis is confirmed by demonstration of the megabacteria in the koilin layer by impression smears from the underside of the koilin layer, by histopathology, or by bacterial culture on MRS (Man, Rogosa and Sharpe) agar (De Man *et al.*, 1960).

Megabacteria are sensitive to synthetic penicillins, but these can encourage fungal growth in the damaged gastric environment. It is therefore better to give a combined antibacterial and antifungal treatment. In addition, the gizzard contractions have to be restimulated. Outbreaks can be stopped only by vacating the unit and leaving it without chicks for a minimum of 6 weeks. Prevention is based on avoiding all contact with pet and wild birds and their faeces, as well as avoiding stress factors (Huchzermeyer, 1994, 1998).

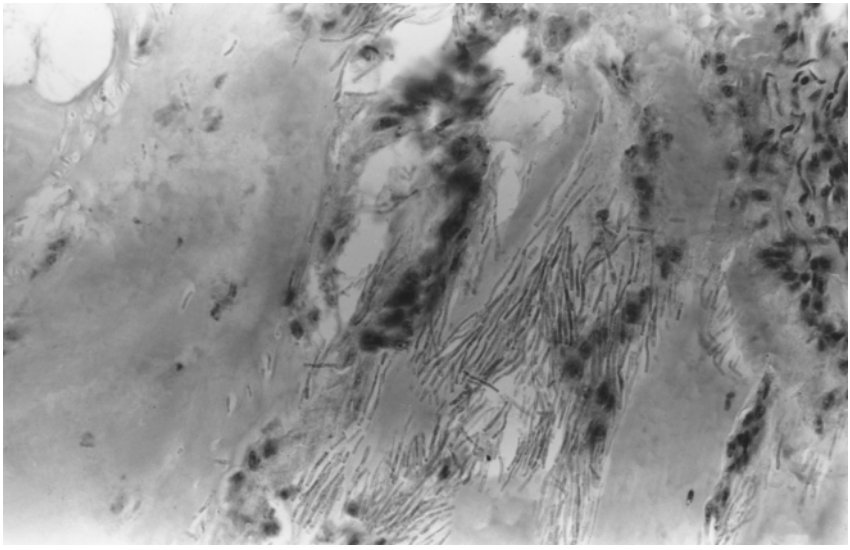

Fig. 12.3. Megabacteria in the koilin layer of an ostrich gizzard (×400).

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Other bacterial infections

In ostriches anthrax, i.e. infection with *Bacillus anthracis*, occurs in two forms: sudden death and anthrax fever, the latter severely depressing the birds but with spontaneous recovery. Both forms may occur simultaneously in the same flock (Theiler, 1912). A cattle vaccine has been used successfully to prevent further outbreaks on farms where this disease occurred. No cases of anthrax have been reported in ostriches during the last 50 or more years. Anthrax can cause human disease.

Campylobacter jejuni is a poultry pathogen shown to cause enteritis and hepatitis in ostrich chicks (Perelman *et al.*, 1992). It is increasingly associated with cases of enteritis in ostrich chicks in South Africa (Verwoerd, personal communication, 1997). Diagnosis is based on bacterial cultures, and the recommended treatment is dosing with furaltadone in the drinking water (250 mg l^{-1}), or injection of norfloxacin (30 mg kg^{-1} live mass; Perelman *et al.*, 1992), followed by restoration of a normal intestinal flora. Prevention is based on the principles outlined for general enteritis problems.

Infections with *Chlamydia psittaci* in ostriches have been reported from several countries. *C. psittaci* can be carried by many species of wild and domestic birds. Infected birds can be asymptomatic carriers, and a severe stress is needed to precipitate clinical disease. In ostriches conjunctivitis as well as generalized disease with severe depression and high mortality have been reported (Kolb *et al.*, 1993; Kösters *et al.*, 1995). In the cases of generalized disease, there were fibrinopurulent tracheitis, pneumonia, pericarditis and perihepatitis. Diagnosis is based on the demonstration of the chlamydia in stained impression smears and histopathological sections or the isolation of the agents. Several serological tests are also available.

For treatment it is necessary to give a prolonged course of tetracyclines, whilst prevention is based on the strict avoidance of all contact with wild or pet birds and their faeces. Chlamydial disease has been reported in persons in contact with infected ostriches (Pericard *et al.*, 1991).

FUNGAL INFECTIONS

Dermatitis

Fungal skin infections can be caused by *Aspergillus* spp., *Trichophyton* spp. and *Microsporum gypseum* (ringworm) (Onderka and Doornenbal, 1992; Perelman and Kuttin, 1996; Pistorius, 1996). Wet conditions, stress and poor health may be contributing factors. The lesions may remain localized or involve larger areas, whilst ringworm lesions may occur in rows of small, round lesions anywhere on the body (Boast, 1996). The scar tissue resulting from these lesions can cause downgrading of affected skins. Treatment consists of dabbing the lesions with a 1:50 aqueous solution of enilkonazole (Imaverol 10%, Janssen) (Pistorius, 1996).

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Infections of the respiratory tract

Respiratory fungal infections are acquired by the inhalation of fungal spores produced by moulds growing in the environment, mainly *Aspergillus* spp., and so the disease is commonly called aspergillosis (Walker, 1912; Rousseaux and Dalziel, 1981; Perelman and Kuttin, 1992a; Fitzgerald and Moisan, 1995). All parts of the respiratory system can be involved, but particularly the lungs in young chicks and the air sacs in older chicks, juveniles and adults. Stress is a predisposing factor. Clinical signs depend on the localization and severity of the lesions, ranging from respiratory noises to shortness of breath. Lesions in the air sacs cannot be detected by auscultation.

Clinical diagnosis can be confirmed by culture of tracheal swabs, radiography and ultrasound, as well as by serological tests (Scott and Garner, 1993; Marks *et al.*, 1994; Brown and Redig, 1994; Huchzermeyer, 1994, 1998). Upon *post mortem*, typical nodular lesions are found in affected organs, from which fungi can be cultured. The presence of fungal hyphae can also be seen on histopathological preparations.

Treatment consists of aerosoling the birds with a 1:50 aqueous solution of enilkonazole (Imaverol 10%, Janssen) or fumigation with enilkonazole (Clinafarm, Janssen) (Perelman and Kuttin, 1996; Huchzermeyer, 1998). The birds to be aerosoled or fumigated are placed in a small, closed room in which they are forced to inhale the aerosol or fumes. Whilst this treatment kills the fungi, it does not remove the fibrin surrounding the lesions and therefore does not lead to an immediate clinical improvement. Prevention of aspergillosis requires strict avoidance of mouldy conditions in the environment of the birds (hay and straw litter, wet patches around water troughs, mouldy feed), providing good ventilation, keeping the birds warm and avoiding stress and malnutrition.

Infections of the digestive tract

Yeasts of the genus *Candida* are the main fungal agents infecting the upper digestive tract, and cause a condition commonly called 'thrush'. This consists of yellow pseudomembranes (fibrin) in the pharynx and upper oesophagus. Protracted lesions can cause beak deformation (Huchzermeyer, 1998).

Infections of the proventriculus and gizzard involve yeasts as well as *Aspergillus* spp., *Mucor* spp. and other fungi penetrating the koilin layer and sometimes also the mucosa leading to gastric stasis (Perelman and Kuttin, 1992b; Jeffrey *et al.*, 1994; Huchzermeyer, 1998). However, fungal infections can also be a sequel to, or a complication of, gastric stasis, particularly after attempts to treat sick chicks with oral antibiotics. Affected birds show all the symptoms and *post-mortem* lesions of birds suffering from gastric stasis. The presence of fungi can be demonstrated by culture and histopathology.

Yeast infections can be treated with nystatin (Mycostatin, Squibb) individually at 20,000–50,000 units kg^{-1} live mass or in the feed at 220 mg t^{-1} for 8–10

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days, while gastric aspergillosis is treated with itraconazole (Sporanox, Janssen) at 10 mg kg^{-1} live mass for 5–10 days (Perelman and Kuttin, 1996). Alternatively, acidified copper sulphate can be given in the drinking water at 0.5 g l^{-1} for 5–7 days for both conditions (Perelman and Kuttin, 1996).

VIRAL INFECTIONS

Newcastle disease

Newcastle disease is a disease of poultry caused by a pathogenic virus of paramyxovirus serotype 1 (APMV-1), but avirulent strains have also been isolated from ostriches (Manvell *et al.*, 1996). Ostriches contract the virus from poultry and wild birds, causing subacute to chronic nervous disease, usually limited to a small number of birds. Nervous signs consist of a slight tilting of the head, frequent scratching of the head, a tic of the neck muscles, later torticollis, uncontrolled head movements and finally inability to lift the head off the ground (Fig. 12.4; Samberg *et al.*, 1989; Huchzermeyer and Gerdes, 1993; Huchzermeyer, 1996b). Usually only one or a few birds are affected in a flock at any one time. In severe cases mortality occurs within 3 or 4 days. Ostriches appear to become more resistant to the infection with increasing age.

Ostriches which have died from Newcastle disease do not show any typical pathological or histopathological lesions. In some cases small foci of gliosis may be seen in the brain stem, while perivascular cuffing is rare (Allwright, 1996; Huchzermeyer, 1996b). Isolation and identification of the virus is the only reliable way to diagnose the disease. The haemagglutination inhibition test is unreliable, tending to give false negative as well as false positive results (Huchzermeyer, 1996b). However, reliable ELISA kits are now available.

There is no treatment for Newcastle disease, although some birds may recover spontaneously. Prevention consists of avoiding contact with poultry or wild birds. The combined use of live vaccines with killed emulsified or aluminium hydroxide-absorbed vaccines gives very good protection (Verwoerd *et al.*, 1997). A disadvantage of the emulsified vaccines is that sometimes they cause severe local reactions. Due to the slow spread of the disease within a flock, it may be sufficient to vaccinate only once the disease has broken out. Trials carried out at Onderstepoort, South Africa, showed that there is no carrier state in slaughter ostriches (Verwoerd, 1998)

Avian influenza

Avian influenza is caused by a number of strains of the influenza virus, and can affect or be carried by a large variety of wild birds with different pathogenicity for various avian species. In 1991 and 1992 severe outbreaks occurred in juvenile

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Fig. 12.4. Ostrich chick (approximately 6 weeks of age) with Newcastle disease, unable to lift its head off the ground.

ostriches in South Africa caused by the strain H7N1 (Allwright *et al.*, 1993). Strains H5N9 and H9N2 have also been isolated from South African cases, and H5N2 from an ostrich in Zimbabwe (Manvell *et al.*, 1996) and ostriches imported into Denmark (Jørgensen *et al.*, 1998). Not all strains are equally pathogenic for ostriches (Manvell *et al.*, 1998).

