Physiology and Functional Anatomy

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Harvey B. Lillywhite

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

Abstract

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

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

Keywords

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

2.1 Introduction

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

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

2.2 Body Temperature, Energetics, and Ectothermy

Non-avian reptiles are characteristically regarded as ectothermic because they are highly dependent on external sources of heat to determine body temperature, in contrast to endothermic birds and mammals that regulate body temperature largely by means of internal metabolic heat production. There is ongoing debate regarding whether extinct reptiles, and especially dinosaurs, were endothermic (Dunham et al. 1989; Padian et al. 2001; Seymour 2013; Grady et al. 2014). Some of the stronger evidence for endothermy of dinosaurs comes from data for rapid growth rates of bone (Erickson et al. 2001; Padian et al. 2001; Lee and Werning 2008). However, when the effects of size and temperature are considered, the metabolic rates of dinosaurs were shown to be intermediate to those of endotherms and ectotherms, suggesting that the controversial dichotomy of endothermic versus ectothermic is overly simplistic (Grady et al. 2014). Putting the controversy aside, smaller reptiles are generally ectothermic and are not capable of sustaining a body temperature above ambient by means of endogenous heat production. However, there are a few notable exceptions, including swimming sea turtles, incubating pythons, digesting rattlesnakes, yolk metabolism of hatchling snakes, and seasonal reproductive endothermy of tegu lizards (Tu et al. 2002; Lillywhite 2014; Pough et al. 2016; Tattersall et al. 2016). These examples are of much scientific interest, and they demonstrate the capacity for limited, facultative endothermy and physiological control of muscular heat production (in several species of pythons during incubation). However, in general, the majority of captive reptiles depend on external sources of heat to determine body temperature, and transient variations of metabolic heat production (independent of external environment) are usually of little significance in captive settings.

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

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

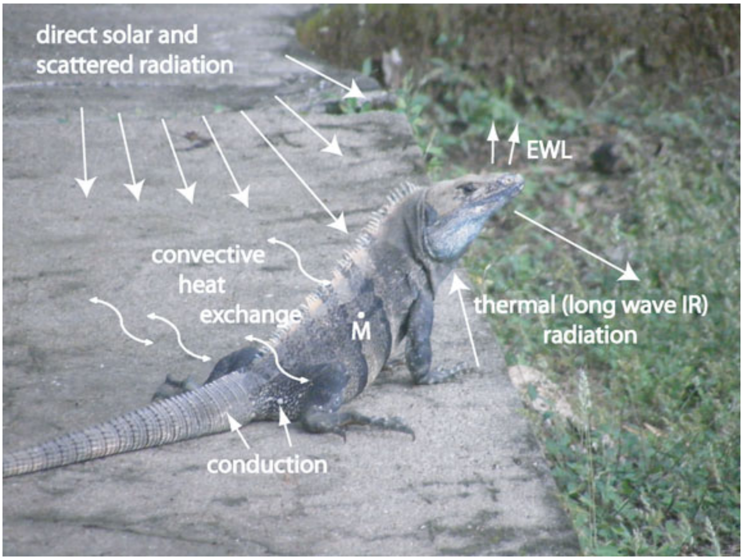

Fig. 2.1 Pathways of heat exchange featuring an iguana on a roadside in Guanacaste, Costa Rica. The hypothetical body temperature of this lizard is determined principally by direct solar radiation that is absorbed by the dorsal skin surfaces and conduction of heat from the heated surface of the road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