The severity of the disease depends on the age of the birds, with chicks being more susceptible than older birds, as well as on complicating secondary respiratory and intestinal infections. Clinically the birds show severe depression, ocular discharge and respiratory signs, and pass green urine.

Post-mortem lesions consist of an enlarged, mottled and friable liver and congestion of the proximal small intestine which is filled with mucoid contents. Outstanding histopathological lesions in the liver consist of coagulative necrosis surrounded by heterophil infiltrate, often in the proximity of blood vessels with varying degrees of vasculitis.

There is no treatment for avian influenza. However, it is important to treat the secondary infections once these have been identified. Whilst the use of an

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experimental vaccine was successful in preventing further mortality in South Africa, it did not prevent the spread of the virus. Vaccines have to be strain-specific, and the multiplicity of avian influenza strains encountered in the field makes it virtually impossible to prepare and use vaccines against future outbreaks. Prevention has to rely mainly on reducing contact between ostriches and wild birds.

Crimean–Congo haemorrhagic fever

Crimean–Congo haemorrhagic fever occurs from the Black Sea to the southern tip of Africa and is transmitted by ticks of the genus *Hyalomma*. In sheep, cattle and ostriches it causes a very short, symptomless viraemia. Human infections, which are often fatal, are contracted through the bite of infected ticks or through direct contact with the blood of a viraemic animal. No case of human infection from the consumption of meat from an infected animal has ever been reported.

In South Africa, ostriches have been found to be serologically positive for the virus, and a labourer on an ostrich farm contracted the infection when handling tick-infested slaughtered ostriches (Shepherd *et al.*, 1987). In 1996 several labourers at the Oudtshoorn ostrich abattoir came into contact with infected ostrich blood and one of them died. However, in experimentally infected ostriches slaughtered during viraemia the virus could not be detected in muscle samples (Swanepoel *et al.*, 1998). Occurrence of the infection in ostriches at abattoirs can be prevented by keeping the birds free of ticks for 14 days before slaughter (Verwoerd *et al.*, Chapter 8).

Other viruses

Whilst both eastern and western equine encephalitis viruses have been isolated from ostriches in the USA, clinical disease and mortality are known from emus only (Smith, 1993). Borna disease is a viral infection of horses and sheep, but in Israel the infection has caused an irreversible spastic paresis in juvenile ostriches. Diagnosis is based on histopathological lesions in the lumbar spinal chord and the demonstration of viral proteins by enzyme-linked immunosorbent assay (ELISA). Serum from surviving paretic birds can be used to prevent further outbreaks on farms where this disease poses a problem (Malkinson *et al.*, 1993; Ashash *et al.*, 1994, 1996).

Avian pox virus is transmitted by a mosquito bite, and poultry and wild birds can be a source of infection for ostriches. The dry form of the disease produces wart-like lesions around the beak and eyes, in severe cases causing the eyes to close up, while the wet form produces pseudomembranes in the buccal cavity, pharynx and larynx. This latter form can cause severe respiratory problems and can interfere with feed intake. In both cases the course of the disease can be protracted, 1 month or longer, and there is no treatment (Perelman *et al.*, 1988; Allwright *et al.*, 1994a). Diagnosis is based on the typical lesions on the head.

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Inclusion bodies can be found on histopathological sections, and the virus can be isolated in embryonated chicken eggs. Where the disease is a problem a commercial fowl pox vaccine can be used to immunize ostrich chicks. Burning mosquito coils in the chick-rearing houses will help to control the mosquitos.

Coronaviruses, probably of poultry origin, have been found in association with outbreaks of enteritis in ostrich chicks (Frank and Carpenter, 1992; Allwright, 1996). However, their role in these outbreaks has not yet been elucidated. Reoviruses have been isolated from ostrich chicks with enteritis as well as from 6-month-old feedlot ostriches (Jensen *et al.*, 1992; Allwright, 1996).

Some adenoviruses isolated from ostrich chicks in the USA were found to cause clinical signs of 'chick fading syndrome' in experimentally infected ostrich chicks (Raines *et al.*, 1996). By contrast, other work on larger numbers of ostriches has shown that at least two isolates are not pathogenic to immature ostriches, and it was concluded that the presence of an adenovirus in dead or sick birds did not necessarily implicate pathogenicity (El-Attrache *et al.*, 1997). An adenovirus isolated from an ostrich chick with pancreatitis in Italy was found to have characteristics similar to virus isolates from cases of guinea fowl pancreatitis (Capua *et al.*, 1996).

Wesselsbron disease is an acute flavivirus infection of sheep, cattle and goats in Africa and is transmitted by mosquitos (Swanepoel and Coetzer, 1994). The virus was isolated from an outbreak of high mortality in a flock of 4-month-old ostriches with splenomegaly. Ostriches on other farms in the area were found to be seropositive (Allwright *et al.*, 1995).

Other viruses have been and are being isolated from ostrich chicks associated with outbreaks of disease and mortality. The role of the viruses in these disease outbreaks is uncertain. In some of the cases it may well be that the viruses find an opportunity to multiply in tissues which already are diseased. However, the likelihood that more of the pathogenic poultry viruses will find their way into ostriches is very real. The strict separation of ostriches from poultry is therefore of great importance.

Spongiform encephalopathy

Bovine spongiform encephalopathy causes central nervous symptoms and is diagnosed by typical histopathological lesions in the brain and by electron microscopical demonstration of scrapie-associated fibrils. Similar histopathological lesions were reported from three adult ostriches from two zoos in Germany in 1986, 1988 and 1989, which had suffered from protected nervous disease with ataxia, balance disorders and uncoordinated feeding. However, the material was never examined electron microscopically. The diet of these birds had included poultry feed containing carcass meal. Allegedly they had also been fed meat from emergency slaughtered cattle (Schoon *et al.*, 1991).

The first of these cases occurred when Germany was officially free of the disease. It is also doubtful that the birds should have eaten the meat. In view of their

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long life span ostriches could well be susceptible to this infection, and due precautions with regard to the feeding of carcass meal should be taken in countries where this disease occurs.

PARASITES

Worms

The wireworm *Libyostrongylus douglassii* lives in the openings of the deep proventricular glands and under the koilin layer of proventriculus and gizzard. In heavy infestations it causes a severe gastritis with subsequent gastric stasis. The eggs are excreted with the faeces of the host, and under optimal conditions the infective larva develops within 60 h. However, eggs containing these infective larvae can resist desiccation for up to 3 years. After such a larva has been ingested by a new host it takes 33 days to reach maturity (Soulsby, 1984). Infestation with wireworm is confirmed by faecal examination and faecal egg count. During *post-mortem* examination, the koilin layer has to be peeled off and the mucosa underneath scrutinized closely for the very small parasites. Levamisole, fenbendazole and ivermectin are used to treat infestations in ostriches (Huchzermeyer, 1994). Dosages depend on the concentration of the active substance in the product, and manufacturer's instructions should be followed.

Codiostomum struthionis is a slightly larger roundworm that inhabits the upper rectum, but is relatively harmless (Huchzermeyer, 1994). Its eggs closely resemble those of the wireworm, and this parasite is suppressed by the anthelminthic treatment for wireworm.

Several species of filariae, very long and thin roundworms, have been found in ostriches in the lungs and air sacs, in the peritoneal cavity and under the peritoneum in the lumbar region. They do not appear to cause any damage (Huchzermeyer, 1994, 1998).

Houttuynia struthionis is a large tapeworm which inhabits the small intestine of ostriches, causing ill-thrift in young birds. Infestation is diagnosed from the presence of mature segments in the faeces which look like white grains of rice and are easily spotted on the ground. The intermediate host of this parasite is unknown. Treatment is with resorantel (130 mg kg^{-1}), niclosamide (100 mg kg^{-1}) or praziquantel (7.5 mg kg^{-1}) (Gruss *et al.*, 1988; Huchzermeyer, 1994).

Protozoa

An as-yet-unidentified *Cryptosporidium* species has been shown to infect the bursa, the rectum and the pancreas of ostrich chicks, and in South Africa caused outbreaks of cloacal prolapse particularly in male ostrich chicks, sometimes with severe losses (Allwright and Wessels, 1993; Bezuidenhout *et al.*, 1993; Penrith *et al.*, 1994; Jardine and Verwoerd, 1997). Cryptosporidia have also been found in the faeces of imported ostriches in Canada (Gajadhar, 1993).

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The infection is diagnosed histopathologically on sections of the affected organs or by the identification of the oocysts in faecal samples. There is no treatment for cryptosporidiosis although the cloacal prolapse can be cleaned, repositioned and held in place by a tobacco pouch suture. A functional intestinal flora appears to be the most important defence mechanism against cryptosporidial infections (Harp *et al.*, 1992; De Simone *et al.*, 1995).

Although an *Isospora struthionis* with spherical oocysts has been described from an ostrich in a Russian zoo (Yakimoff, 1940), no outbreaks of coccidiosis in farmed ostriches have been documented. Outbreaks of haemorrhagic enteritis caused by *Clostridium perfringens* sometimes are mistaken for coccidiosis. The use of coccidiostats in ostrich rations is wasteful and possibly also dangerous as some of the ionophore coccidiostats are toxic for ostriches (Gregory *et al.*, 1992; Jensen *et al.*, 1992).

The flagellate *Histomonas meleagridis* is a parasite of turkeys and other gallinaceous birds and causes inflammation of caeca and liver (typhlohepatitis). It can infect ostriches in close contact with such birds and cause a similar disease (Borst and Lambers, 1985). A *Trichomonas* infection can be acquired by ostriches via contact with pigeons and doves. It causes pseudomembraneous lesions in the upper digestive tract (Massi *et al.*, 1995). Other trichomonads and other types of flagellates are found from time to time in fresh intestinal smears, but these are probably entirely harmless. Flagellate infections are treated by individual dosing with dimetridazole, 50 mg kg^{-1} live mass. Continuous feeding of dimetridazole in ostrich rations is inadvisable as it deleteriously affects the intestinal flora. Flagellate infections are prevented by strict separation of ostriches from poultry, pigeons and wild birds.

Balantidium struthionis (Hegner, 1934) is a ciliate and a normal inhabitant of ostrich intestines, probably capable of becoming somewhat pathogenic under favourable conditions. Its cysts could also be mistaken for coccidial oocysts. Amoebae and *Blastocystis* spp. are harmless inhabitants of normal ostrich intestines. On faecal smears their cysts could be mistaken for coccidial oocysts.

Under favourable circumstances, ostriches are susceptible to infection with avian species of *Plasmodium* transmitted by mosquitos (Fantham and Porter, 1943). *Leucocytozoon struthionis*, transmitted by blackflies, commonly infects ostrich chicks in South Africa, normally without causing clinical disease (Bennett *et al.*, 1992; Huchzermeyer, 1994).

Arthropod ectoparasites

Feather lice (*Struthiolipeurus struthionis*) do not suck blood but feed on the feathers, sometimes causing considerable damage and irritation. They are difficult to spot as they can easily vanish under the feathers. Their eggs are deposited on the feather barbs on both sides along the shaft (van Heerden *et al.*, 1983; Huchzermeyer, 1998).

The hippoboscid fly *Struthiobosca struthionis* spends most of its time on the

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host, only flying directly across to another ostrich. It sucks blood and can cause considerable irritation (Ormerod, 1900; Mertins and Schlater, 1991; Huchzermeyer, 1998). Mosquitos and blackflies (*Simulium* spp.) regularly feed on ostriches, and in addition to causing irritation and stress they can also transmit a number of infectious diseases (Beavers, 1990; Huchzermeyer, 1994, 1998).

Ostrich quill mites (*Gabucinia* spp.) live in the ventral groove of feather shafts where they feed on the gelatinous contents of the shaft of the growing feather (Huchzermeyer, 1998). As ostriches moult continuously there always are immature feathers for them to feed on. However, when their population grows out of control they also attack the skin causing mange-like damage. Neither mites nor lice cause feather loss; bare patches on the backs of ostriches are due to feather pecking caused by behavioural stress (Sambraus, 1995; Huchzermeyer, 1997b).

Many species of hard and soft ticks are found on ostriches on pasture (Mertins and Schlater, 1991; Huchzermeyer, 1994, 1998). A preferred site of attachment is under the chin. Some ticks attaching to the body can cause scars which later may lead to the downgrading of affected skins. Ticks are also capable of transmitting several infectious diseases (Huchzermeyer, 1994).

Infestations by lice, flies, mites and ticks are treated by regular and thorough spraying with synthetic pyrethroids or by dosing or injecting with ivermectin (Huchzermeyer, 1998). Preparations containing lindane should not be used as this is highly toxic to ostriches (Jensen *et al.*, 1992).

NUTRITIONAL PROBLEMS

Overfeeding causes the deposition of excessive amounts of fat under the skin and in the abdomen. Overfed breeding birds are poor producers, and overfed birds suffering from lack of exercise may also be prone to sudden death caused by the rupture of the aorta (Mitchinson and Keymer, 1997). Excessive fat deposits in slaughter birds indicate wasteful feeding regimens.

The lack of calcium or phosphorus in the ration can lead to the development of soft bones leading to frequent and multiple fractures (Cooper and Gimbi, 1994). This happens with ostrich chicks reared on broiler rations, or with chicks on a normal ration but suffering from enteritis which interferes with the absorption of phosphorus. Clinically such birds can be recognized by the deformability of the beak (rubber beak). Rickets is a form of soft bone disease caused by the lack of vitamin D_3. Often this causes a deformation of the rib cage (Huchzermeyer, 1998). Ostriches kept indoors for part of the year may be prone to develop this disease.

A deficiency of vitamin E and/or selenium causes the degeneration of the muscles, also referred to as 'white muscle disease', with resulting inability to stand up and to walk (van Heerden *et al.*, 1983). Affected birds remain alert and hungry. Clinically, other causes of recumbency have to be eliminated, such as gastric

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stasis, impaction, injuries, exertion myopathy and botulism. Prolonged recumbency can also lead to degeneration of the leg muscles. For the histopathological diagnosis it is therefore important to examine the heart muscle as well. The treatment consists of vitamin E and selenium supplementation and non-weight-bearing exercise in a sling or in water, e.g. in a swimming pool (Huchzermeyer, 1998).

Ostriches fed on grain rations without vitamin supplements can develop vitamin B deficiencies, mainly affecting the skin of the head. The signs are retarded growth, and crust formation on the eyelids, the skin of the head and the corners of the beak (Perelman, 1991; Foggin, 1992).

POISONING

Common remedies

All orally dosed antibacterials can destroy the intestinal bacterial flora and thereby predispose the treated ostrich to enteritis and related diseases. Overdosing with furazolidone can cause nervous symptoms (Foggin, 1992). Other antibacterial agents with toxic effects are lincomycin, dynamulin, streptomycin and colistin (Huchzermeyer, 1994, 1998). Ionophore coccidiostats can cause ataxia, paralysis and death, and their use in ostrich rations should be avoided, particularly as there have been no reports of confirmed cases of coccidiosis in farmed ostriches (Gregory *et al.*, 1992; Jensen *et al.*, 1992). Morantel is an anthelminthic used in sheep and cattle, but its use in ostriches can cause severe mortality (Huchzermeyer, 1994, 1998). Benzene hexachloride (lindane) is extremely toxic for ostriches, even at dilutions recommended for spraying other livestock species (Jensen *et al.*, 1992). Overdoses of selenium intended for the prevention of nutritional muscular dystrophy can cause high mortality in ostrich chicks (Shivaprasad, 1993). Rat poisons containing the anticoagulant warfarin may be ingested accidentally by ostriches, which then become somnolent and pale with subcutaneous haemorrhages. The antidote is vitamin K (Huchzermeyer, 1994, 1998).

Dietary problems

Clostridium botulinum is commonly found in the bodies of dead animals. If ostriches swallow bones to satisfy their mineral needs, or consume a dead mouse in hay, they can be exposed to toxin produced by *C. botulinum* and this may cause paralysis and death. Usually such birds are completely paralysed, unable to move the head and neck. The toxin can be identified in the serum, and depending on the toxin the affected birds can be treated with the specific antitoxin (Allwright *et al.*, 1994b).

Ostriches are very resistant to high levels of salt (NaCl) except when their

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water intake is restricted. Affected birds become somnolent and may die with nephrosis and visceral gout (Huchzermeyer, 1998).

Fungal toxins such as sporodesmin and aflatoxin can be present in mouldy feeds. Ingestion can lead to liver damage, and affected birds produce green urine (Foggin, 1992; Scheideler and Kunz, 1997). Mycotoxins can also suppress the immune system, increasing the birds' susceptibility to infections, and can cause photosensitivity (Huchzermeyer, 1998).

Normally ostriches avoid poisonous plants, but under behavioural stress, particularly when disoriented, the resulting disturbed feeding pattern can include the eating of otherwise avoided plants. The ingestion of parsley caused photosensitivity (Perelman and Kuttin, 1988). The ingestion of avocado leaves caused mortality with epicardial oedema and degeneration and necrosis of the myocardium (Burger *et al.*, 1993). Consumption of large quantities of acorns caused severe enteritis (Robertson, 1911).

MISCELLANEOUS CONDITIONS

Ostriches chased by dogs develop exertion or capture myopathy in the leg muscles and become recumbent (van Heerden, 1977). These cases closely resemble nutritional muscular dystrophy, except that here there is a history of recent overexertion, sometimes combined with other injuries. The recumbent birds need gentle exercise in a sling, or in water, several times a day (Huchzermeyer, 1998).

Arthritis is caused either by direct injury to the joint, or by the localization of an infection after a bout of septicaemia. In both cases lameness results and the affected joint is visibly swollen. Treatment of these cases of arthritis may be difficult and even unsuccessful. As ostriches cannot stand on one leg, severely affected birds may have to be culled (Huchzermeyer, 1998).

The injection of irritant substances, such as certain antibiotics, into the muscles of the thigh can result in a severe inflammatory reaction, which later at the abattoir may cause part of the carcass to be rejected. To avoid this all intramuscular injections should be given into the muscles of the upper wing (Huchzermeyer, 1998).

Subcutaneous emphysema of the neck is caused by the rupture of the clavicular air sac which can happen when an ostrich runs into an obstacle. Stitching a cotton swab into a small incision in the skin of the neck allows the air to escape, whilst the air sac will mend itself in due course (Huchzermeyer, 1994, 1998).

Intussusception of the intestine is caused by a disturbed peristalsis which may be due to a sudden feed change or to cryptosporidial infection. Torsion of the intestines may be due to sudden feed change as well, but can also be caused by frequent stumbling and falling. In both cases the affected bird is very ill and will die within a very short time. An operation to resolve the case may be tried but usually comes too late (Huchzermeyer, 1998).

During the breeding season the phallus of the male bird sometimes remains

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everted for long periods and can become damaged and consequently stay prolapsed. Extreme weather variations, particularly cold conditions, can cause the phallus to prolapse (Hicks, 1992). A breeding bird with prolapse should be separated from the hens, and the injuries should be cleaned and treated. In other cases the affected bird should be kept at an even, warm temperature; and usually this will suffice for the prolapse to resolve itself. If not, the oedematous tissue is shrunk by the application of dimethyl sulphoxide or terramycin powder, and the phallus manually reduced. The cloaca then is secured by a purse-string suture (Aarons, 1995).

Injuries occur due to rough handling (broken neck, broken wings); running in panic into obstacles (skin lacerations, broken ribs); getting caught in a fence (skin lacerations, broken legs); fighting; and slipping on ice (fracture of sternum or of pubic symphysis). While skin lesions tend to heal easily, leg bone fractures usually lead to the destruction of the bird (Huchzermeyer, 1998).

IN CONCLUSION

In a commercial situation the treatment of individual birds tends not to be affordable. The greatest emphasis must be placed on disease prevention. The most effective way to reduce the cost of production is to increase rearing efficiency. To this end, existing knowledge should be applied and more funds should be made available for research in this field, particularly at times when the industry finds itself under economic pressure. Research is an investment in the future of the industry. An industry shying away from funding research appears to be burying its head in the sand.

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Health Management and Veterinary Procedures

13

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Since the worldwide expansion of the ostrich industry over the past 10 years, emphasis has been put on the description of diagnosis and treatment of individual ostriches. The exaggerated prices paid for breeding birds in the late 1980s forced veterinarians and farmers to try to treat and 'save' every sick ostrich. Surgical techniques were developed in order to try to correct twisted legs, stomach impactions and infected yolk sacs, instead of trying to investigate with a more serious effort the aetiology of these disorders, in order to develop and apply preventive measures which would be much more cost effective.