2.2.1 Temperature and Energy Expenditure

The significance of ectothermy in context of coupled biological advantages has been discussed by Pough (1980). Two important consequences of ectothermy are very relevant to the husbandry of reptiles. First, the rate of energy expenditure derived from food or fat stores is comparatively low because metabolic heat is not required to maintain body temperature. Therefore, to maintain a steady state with respect to energy balance, relatively few calories from food are required as input to match the low rate of energy use. The requirement for food is further lowered by behaviours that might include relatively long periods of inactivity and nocturnal seclusion. Thus, night-time cooling and long periods of inactivity contribute to a low rate of energy expenditure of many reptiles, roughly 2–5% of that of a bird or rodent of equivalent size (Nagy 1983). Energy requirements are minimal for fasting and inactive reptiles at low body temperature, and they increase to substantially higher levels in animals that are active at elevated body temperature. As an example, a red-eared turtle (*Trachemys scripta*) has a rate of aerobic metabolism during vigorous movement at 40 °C that is 270 times as great as during rest at 10 °C (Gatten 1974). The coupling of food requirements to both temperature and activity varies with species and the circumstances of captivity. One should be vigilant of animals that might experience weight loss due to excessive energy expenditure related to ‘escape’ or exploratory activity whilst in new or inadequate enclosures, conspecific aggression or related stress, and disease or parasitism (see Warwick 2023). The reproductive status of females should also be taken into account and monitored carefully.

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

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

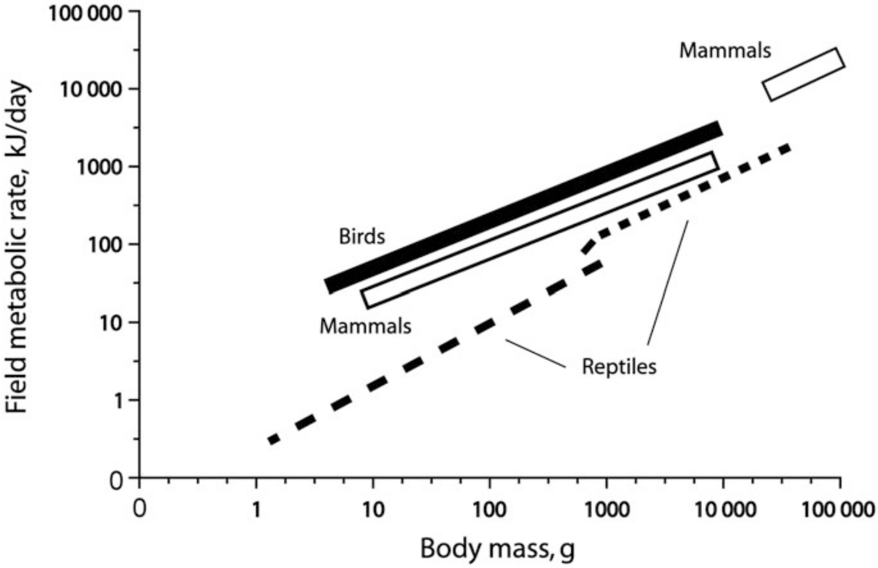

Fig. 2.2 Field metabolic rates shown as a function of body mass in 229 species of non-avian reptiles, birds, and mammals. The bars represent the central densities of collective data points for the various taxa, estimated by eye. The relationships are adopted from data in Nagy (2005)

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

With respect to husbandry, persons unfamiliar with reptiles may not fully appreciate the comparatively low rates of feeding (either frequency or quantity) required to sustain individuals in a healthy state. Daily or frequent feeding is often not necessary, and voluntary periods of fasting are not harmful, especially for intermittent feeders such as snakes. In fact, many reptiles such as snakes and crocodylians that are kept for public display are abnormally obese compared with conspecific individuals that are living in nature. Our current understanding of the health risks of obesity in reptiles is minimal, but optimal care most likely involves balancing energy availability and energy expenditure. Allowing animals to fatten excessively represents poor husbandry. The low requirement of energy by reptiles is often misunderstood or not appreciated. The amount of food that is fed or offered to captive reptiles should be based on direct observations of the condition of animals and at least a basic understanding of seasonal behaviour and dietary requirement of each species rather than a uniform protocol that is intended for application to all species. For further review of the energetics and feeding of ectotherms, see McNab (2002), McCue (2012), and Andrade et al. (2016). There is also veterinary literature on topics potentially related to obesity; examples include hepatic lipidosis (Divers and Cooper 2000; Gumpenberg et al. 2011), cardiovascular disease (Schmidt and Reavill 2010; Stephens and Rosenwax 2018), and intestinal obstruction (Corbit et al. 2014).