The way in which the ostrich industry has developed during recent years has increased the exposure of this bird to a variety of management and environmental conditions, as well as to many different infectious agents capable of causing serious and sometimes devastating diseases. From an epidemiological point of view, ostriches are somewhat different from other birds: they are susceptible not only to diseases of poultry, but also to a wide range of pathogens affecting domestic livestock (Huchzermeyer, 1994). They can also be carriers of zoonotic diseases usually related to mammals, such as Borna virus (Weisman *et al.*, 1993), Wesselsbron disease (Huchzermeyer, 1994; Allwright, 1996), and Crimean–Congo haemorrhagic fever (Shepherd *et al.*, 1987; Swanepoel *et al.*, 1998). Furthermore, the extensive movement of ostriches from one country to another has exposed these birds to many new infectious agents, some of them pathogenic, but others innocuous to ostriches but potentially pathogenic to other species including humans (Shepherd *et al.*, 1987; Cadman *et al.*, 1994; Kelly *et al.*, 1996).

The only way to maintain a healthy and profitable ostrich industry in the long term is by the implementation of comprehensive, practical and effective methods of health management and preventive medicine. Biosecurity and

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preventive medicine are probably two of the most important issues in the future development of the ostrich industry. Unfortunately, they have been only briefly discussed in the literature, and only partially applied during the development of ostrich farming (Shane and Minter, 1996).

CLINICAL APPROACH

Today, ostriches are raised in large numbers as farm animals in order to be slaughtered for their meat and skin, and the veterinary approach should be based on flock medicine. Diagnostic work in ostrich farming should be based on a good clinical history and clinical examination, a good *post-mortem* examination, and the use of pathological and laboratory work, which are indispensable for a rapid and accurate diagnosis to minimize economic damage. The main purpose of this chapter is to provide the veterinarian or the farmer dealing with ostriches with a basic and practical medical approach to veterinary procedures applied in ostriches raised as farm animals.

Probably the most important starting point whilst dealing with a medical problem in ostriches is to obtain the most accurate and extensive clinical history (anamnesis) of the flock, and the individual, before starting with the clinical inspection of the sick birds. The most common medical problems observed in ostriches are in some way management- or nutrition-related, which makes it imperative for the veterinary practitioner to have good basic knowledge on every aspect related to ostrich nutrition, management and handling. Factors such as incubation and hatching conditions, as well as over-crowding, environmental temperature, handling and stress, position of drinkers and feeders, kind of litter, exercise space, changes in diet, and many other factors (Verwoerd *et al.*, Chapter 8) may be related to medical problems within the flock. All possible factors should always be checked while investigating a clinical case in ostriches.

BIOSECURITY IN OSTRICH FARMING

Biosecurity encompasses many apparently simple but very important issues that should always be taken into consideration while planning an ostrich enterprise. Here some of the most important points in biosecurity are considered.

The location and design of an ostrich farm, particularly the proximity to poultry, other ostrich farms, or processing plants, are amongst the most important points in biosecurity. The presence of serious infectious diseases in nearby premises not only increases the risk of infection, but could also have a severe and devastating impact on the marketing of live birds, fertile eggs and ostrich products, due to quarantine regulations.

Farms should not be located adjacent to public roads where there is

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significant traffic of poultry or poultry house litter. Small particles of contaminated material can be carried by the wind into farms and introduce infectious agents. Many of the important infectious diseases can be transmitted in airborne particles, and the possibility of infection increases in direct correlation with the density of livestock in the surrounding area.

Ostrich farms should be fenced so as to prevent undesired visitors from entering the farm. Access should be limited to company personnel and authorized visitors. All staff and visitors should be provided with coveralls and boots, as many potential pathogens may remain viable for long periods of time in soil and faeces which may have adhered to footwear and clothing. Access of cars and trucks near or on to the premises should also be restricted.

Separate facilities should be established for breeding, incubation facilities, rearing, feedlots and processing facilities. Although these activities may be conducted on the same farm, the maximum possible distance is recommended for the separation of different classes of stock.

Ostriches should be the only livestock raised in ostrich farms. Multi-species farming will increase the risk of infection from disease-causing agents. Salmonellosis has been reported to be transmitted to ratites from pigs, goats, alligators and poultry (Vanhooser and Welsh, 1995; Welsh *et al.* 1997a). Ostriches are susceptible to diseases such as pox (Perelman *et al.*, 1988), Newcastle disease (Samberg *et al.*, 1989), campylobacteriasis (Perelman *et al.*, 1992), and many other serious diseases common to poultry (Huchzermeyer, Chapter 12, this volume).

The introduction of new birds to the farm always increases the risk of introducing infectious diseases. Birds and eggs for incubation should be purchased from farms free from medical problems. The breeding flock of origin and the purchased birds should be checked and tested as free of infectious agents before being introduced to the existing flock. Whenever possible, newly purchased birds should be quarantined for at least 4 weeks, and during this period regular examinations, as well as laboratory tests and prophylactic treatments against external and internal parasites, should be performed. Ostriches should be transported only in adequate and disinfected vehicles.

Bulk feed tanks should be located as far as possible from the bird premises to eliminate the need for feed vehicles to enter the area where ostriches are kept. Any kind of equipment used in other farms, such as portable holding chutes or vaccination equipment, should be thoroughly disinfected before being introduced into the farm and ostrich enclosures.

The water supply should fulfil the requirements for drinking quality. Chlorination of water at 2 p.p.m. is recommended. Water used for irrigation of lucerne (*Medicago sativa*, alfalfa) fields should be of drinking quality. The use of sewage water for irrigation may cause severe infectious diseases because enteropathogenic agents, e.g. *Campylobacter*, could be transmitted in this way (Perelman *et al.*, 1992). Lucerne sprouts grown hydroponically have been reported to be related to *Klebsiella* pneumonia infections in ostrich chicks (Welsh *et al.*, 1997b).

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Flocks should be kept under veterinary surveillance. Sick or dead birds should be subjected to clinical or *post-mortem* examination, as well as any relevant laboratory test in order to make accurate and prompt diagnoses. Appropriate and approved methods and sites should be used for the disposal of dead birds. Veterinarians and farmers should always take into account the potential threat of infectious diseases and try to prevent them.

These basic biosecurity measures, and greater control over the trading and movement of birds, are necessary to prevent infection and dissemination of diseases in ostriches and to help prevent any severe negative economic impact on the industry.

PREVENTIVE VETERINARY MEDICINE

Prevention of non-infectious medical problems

Preventive medicine includes all those measures applied in order to prevent or minimize potential damage caused by medical problems. Such measures apply not only to the prevention of infectious diseases, but also to non-infectious problems; that is, to any problem causing mortality, reduction of production (fertile eggs, fertility, hatchability, viability of the progeny), or affecting the quality of the final products. Non-infectious medical problems may have a genetic origin (Perelman *et al.*, 1995), or be related to management, nutrition, or toxic agents (Perelman *et al.*, 1988; Gregory *et al.*, 1992; Huchzermeyer, 1994).

Prevention is a much more profitable approach than trying to solve problems that have already appeared in the individual bird or the flock. Such an approach is based on good management and procedures and will include: handling; adequate fences and gates; size of and density in the enclosures; selection of breeders for production and elimination of genetic or hereditary problems; good nutrition based on quality and quantity according to age of bird; egg handling; and incubation conditions. Only trained and qualified people should carry out handling of young and adult birds. Stress, physical damage and mortality can be caused when ostriches are not handled properly.

Fences and gates should not only keep ostriches inside the enclosures, but also prevent predators from gaining entrance and causing damage to chicks and breeders. For example, attacks by feral dogs can cause extensive direct damage to ostriches and can also have a dramatic impact on production, since breeders may completely stop egg production during the season after such an episode. Loose or inadequate fences or gates can also cause heavy damage by themselves, since ostriches may entangle themselves in the fencing wires sustaining severe injury to the legs and neck, or may even kill themselves. Moreover, sharp wires or other protrusions in the fences may cause wounds and scars in the skin, which reduces the quality of any leather subsequently produced.

Nutrition is probably one of the most important aspects in the prevention of

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medical problems in both breeding flocks and progeny. High-quality, well-balanced diets should be provided according to the age and stage of production. Deficiencies or imbalance of calcium, phosphorus or vitamins may increase predisposition to rickets or other leg problems. Drastic changes in the diet, or the use of high levels of low-quality fibre such as straw or beet leaves, may cause intestinal problems such as impaction or torsion of the intestine, and mortality rates as high as 30% (Perelman, personal observation, 1984). The addition of pebbles or stones according to the age and size of the birds will help prevent impaction of the stomach in those farms where birds have access to vegetation. It is important to note that any change in the diet of ostriches should be made gradually.

Toxicological problems can be a serious threat to the ostrich flock (Huchzermeyer, Chapter 12). Overdose of any medication, or the introduction of potentially toxic compounds, can poison ostriches. Some of the compounds commonly used in animal farming, such as urea, rodenticides, lindane, thiabendazole or ionophore antibiotics, may lead to severe damage causing mortality or a drastic reduction in the performance of the flock (Gregory *et al.*, 1992; Huchzermeyer, 1994). Potentially toxic plants, including avocado (Burger *et al.*, 1993), common fern, parsley (Perelman and Kuttin, 1988) and milkweed, should be considered in planning the location of an ostrich farm, or when adding new ingredients to the diet of ostriches.

Control and prevention of infectious diseases

Egg handling and disinfection are key factors in the prevention of bacterial and fungal diseases in young ostriches. Eggs are laid at the bird's body temperature, but a drop of temperature of the egg causes a reduction in the volume of the egg contents, causing a negative pressure and vacuum. If the surface of the egg is wet and contaminated with fungi or bacteria, these potential pathogens can be 'sucked' into the egg through the pores in the eggshell.

The same mechanism of contamination can occur when eggs are washed or dipped in an antiseptic solution, if the temperature of the solution used is lower than the temperature of the egg. Dipping eggs, even in antiseptic solutions, will in most cases increase movement of bacteria through the shell pores, increasing contamination of the internal contents of the egg and subsequent infection of the embryo (Deeming, 1997).

Cleaning and disinfection of incubators and hatchers are of primary importance in the prevention of bacterial and fungal infections in the young ostriches, as the conditions maintained in the hatchers are optimal for the growth of potential pathogens. Pathogenic bacteria and fungi may infect the newborn chick via the respiratory or digestive tract, as well as through the open navel, causing severe infections and mortality of young ostrich chicks (Perelman and Kuttin, 1992a; Welsh *et al.*, 1997b; Verwoerd *et al.*, Chapter 8; Huchzermeyer, Chapter 12).

There are several techniques in egg handling and disinfection which will

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help to minimize infection of eggs and chicks (Deeming, 1997). Keep the nest as clean and dry as possible. This can be facilitated by the use of sand or gravel as a substrate, which helps with drainage of the nest. Eggs should be collected as soon as possible after laying, and cleaned as soon as possible with a dry, clean cloth or a soft abrasive. Very dirty eggs should be discarded. If possible, do not wash or dip eggs as these procedures may enhance contamination. In case washing of eggs cannot be avoided, use only warm tap water or pre-warmed (40–41°C) disinfectant solutions. Pre-warmed disinfectant solutions can be sprayed on the surface of the eggs and the shell can be wiped dry with a clean paper towel for each egg. Use only approved egg disinfectants according to the recommendations of the manufacturer.

Fumigation with formaldehyde can be very effective as a surface and shell disinfectant, but the compound is highly irritant and potentially carcinogenic, and should be used only according to the regulations of the Occupational Safety and Health Administration of each country. Eggs should be stored for as short a time as possible in a clean room at 18°C and 65–70% relative humidity (Deeming and Ar, Chapter 7). Incubators and hatchers should be cleaned and disinfected after each hatch using effective antibacterial and antifungal agents.

All attempts to prevent bacterial and fungal diseases of young ostriches should be made, since treatment of problems is usually not cost-effective. A common mistake of farmers and veterinarians is to use antibiotics for the prevention of bacterial infections in young birds. The long-term use of antibiotics should be avoided because they will predispose birds to fungal infections of the mouth and the digestive tract (Perelman and Kuttin, 1996).

Vaccinations used in ostriches

In countries or areas where infectious diseases are endemic, vaccination with adequate vaccines can help to prevent the development of disease, and contribute to the reduction of its spread and subsequent economic damage. Vaccination should be carried out according to the regulations and recommendations of the local veterinary services of each country.

Vaccination against Newcastle disease is recommended where this disease is endemic, since it may cause extensive damage and mortality in ostriches (Samberg *et al.*, 1989). Vaccination schedules against Newcastle disease include the use of live (La Sota-like) vaccines applied by eye drop or spray into the eye between 6 and 8 weeks of age, followed by subcutaneous injection of an inactivated emulsified or alum-precipitated La Sota ND vaccine given at the same time or within 3 weeks of the application of the live vaccine (Blignaut *et al.* 1998). Vaccination should be repeated at 6 months of age and once a year thereafter in breeding flocks. The age of vaccination of chicks depends on the levels of antibody titres in the breeding flock and the pressure of infection in the area. In some cases, local reactions characterized by the development of large sterile abscesses occur after vaccination with emulsified inactivated vaccines.

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Serological monitoring of Newcastle disease in poultry is based mainly on the haemagglutination inhibition (HI) test (Alexander, 1997), but in ostriches the use of this test may sometimes be confusing, especially when titres are low (after vaccination) and false negatives are common (Allwright, 1996). Williams *et al.* (1997) found that the ELISA (enzyme-linked immunoassay) test was ten times more sensitive than HI tests conducted on the same samples.

Severe outbreaks of avian influenza occurred in ostriches in South Africa during the 1970s and 1980s, and more recently outbreaks due to the H7N1, H5N9, H5N2 and H9N2 strains of avian influenza have been reported in South Africa (Allwright, 1996; Manvell *et al.*, 1996) and Denmark (Jørgensen *et al.*, 1998). While ostriches of all ages have proved to be susceptible to infection, mortality is age-related and is much higher among young birds of less than 4 months of age. However, the relationship between the virus and host can be complex: Manvell *et al.* (1998) showed that an H5 strain of avian influenza was highly pathogenic to domestic fowl, but ostrich chicks at 2 weeks of age failed to show any clinical signs despite seroconversion and re-isolation of the virus. Vaccination with autogenous inactivated oil-based vaccine has controlled disease and mortality in South African outbreaks, but has failed to prevent shedding of the virus (Allwright, 1996).

Avian pox, a common disease observed in ostrich chicks in areas where the disease is endemic, can cause mortality as high as 30% because of blindness caused by infection of the eyelid. The disease can be prevented and controlled almost completely by vaccination at 2 weeks of age with commercial fowl pox vaccines by wing-web puncture administration (Perelman *et al.*, 1988).

Ostriches are susceptible to a wide range of bacterial diseases, some of which are common in poultry (Huchzermeyer, Chapter 12). As with other infectious diseases, the best method for prevention of disease is by the application of biosecurity measures, but in areas where anthrax or clostridiasis is common vaccination is recommended. On farms where anthrax has occurred, a single dose of cattle anthrax vaccine has proved to be effective in preventing the disease in ostriches (Theiler, 1912).

Clostridium perfringens types A and D can be fairly common in ostriches, causing necrotic and haemorrhagic enteritis and enterotoxemia. Snyman *et al.* (1992) reported a reduction of losses in ostriches after vaccination with enterotoxemia vaccine. The present recommendation in areas where this problem is prevalent is to use *C. perfringens* type B and D vaccines at 1 week of age, with repetition at 30 days of age (Huchzermeyer, 1994). The use of *C. septicum* type D bacterine has caused anaphylactic shock and death in ostriches (Huchzermeyer, 1994).

Prophylactic treatments

Preventive medication in feed or water is quite common against certain poultry diseases, but with ostriches this procedure is less accepted. It is necessary to

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establish a medication protocol based on risk of exposure to an agent and the resulting costs following infection. Preventive medication in ostriches can be applied against bacterial, fungal, protozoal and parasitic diseases.

A common practice in ostrich hatcheries is to keep hatchlings in the hatchers for 24–48 h after hatching, in order to accelerate the absorption of the excess oedema which is a common characteristic of many ostrich chicks. Any kind of contamination of the hatchers may cause infection of the birds during this period. Fungal infection of the birds at hatch is a serious threat and can cause heavy damage in ostrich chicks (Perelman and Kuttin, 1992a, 1996). In those hatcheries where airborne fungal infections occur despite disinfection of the hatchers, the use of smoke candles of enilconazol (Clinafarm, Janssen) can help in the reduction of lung aspergillosis (Braem, 1985; Perelman and Kuttin, 1996). Disinfection of the open navel of chicks with any commercial iodine solution or an antiseptic spray containing gentian violet can help in the reduction of navel infections.

Gastro-intestinal microflora populations are formed almost immediately after a bird hatches and act as an important barrier against colonization by potentially pathogenic microorganisms. In poultry, the use of commercial products which contain mixtures of live microorganisms is becoming a common practice. In ostriches, this goal is achieved on some farms by the administration of fresh faeces from 'apparently healthy' adult birds. This empirical method may have some advantages, but it has many serious disadvantages, as there is no way to demonstrate that by the use of fresh faeces the small chicks will receive the right amounts of beneficial bacteria and fungi required to protect the intestinal tract. This practice may also increase the transmission to the young birds of intestinal parasites or pathogenic bacteria such as *Salmonella* (Welsh *et al.*, 1997b) and *Campylobacter* (Deeming *et al.*, 1996), and should be discarded in commercial-scale ostrich farming.

Commercial products used in poultry have been tried on some ostrich farms to treat newborn ostrich chicks, but to date there has not been enough scientific information on this issue reported for ostriches. Commercial bacterial mixtures act as competitors to pathogenic bacteria in the intestine, or lower the pH levels in the intestines through the production of lactate and volatile fatty acids, which may have a positive effect on the development of a normal flora in newborn ostrich chicks, and in the prevention of intestinal infections with pathogenic bacteria. Further research is necessary before these prophylactic methods are applied as common practice in ostrich farming

Specific bacterial diseases such as clostridial enteritis can be successfully prevented by the addition in the food of zinc bacitracin at 300 p.p.m. Clostridial enteritis is more common in young birds and so this additive is provided from day 1 to 6 months of age, depending on the incidence of the disease. The long-term use of antibiotics is not recommended as their use may induce the development of serious fungal diseases in the mouth and digestive tract of ostriches (Perelman and Kuttin, 1992b, 1996). The excessive use of antibiotics may enhance the development of bacterial resistance to many different antibiotics. Resistance to

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antibiotics may have a direct effect on their possible use in ostriches during severe bacterial infections, and constitutes a serious threat to public health (Olivier and Henton, 1998).

Various protozoal parasites have been reported in ostrich chicks, in some cases causing severe intestinal disorders and high mortality (Huchzermeyer, Chapter 12). In farms where intestinal disorders are caused by these protozoal parasites, prophylactic treatment can be attempted by the use of dimetridazol (Emtryl, Salsbury) or metronidazol (Flagyl, Searle) in the drinking water or feed. An unexplained increase in mortality has been observed after the introduction of dimetridazol in the feed at 300 p.p.m. (Perelman, personal observation, 1995). The use of any drug as a prophylactic treatment should be carried out according to the recommendations of a veterinary specialist.

HANDLING, RESTRAINT AND PHYSICAL EXAMINATION

Physical examination of ostriches should start with watching the birds in their enclosure, because this can provide the veterinarian with some useful information. Sick or stressed birds usually stay apart from the rest of the flock, walking slowly and spending most of the day near the fences and away from other birds. Sick and weak ostrich chicks tend to walk slowly with an S-shaped neck and low head. Reluctance to move may indicate locomotive and neurological problems, and could be indicative of nutritional, toxicological or infectious disorders.

The physical examination of ostriches should be as complete as possible, and should include visual and manual examination from the head to the tail. A proper physical examination in ostriches requires good physical restraint of the bird. Ostriches have only recently been domesticated and their response to handling and restraint can be unexpected and dangerous to both birds and handlers.

Handling and restraint

On many occasions, a simple action such as moving birds from one enclosure to another, or attempts to separate one or more birds from the flock, may end with injured or dead birds. Ostriches tend to panic if frightened and run as a group against the fences and corners of the enclosure, or try to climb the fences and gates, causing severe damage to themselves or others. While entering an enclosure, do it in a slow and methodical way and try always to work with experienced attendants.

Small chicks are easy to catch and handle, as they tend to sit when threatened. Very young birds can be grabbed gently by the base of the neck and then held by placing one hand under the chest bone and the other below the pelvic bone; ostrich chicks held in this way tend to paddle with the legs using strong movements. While holding ostrich chicks in order to perform any medical

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procedure, it is necessary to hold both legs of the bird tightly (Deeming *et al.*, 1996).

Never enter an enclosure containing subadult or adult birds alone: ostriches may attack without any warning. The best way to enter an enclosure is with a long, smooth shepherd's hook so that you can gently reject aggressive birds, or can use the hook to grab the birds.