2.2.2 Regulation of Body Temperature

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

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

Thermoregulatory behaviours commonly employed by reptiles include shuttling movements between a heat source (such as sunlight or warm substrate) and a heat sink (such as shade, water, or burrow), as well as precise adjustments of body volume, shape, orientation, and posture. Postural adjustments can be subtle and are capable of providing remarkably precise control over body temperature (DeWitt 1967). All thermoregulatory behaviours require some heterogeneity of environment in terms of the physical factors affecting heat exchange (Tracy 1982). Indeed, both mean environmental temperatures and spatial heterogeneity potentially influence thermoregulation, movement, and energetics of reptiles (Sears and Angilletta 2015).

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

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

2.2.3 Variation of Body Temperature

Many reptiles experience variation of body temperature during a season and even during a single day. Tropical or aquatic species may experience comparatively little temperature variation and can be sensitive to temperature changes readily tolerated by temperate, terrestrial, and amphibious species (Inger 1959; Ruibal 1961; Hertz 1992). Indeed, non-basking species constitute a major component of the diversity of lizards in the neotropics (Huey et al. 2009). The marine file snake (*Acrochordus granulatus*), for example, thrives at water temperatures near 30 °C, but does not tolerate prolonged exposure to temperatures below about 25 °C (Lillywhite 1996). Tuataras (*Sphenodon punctatus*) are active at body temperatures well below those of most other reptiles and have a temperature for peak aerobic activity much lower than that of turtles, lizards, and snakes (see Avery 1982, for review). On the other hand, some terrestrial species inhabiting the tropics actually experience and may require greater microclimatic variation of temperature than might be presumed solely from macrogeographic considerations (Hertz 1992).

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

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

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

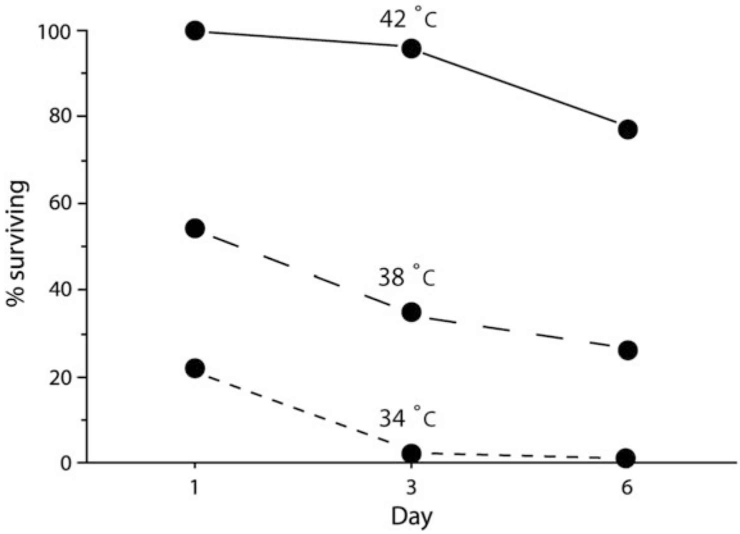

Fig. 2.3 Percentage survival of desert iguanas, *Dipsosaurus dorsalis*, injected with bacteria, *Aeromonas hydrophila*, and maintained at temperatures of 34 to 42 °C. The number of lizards in each group is 12 at 34 °C, 36 at 38 °C, and 24 at 42 °C. Adopted from data published in Kluger et al. (1975)