Catching a bird with a hook should be done in the gentlest possible way. Position the hook in the upper third of the neck, let the bird pull backwards, and follow the bird's movement. Never pull the hook with sharp or strong movements as this may cause neck dislocation and death of the bird. After the ostrich is caught, pull gently to reach the head in order to hood the bird. Ostriches grabbed by the head or the neck tend to jump and kick forward – holding the base of the tail, and pulling it back at the same time as the head of the ostrich is pulled to hood the bird, will reduce the tendency of the bird to jump. The handler should keep himself and the ostrich's head as far away as possible from the bird's legs, holding the bird's head below the level of its chest until the hood is in position (Wade, 1996).

Most ostriches may become quieter and easier to handle when hooded. It is important that the hood is made of dark or black cloth, and the open end should fit down the neck so that the hood does not fall from the head as the bird tries to get rid of it. After the hood is in place, one of the handlers should hold the ostrich by the chest while standing on one side of the bird, and a second handler keeps the bird from moving backwards by upward and forward pressure to the pelvis.

To move a hooded ostrich, hug the bird around the chest and back, and make it walk backwards, always standing at the side of the bird and never at the front or back, as some birds may try to jump and kick forward or fall back. Do not grab a hooded ostrich by the neck, as it may cause distress and panic. Do not try to move big birds by pulling forward by the wings, as this procedure may cause dislocation or fracture of wing bones. Bring the bird to a safe place where it can be examined or treated. Healthy ostriches tend to attack hooded birds and could harm not only other birds, but also the handlers.

Physical examination

Physical examination of the bird should be performed in a safe enclosure where the bird will not harm itself. The enclosure should have plain, solid walls without any sharp edges, corners or pipes where the bird could introduce its legs or head whilst the examination is performed. An ostrich stanchion may help in some cases to keep the bird in place while performing the physical examination, but the use of such a device is necessary only while working with very difficult birds. If the bird is handled properly, a hood over the head and manual restraint may be enough to perform a physical examination or take samples of blood, joint or abscess fluid, or even perform minor surgical procedures like small biopsy sampling or stitch closure of skin lacerations.

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Physical examination is based mainly on visual and manual examination of the bird in order to evaluate its physical condition and aid in the diagnosis of many medical problems. The examination should be as complete as possible. Examinations of the eyes, nostrils, mouth and throat are of great importance in the diagnosis of nutritional deficiencies, as well as for infectious diseases such as pox or fungal diseases like candidiasis, especially in young ostriches. Watching the colour and texture of the faeces or the colour of the urine may be indicative of dehydration (Skadhauge and Dawson, Chapter 3), intestinal disorders or liver damage, as in the cases of campylobacteriasis or influenza which may cause a green coloration of the urine.

In young ostriches, auscultation and palpation of the abdominal cavity may help in the evaluation of some mechanical disorders such as stomach impaction or the presence of foreign bodies in the stomach. In big birds, palpation of internal organs is very difficult and quite ineffective; the big mass of intestines in the abdominal cavity and the location of the liver and other internal organs make any attempt to detect internal disorders by physical examination almost impossible.

Blood sampling

Taking blood samples for haematological, biochemical or serological testing is an easy procedure in ostriches. In very young ostriches, the large right external jugular vein of the neck or the medial metatarsal vein (Bezuidenhout, Chapter 2) can be used to take blood samples. Small ostrich chicks have a tendency to hiccup whilst being held, making the task of blood sampling somewhat difficult. In bigger ostriches the ulnar vein of the wings or the jugular veins in the neck are easy to detect for sampling.

The use of butterfly needles simplifies blood sampling and reduces the risk of tearing the vessels. To take blood samples from young birds, 20–22 G needles can be used, while 19–20 G needles are recommended in ostriches above 30 kg, as the blood can be collected faster without causing haemolysis. Vacuum tubes or syringes are suitable for taking blood samples (Fudge, 1996). Before the samples are taken it is important to determine what kind of tests are required in order to prepare any necessary equipment and save time and stress to the birds. Blood can be collected in tubes with or without anticoagulants depending on the tests to be carried out. To obtain serum for clinical serology or biochemistry, the containers must be new or completely clean without residues of detergent or organic matter. Blood should be taken slowly in order to prevent cell disruption and haemolysis.

To obtain the maximum amount of serum from a blood sample, it is necessary to tilt the tube to a 45° position to increase the contact surface of the blood and the container, let the blood coagulate at room temperature, and then keep the samples at low temperature to maintain the quality of the serum. Ostrich serum tends to coagulate if samples are not handled properly or if the blood has not coagulated completely before one tries to separate the serum.

In order to perform haematological studies or when biochemistry is required,

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blood must be collected in containers with an adequate anticoagulant. The same anticoagulants used in mammalian haematology can be used in ostriches, although the use of certain anticoagulants depends on the tests to be performed. EDTA (1.5 mg ml^{-1}) is the anticoagulant of choice for haematology in mammals, but ostrich blood may be adversely affected by EDTA, thus making sodium citrate a better choice (Fudge, 1996). Heparin (25 IU ml^{-1}) is the most accepted anticoagulant for biochemistry tests, but it is important to remember that EDTA and sodium heparin may change the levels of calcium and sodium in the serum, thus leaving lithium heparin as the anticoagulant of choice whenever mineral or electrolyte values are required.

Blood samples should be processed as soon as possible: haematological and chemical changes may occur quite rapidly at room temperature or if samples are not collected and maintained in optimum conditions. Plasma or serum should be refrigerated (4°C) if analysis is to be performed within 4 h, or frozen (–20°C) if the samples are kept for longer periods.

It is better to prepare blood smears for microscopic examination directly from fresh blood. There are two common methods used to prepare a blood smear from avian blood (Dein, 1986): the two-slide push smears technique, and the slide-and-coverslip method. The two-slide push method may cause margination of the granulocytes in some cases, while the slide-and-coverslip or coverslip-to-coverslip methods usually produce a more uniform distribution of the cells (Dein, 1986; Fudge, 1996).

Staining of the blood cells is a critical point in the preparation of blood smears for microscopic examination. Stains used in avian haematology (Lane, 1991), such as Wright or Wright/Giemsa stains, can be used in ostriches (Levy *et al.,* 1989a; Dein, 1986). The most crucial aspects of staining methods are consistent staining results and the preservation of all the cells present. Quick stains may cause damage to certain groups of cells thus affecting the differential counts (Dein, 1986). Whilst using Giemsa stains, it is important to use buffered solution because buffer/water pH may affect the colour of the cell components, enhancing red colours if the pH is too acid or blue colours if the pH is too alkaline (Dein, 1986; Lane, 1991). According to Lane (1991), the best staining results are obtained with a buffer pH between 7.0 and 7.5.

CLINICAL HAEMATOLOGY AND SEROLOGY

Clinical pathology has been used for some time as a medical aid in veterinary medicine (Coles, 1986). In ostriches, as in other avian species raised as farm birds in large flocks, haematology and serum or plasma chemistry have seldom been used in the evaluation of the flock's health or a pathological situation, because results will rarely provide an aetiological diagnosis. The evaluation and interpretation of the results obtained are possibly the most complicated task in ostrich clinical pathology. There is a lack of information on the correlation between

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clinicopathological values and specific pathological entities. There are also numerous variables, such as age, sex, physiological condition, handling, stress, nutrition, and the way the samples were collected or harvested, which may affect the results obtained (Stoskopf *et al.*, 1983a,b; Dein, 1986; Fudge, 1996; Hochleithner, 1994).

Haematology

Haematology has been used for many years in veterinary medicine as a useful tool in the evaluation of the health status of sick birds (Coles, 1986). The fact that physiological or pathological inducing factors may cause qualitative as well as quantitative changes in haematological values makes such studies an important aspect of the diagnostic panel.

In ostriches, haematological studies have been reported as reference values (Gray *et al.*, 1988; Levy *et al.*, 1989a; Fudge, 1996; Robertson and Maxwell, 1996), but there is still a lack of basic information with regard to the relation

Table 13.1. Haematological reference values (means only) for ostriches of both genders and for a variety of ages. Based on Levy *et al.* (1989a).

				Age in months		
Parameter	Pooled	Males	Females	1–3	5–6	12–72
Haematocrit (%)	32	30	30	30	30	40
TRBC (10^{12} l^{-1})	1.7	1.8	1.7	1.3	2.1	1.5
Hb (g l^{-1})	1.22	1.25	1.18	0.89	1.44	1.38
MCV (fl)	174	170	177	159	165	193
MCHC (g l^{-1})	3.3	3.3	3.3	3.0	3.4	3.7
TWBC (10^{9} l^{-1})	5.5	5.5	5.6	–	7.5	5.2
Lymphocytes (%)	34.1	–	–	39.8	–	27.1
Heterophils (%)	62.6	–	–	56.1	–	63.6
Monocytes (%)	2.8	–	–	3.0	–	1.9
Eosinophils %)	0.3	–	–	0.6	–	0.1
Basophils (%)	0.2	–	–	0.5	–	0.1

TRBC, total red blood cell; Hb, haemoglobin concentration; MCV, mean corpuscular volume; MCHC, mean corpuscular haemoglobin concentration; TWBC, total white blood cell count; –, not determined.

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between abnormal health entities and the haematological changes observed. A summary of the haematological reference values reported by Levy *et al.* (1989a) are presented in Table 13.1.

Microscopic examination of peripheral blood may help in the diagnosis of some infectious diseases, and should be performed whenever a protozoal blood infection is suspected (Bennett *et al.*, 1992). Differential counting and cell characteristics can be indicative of pathological situations, but lack of consistency in the preparation, staining and evaluation of samples may limit the value of the results (Fudge, 1996). The morphological characteristics of ostrich blood cells are similar to those described in any other avian species. Excellent morphological descriptions of avian blood cells have been published (Lucas and Jamroz, 1961; Campbell, 1988) and can be used as a guide for identification and differential counts in ostrich blood.

Basic characteristics of blood cells in ostriches are very similar to those observed in other avian species (Lane, 1991). Mature erythrocytes are oval with a dense purple nucleus and an orange cytoplasm. Reticulocytes are rounded, the cytoplasm is blue-tinged, and the nucleus is less dense. Thrombocytes are small cells with a rounded-to-oval shape, the cytoplasm is slightly blue, and the nucleus is not centred, is relatively large and occupies most of the cell content. Ostrich thrombocytes tend to clump together, thus making accurate counting quite difficult. Heterophils are the most common white blood cells observed in ostrich blood. They are relatively large, have a multi-lobulated nucleus and light eosinophilic granules in the cytoplasm. Eosinophils are large cells with a multi-lobulated nucleus and large eosinophilic granules in the cytoplasm. These cells may be confused with heterophils if the blood smear is not stained properly. Basophils are relatively rare in ostrich blood (Fudge, 1996; Levy *et al.*, 1989a), and usually only a few of these cells can be observed in a smear. Robertson and Maxwell (1996) reported a range of 3.9–7.3% basophils in ostrich blood. The characteristic feature of these cells is the presence of the basophilic granules in the cytoplasm. Mature monocytes are easy to distinguish from other cells in ostrich blood smears because they are relatively large and have a typical kidney-shaped nucleus. When monocytosis is observed, young monocytes may be confused with large lymphocytes.