2.2.4 Functional Significance of Body Temperature Variation

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

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

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

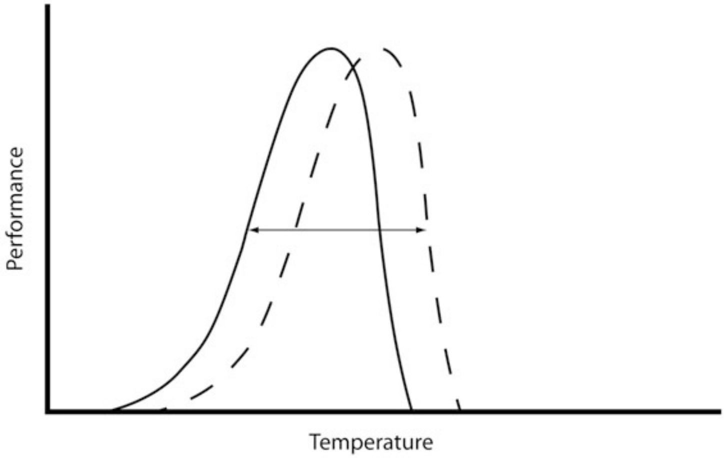

Fig. 2.4 Hypothetical 'performance curve' depicting how a rate variable (such as running speed, digestion) changes with temperature. The shift in the curve illustrates hypothetical changes that might be attributable to acclimation. The shift in performance could occur in either direction depending on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

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

2.3 Light and Photoreception

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

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

The effects of variation in the intensity or spectral composition of light are poorly understood. Some reptiles require ultraviolet light for mineral metabolism and normal behaviour (Moehn 1974; Regal 1980; Townsend and Cole 1985; Adkins et al. 2003). Like birds and mammals, some species of reptile require UV light for cutaneous synthesis of previtamin D_3 and the maintenance of levels of the active vitamin in the blood (Pough 1991; Holick et al. 1995). Indeed, there is evidence that some lizards might adjust basking and UV exposure in relation to requirements for vitamin D_3 (Ferguson et al. 2003). On the other hand, some reptiles have been raised or maintained successfully, sometimes for multiple generations, without UV light, but with dietary supplementation of vitamin D_3 (Gehrmann et al. 1991; Pough 1991). Some reptiles may have multiple types of previtamin D_3 in their skin (Holick 1989). Neither the biochemistry of vitamin D synthesis nor the spectral qualities of UV light involved in the process are well studied in reptiles.

There is relatively little information concerning the range of irradiance that is appropriate for a given species of reptile. Ferguson et al. (2010) quantified the UV exposure of 15 species of reptiles in the field and suggested that knowledge of basking behaviour and daytime exposure to light can provide a reasonable estimate of likely UV exposure experienced or required for a species. Based on this information, species can be grouped into four zones (termed 'Ferguson zones') according to thermoregulatory behaviour and preferences for microhabitats, and each such zone can be used potentially for guidelines for UVB based on the quantitative measurements reported from the field work. The Ferguson zones extend from crepuscular or shade-dwelling to basking in the midday sun. Further discussion of such irradiance criteria can be found in Ferguson et al. (2010, 2014), Carmel and Johnson (2014), and Baines et al. (2016).