Haematological parameters in ostriches according to age and sex are shown in Table 13.1. According to Levy *et al.* (1989a) the total number of white blood cells ranges between 5.5 and 7.5×10^3 l^{-1}, whilst Fudge (1996) reported a range of $10–24 \times 10^3$ l^{-1}. Young ostriches may have relatively higher numbers of white blood cells, but there are no differences between males and females (Levy *et al.*, 1989a). Levy *et al.* (1989a) reported lymphocytes as ranging from 39.8% in young ostriches to 27.1% in mature birds, while Fudge (1996) reported a range of 12–41%, and Robertson and Maxwell (1996) reported a range of 11.9% in young ostriches to 14% in adult birds. The heterophil count shows an increase in the percentage of these cells from 56.1% in young birds to 63.6% in adult birds (Levy *et al.*, 1989a). Fudge reported a range of 58–89% in adult birds, and Robertson and Maxwell (1996) reported a range between 79.8 % in 1-day-old ostriches to 74.5% in adults.

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Haematocrit increases from 30–35% in young ostriches to 40.2–45% in adult birds (Levy *et al.* 1989a; Brown and Jones, 1996). Total red blood cells range from $1.7–2.1 \times 10^{12}$ l^{-1} with no significant gender differences. Haemoglobin concentration is significantly lower in young ostriches (0.89 g l^{-1}) compared with adult birds (1.38 g l^{-1}; Levy *et al.* 1989a). The mean corpuscular volume in the ostrich tends to increase with the age. In young ostriches (1–3 months), the mean corpuscular volume is 159 fl compared to 193 fl in adult ostriches. This finding is interesting because, in humans and other mammals, the size of the red blood corpuscle tends to decrease with age. Mean corpuscular haemoglobin concentration in ostriches varies with age, with chicks at 1–3 months of age showing a value of about 30%, while in adult birds it is about 37%. Mean corpuscular haemoglobin in the ostrich ranges between 51 pg in chicks at 1–3 months old to 71 pg in adult birds.

Red blood cell parameters may be of importance as indicators of the functioning of the haematopoietic system. A drop in haematocrit and haemoglobin levels will indicate anaemia. Mean corpuscular volume may be indicative of haematopoietic activity; macrocytic cells are usually young cells and may indicate a regenerative response, while microcytic anaemia may be indicative of chronic processes with poor regenerative response.

Haematological parameters reported in the literature can be used as a reference for the evaluation of values observed in ostriches, but significant differences in the haematological parameters have been reported by different authors and should always be taken into consideration (Stoskopf *et al.*, 1982; Gray *et al.*, 1988; Levy *et al.*, 1989a; Palomeque *et al.,* 1991; Fudge, 1996; Robertson and Maxwell 1996; Olowookorun and Makinde, 1998). The lack of published information dealing with specific pathological entities and the haematological parameters makes the interpretation of results a complicated task in ostrich medicine.

Clinical blood chemistry

Together with a good anamnesis and physical examination, clinical pathology data is probably the most specific medical tool for the differential diagnosis of organopathies (Coles, 1986; Hochleithner, 1994). Physiological as well as pathological situations may induce changes in the chemical content of the plasma or serum. When these changes are accurately measured and comprehensively evaluated, it is possible to determine specific organopathies or homeostatic imbalances. As in the case of haematology, there are published reports of chemical values obtained in ostriches (van Heerden *et al.*, 1985; Levy *et al.*, 1989b; Okotie-Eboh *et al.*, 1992; Brown and Jones, 1996; Fudge, 1996; Olowookorun and Makinde, 1998). Blood chemical values in ostriches, according to age and gender, are shown in Table 13.2: most of the biochemical values in ostriches reported by different authors are within an acceptable range of variation. Lack of information on the correlation of specific pathological entities and the chemical parameters in the plasma makes the interpretation of the results more speculation than scientific evaluation. Factors including age, gender, season, stress, handling

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and nutrition, as well as technical mistakes, may affect some of the parameters (Lewandowsky *et al.*, 1986; Hochleithner, 1994; Fudge, 1996) and make the evaluation and interpretation of results even more complicated.

When taking blood samples for biochemistry, it is important to keep in mind that some parameters may be affected by the kind of anticoagulant used and the way the sample is handled during collection and processing (e.g. sodium heparin or EDTA). It should always be taken into consideration that 'reference' values reported in ostriches are based on very small sample populations, and extrapolation for comparison with values obtained under different conditions may cause mistakes in the evaluation of the results. The best way to obtain accurate reference values to compare with a clinical case is to take a significant number of samples from apparently healthy birds from the same group kept under the same conditions.

Diagnostic value of blood chemical parameters

Total protein (Table 13.2) is a useful indicator of the health status, with levels lower than 0.3 g l^{-1} probably suggesting hypoproteinaemia and probably hypoalbuminaemia which may occur in chronic disease, stomach impaction, malabsorption, chronic and severe parasitism or hepatic diseases (Lewandowsky *et al.*, 1986; Hochleithner, 1994; Mushi *et al.*, 1998). Changes in protein levels may occur due to dehydration (hyperproteinaemia) or during infectious diseases that cause a stimulation of the immune system due to an increase in the levels of immunoglobulins (Hochleithner, 1994).

Serum or heparinized plasma can be used for determination of glucose levels (Coles, 1986; Hochleithner, 1994). Plasma levels in ostriches range from 16.4–33.0 mg l^{-1} (Fudge, 1996) and glucose levels lower than 12.0 g l^{-1} are suggestive of hypoglycaemia, but variations also occur due to age, gender, time of day, stress, starvation or feeding time (Table 13.2).

Levels of lipids in ostriches are shown in Table 13.2. Hypercholesterolaemia may be related to high levels of fat in the diet, starvation, liver disease and hypothyroidism (Hochleithner, 1994). Reduced cholesterol levels have been reported in other species related to aflatoxicosis, endotoxaemia and low fat levels in the diet (Hochleithner, 1994).

Uric acid is the primary catabolic product of protein and purines in birds. The avian kidney excretes it mainly by tubular excretion, and therefore impaired renal function or dehydration may induce increased levels of uric acid. Levels of uric acid in ostriches are described in Table 13.2. Increased levels of uric acid may indicate renal disease and decreased tubular excretion, and these levels may increase in emaciated birds. Urea is not a useful test of renal function in ostriches. As with other birds, the value of creatinine as a diagnostic test is questionable in ostriches. During severe kidney damage, if filtration rate is decreased the levels of creatinine may increase.

Bilirubin represents only a small part of the total bile pigments in birds;

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Table 13.2. Reference values (means only) for the biochemical values in blood from ostriches from a variety of ages and both genders (based on Levy *et al.,* 1989b).

				Age in months			
Parameter	Pooled	Males	Females	1–3	4–5	6–9	12–72
Protein (g l^{-1})	0.37	0.38	0.35	0.36	0.36	0.37	0.45
Glucose (mg l^{-1})	24.8	25.1	21.3	24.3	22.7	28.1	16.3
Triglycerides (mg l^{-1})	9.0	8.8	9.2	8.8	10.2	9.9	5.6
Cholesterol (mg l^{-1})	9.7	10.1	9.2	10.0	10.2	10.6	6.7
Uric acid (µmol l^{-1})	487	476	499	561	446	360	375
Bilirubin (mol l^{-1})	5.9	5.9	5.8	7.0	5.2	4.0	6.0
Creatinine (mg l^{-1})	0.03	0.04	0.05	0.03	0.04	0.04	0.03
Alkaline phosphatase (IU l^{-1})	575	626	531	531	730	531	330
Alanine aminotransferase (IU^{-1})	2.0	2.0	2.1	1.9	2.5	1.5	1.9
Creatinine phosphokinase (IU l^{-1})	688	682	694	708	725	640	603
Lactate dehydrogenase (IU l^{-1})	1565	1575	1556	1656	1881	992	1101
Aspartate aminotransferase (IU l^{-1})	131	125	124	126	146	112	117
γ-Glutamyltranspeptidase (IU l^{-1})	1.5	1.6	1.5	2.8	1.1	1.0	1.4
Sodium (mmol l^{-1})	147	153	139	157	139	145	151
Potassium (mmol l^{-1})	3.0	3.0	3.0	2.7	3.1	3.2	2.8
Chlorine (mmol l^{-1})	100	99	105	102	97	100	106
Magnesium (mmol l^{-1})	1.1	1.1	1.1	1.2	0.9	1.0	1.4
Phosphorus (mmol l^{-1})	1.6	1.5	1.5	2.0	1.6	1.3	1.4
Calcium (mmol l^{-1})	2.3	2.4	2.1	2.2	2.4	2.0	2.5

plasma levels of bilirubin in ostriches can be found in Table 13.2. In the domestic fowl the major bile pigment is biliverdin, because these birds lack the enzyme biliverdin reductase and biliverdin is not transformed into bilirubin. The situation in ostriches is unknown, but probably the level of bilirubin may increase during severe hepatic damage.

Each organ has cells containing enzymes designed to perform particular functions. These enzymes may be specific to certain cells within an organ or may be present in different quantities in many different organs and cells. When the integrity of these cells is disrupted, the enzymes escape and their levels in the blood

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increase (Table 13.2). The concentrations of the different enzymes in the blood are usually directly correlated to the damage caused to the cells (Hochleithner, 1994).

The highest activity of aspartate aminotransferase occurs in the heart muscle, skeletal muscle, liver and kidney (Coles, 1986; Hochleithner, 1994). In birds, aspartate aminotransferase is not liver-specific, but hepatocellular or severe muscular damage may cause increased activity.

Levels of alanine aminotransferase activity differ in different tissues according to the species. This enzyme is found in birds in many different tissues, and elevated levels have poor diagnostic value in organopathies. Haemolysis may cause an increase in the levels of alanine aminotransferase because activity in erythrocytes is 1.6 times higher than in plasma (Hochleithner, 1994).

In birds, alkaline phosphatase appears to be related to intestinal and bone activity. The significance of this enzyme in ostriches has not been determined, but the variations in the levels may be related more to physiological changes than to specific organopathies.

The highest activity of lactate dehydrogenase in birds is found in the skeletal and cardiac muscle, liver, lung and red blood cells. Haemolysis may induce an artificial increase in the levels of lactate dehydrogenase in serum or plasma.

Creatinine phosphokinase is present and active in skeletal muscle, heart muscle and brain tissue (Hochleithner, 1994). Muscle cell damage, stress, intensive physical activity and liver damage may cause elevated levels of creatinine phosphokinase (Fudge, 1996). The significance of gamma glutamyltranspeptidase has not been determined in birds. In ostriches the levels found in sera are very low and probably useless as a diagnostic aid.

Sodium and potassium levels in ostriches are quite stable, and even during dehydration the levels of these electrolytes remain within normal range (Gray *et al*., 1988). Potassium levels are released from thrombocytes during the coagulation process and the levels in serum are higher than in plasma; thus haemolysis may cause abnormalities in the measurement of potassium. Hyperkalaemia may be observed after severe tissue damage, reduced excretion due to kidney damage or haemolytic anaemia. Hypokalaemia can be observed during alkalosis, chronic diarrhoea and decreased potassium intake (Hochleithner, 1994). Chloride is the major extracellular anion and, together with sodium, represents most of the osmotically active constituents of plasma. Chloride levels have low value in diagnostics as their value is quite constant (Table 13.2) and elevations are rare. Hyperchloridaemia may occur during severe dehydration (Hochleithner, 1994).

Magnesium levels (Table 13.2) may vary according to the content in the diet (Brown and Jones, 1996). The clinical value of phosphorus levels is not clear; changes in phosphorus concentrations may occur during different diseases but not on a consistent basis. Slightly higher levels have been reported in young ostriches when compared to adults (Brown and Jones, 1996). The diagnostic value of phosphorus levels in the blood is difficult to evaluate.

In most chemical determinations, the calcium measured is bound to serum protein, therefore calcium levels will rise and fall according to protein (albumin) levels, higher levels usually being observed in young ostriches (Brown and Jones,

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1996). Chang *et al.* (1988) reported low plasma calcium levels (1.55–1.80 mmol l^{-1}) in young ostriches with bow-leg syndrome.

Serology

Serology is probably one of the most important diagnostic tools in modern ostrich medicine. Serology can help the veterinarian and the farmer to monitor the response to vaccines for diseases such as Newcastle disease or avian influenza, and also provide useful information for the diagnosis of several infectious diseases (Samberg *et al.*, 1989; Allwright, 1996). As any other animal, ostriches usually respond after exposure to an infectious agent or a vaccination with an increase in the levels of specific antibodies. However, non-pathogenic agents, which are able to infect and reproduce in the ostrich without causing any apparent disease, may induce an increase in the levels of specific antibodies (Cadman *et al.,* 1994).

While using serology as a diagnostic tool, it is important to take into consideration that ostriches may have antibodies to many different infectious organisms. In order to base a diagnosis on serology, it is important to have a baseline of the antibody levels of the flock (not only from a single bird) as soon as the first clinical signs are observed. It is imperative to obtain a second sample at least 10–15 days apart in order to compare the levels of specific antibodies to the suspected disease or diseases. A sharp increase in the levels of specific antibodies may be indicative of a new infection. The fact that specific antibodies to a certain agent may be found in the sera of clinically sick birds does not mean that that agent is related to the disease.

In general, serology in ostriches is based on the same serological procedures as are used in any other species, but ostrich sera may not respond in the same way as sera from other birds. The commonest and most debatable test applied in ostriches is the HI test, used extensively in poultry in order to determine the levels of antibodies to Newcastle disease virus. In ostriches this test has been reported by some authors to be insufficiently sensitive to accurately detect low levels of antibodies (Williams *et al.*, 1997), while other authors have reported a high correlation between the HI test and the ELISA or virus neutralization test (Blignaut *et al.*, 1998; Czifra *et al.,* 1998; Koch *et al.*, 1998; Schaetz *et al.*, 1998).

When using serology as a diagnostic tool in ostriches, it is important to recognize that ostriches may have a different immunological response to vaccination or infectious agents compared to other species, and the techniques used in other animals may not be adequate to detect the specific antibodies in the ostrich sera. It should always be taken into consideration that ostrich antibodies are somewhat different from fowl or turkey antibodies (Cadman *et al.*, 1994), and ELISA tests should be performed using specific anti-ostrich conjugates. The use of commercial kits used in poultry for the detection and measurement of antibody titres of specific diseases may be not adequate to test ostrich sera, and should be adapted, tested and standardized in ostriches before they are used for diagnostic or monitoring purposes in this species.

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CHEMICAL RESTRAINT AND ANAESTHESIA

The principle of veterinary treatment of ostriches as whole flocks suggests that surgery is largely unnecessary. Nevertheless, surgery has been carried out for a variety of conditions, including yolk sac removal, wound management, relief of impaction and egg binding. Jensen *et al.* (1992) and Crabill and Honnas (1996) review the surgical techniques carried out on ostriches.

Having worked with ostriches for almost 20 years, I have found that these birds are relatively resistant to pain and many small surgical procedures may be performed using only an opaque hood on the head and experienced physical restraint. Ostriches can be quite unpredictable birds, however, and attempts to perform surgical procedures with only sedation may end in heavily injured birds or handlers. Whenever immobilization is required, it is recommended to perform the surgical procedure with the bird well anaesthetized. Induction and recovery of anaesthesia in ostriches should be as smooth and quick as possible in order to prevent the bird struggling and causing injury to itself or the handlers. Cornick-Seahorn (1996) provides an excellent overview of anaesthesiology in ratites.

The different injectable drugs that have been used to sedate and induce anaesthesia in ostriches include: xylazine; diazepam; tiletamine/zolazepam (Honnas *et al.,* 1991; Cornick and Jensen, 1992); carfentanil (Cornick and Jensen, 1992; Raath *et al.*, 1992); ketamine hydrochloride, either alone (De Lucas *et al.*, 1998) or in conjunction with either xylazine or diazepam (Cornick and Jensen, 1992; Stewart, 1994); alphaxalone/alphadolone (Gandini *et al.*, 1986); etorphine (Jacobson *et al.* 1986); and nembutal (Perelman, personal observations, 1998).

As a general observation, ostriches seem to be quite resistant to sedation. The use of some of these drugs in ostriches, such as ketamine alone at recommended levels, may cause only severe lack of coordination, partial ataxia and a struggling response (Robinson and Fairfield, 1974). Included here are some of the protocols reported for the induction of anaesthesia in ostriches.

Tiletamine (2–8 mg kg^{-1}) and zolazepam (4–12 mg kg^{-1}) administered intravenously, should be followed by inhalation anaesthetics such as halothane or isoflurane (both at 2–4%; Stewart, 1994). Tiletamine–zolazepam may induce anaesthesia within 15 s with a duration of approximately 30 min (Stewart, 1994). In small ostriches, induction of anaesthesia can be effected by direct inhalation of isoflurane.

Lin *et al.* (1997) reported four anaesthetic regimes: (i) induction and maintenance of anaesthesia with isoflurane; (ii) pre-anaesthetic tranquillization with xylazine and butorphanol followed by anaesthesia with isoflurane; (iii) induction with tiletamine–zolazepam and maintenance with isoflurane; and (iv) tranquillization with xylazine and butorphanol followed by induction of anaesthesia with tiletamine–zolazepam and maintenance with isoflurane. Tiletamine–zolazepam produced a smooth induction of anaesthesia in adult ostriches.

Alphaxalone/alphadolone (2.2–4.8 mg kg^{-1}) by intravenous injection has been reported to induce and maintain anaesthesia in relatively small ostriches

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(Cullen *et al.*, 1995). This steroid anaesthetic is quickly metabolized and non-cumulative, providing a short and smooth anaesthesia and recovery.

Under field conditions, when ostriches can not be transported to hospital facilities nembutal (60 mg ml^{-1}) can be used as the only anaesthetic (2.5 mg kg^{-1}; Perelman, personal observation, 1998). It is important to premedicate ostriches with atropine in order to avoid accumulation of mucus and fluids in the trachea. Administration of the nembutal must be intravenous and the injection of half the dose of the drug must be relatively fast. Induction of anaesthesia takes about 30–60 s in adult birds. It is important to continue a gradual injection of the drug until the bird is anaesthetized: the anaesthesia level is gradual, and it may take the drug 10–15 min after administration to reach the maximum effect. For this reason it is important to wait a few minutes each time before more drug is administered, as an overdose may cause apnea and even death. The main problem with this kind of anaesthesia is the long recovery time and the excitation observed during the ataxic phase of anaesthetic recovery.

Control of depth and duration of anaesthesia is better achieved with inhalation agents. Halothane (2–4%) or isoflurane (2–4%) are the most suitable gas anaesthetics in ostriches. The low blood-gas solubility and the low hepatic metabolism of isoflurane permit a rapid recovery even in birds with hepatic disorders.

Apnea, or bradycardia, observed many times in ostriches under anaesthesia, may be reversed with glycopyrrolate (0.011 mg kg^{-1}; Stewart, 1994), or atropine (Lin *et al.*, 1997). A respiratory rate of less than 30 breaths min^{-1} should be corrected with intermittent positive pressure ventilation (15–20 cm water; Stewart, 1994).

Post-anaesthesia recovery is as important as the anaesthesia itself. Ostriches may injure or kill themselves during the recovery period, particularly following injectable anaesthetics, thus making the inhalation agents the best choice. A smoother recovery after use of injectable agents can be obtained by the administration of diazepam i.v. at 0.2–0.3 mg kg^{-1} during recovery, or azapaerone i.m. at 1–2 mg kg^{-1} following induction (Stewart, 1994). The recovery room must be padded with straw or mats and the walls must be smooth and solid. It is important to keep the bird in the sternal position and to limit its movement. Cover the head with a dark hood or keep the bird in a dark and quiet environment until it is completely recovered.

CONCLUSIONS

Dramatic changes have occurred in the ostrich industry over the past 20 years. The amount of scientific information published during the past two decades is many times more than all the information published during the previous 100 years of ostrich farming. The worldwide expansion and intensification of the ostrich industry have exposed these birds to many management- and nutrition-related problems, as well as to many new infectious agents. Ostrich farming is still

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in its infancy compared to the poultry industry, and many years of research and development are needed in order to reach levels of medical and technological development similar to those found in poultry farming today.

Probably the most important point in this chapter is the introduction of a different concept in ostrich medicine. Preventive medicine, welfare of ostriches as farm animals and public health are the most important issues in the future development of the ostrich industry. Application of comprehensive measures of preventive medicine and biosecurity will reduce the risk of infection, reduce to a minimum the use of antibiotics, and improve the quality and safety of ostrich products for human consumption.

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