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

2.4 Water Exchange and Humidity

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

2.4.1 Water Exchange

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

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

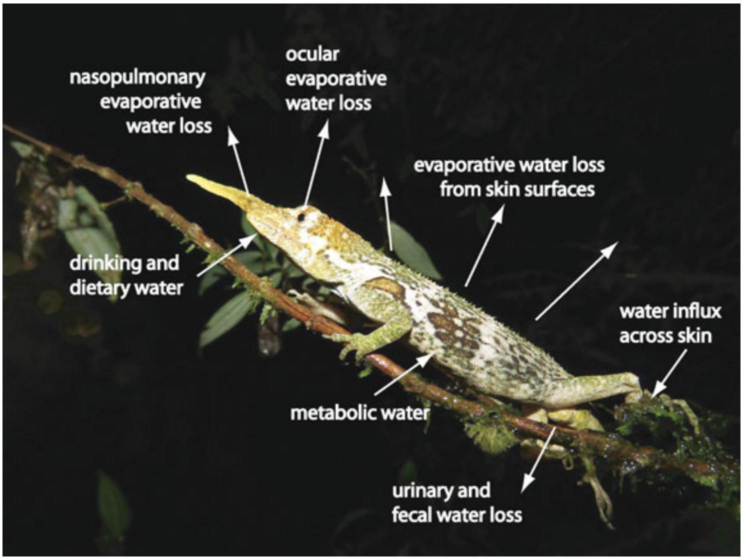

Fig. 2.5 Pathways of water exchange featuring a Pinocchio lizard, *Anolis proboscis*, climbing on a tree branch in the lower montane Andes of western Ecuador. Photograph by Michael Miyamoto

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

2.4.2 Water Loss and Integument

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

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

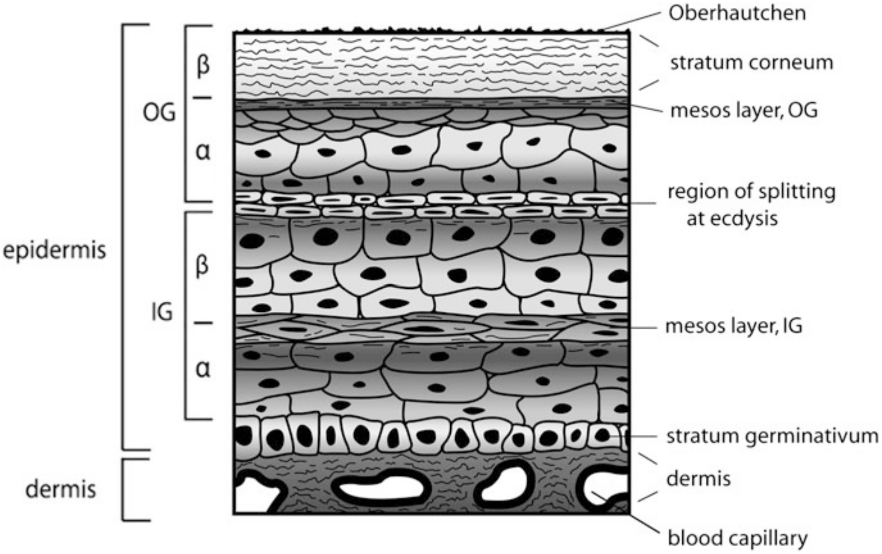

Fig. 2.6 Schematic illustration of a cross section through skin of a generalised squamate reptile, with emphasis on details of the epidermis. Two generations of epidermis are illustrated. The outer generation (OG) represents 'skin' (*stratum corneum*) that will be shed from the body during ecdysis, whilst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

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

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

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

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

[a] Values represent the reciprocal of water vapor conductance and express the difference of water vapor density between saturated skin and external environment per unit of evaporative flux

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

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

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

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

2.5 Ecdysis

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

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

2.6 Osmoregulation and Nitrogen Metabolism

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

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

Excretion of nitrogenous wastes that result from metabolism of protein comprises an important component of the overall water budget of animals. Terrestrial reptiles excrete nitrogenous wastes largely in the form of urates or uric acid, which readily precipitates from solution and can be excreted with comparatively small losses of accompanying water. The white to yellowish semi-solid material characteristic of reptilian excreta consists largely of urates together with co-precipitated salts. On the other hand, nitrogenous wastes of aquatic or amphibious reptiles are excreted largely in the form of ammonium ions (with lesser amounts of urea), which are very soluble in water and require substantial water efflux for elimination. High concentrations of ammonium ions are cytotoxic, and the ion cannot be concentrated by the kidney. Urea is more soluble in water than ammonia and is less toxic.

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

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

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

2.7 Digestive Physiology and Nutrition

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

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

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

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

The digestibility and assimilation of energy and nutrients from food vary with the nature and size of food particles and are generally higher for carnivorous than herbivorous diets (Johnson and Lillywhite 1979; Bjorndal 1989, 1991; Bjorndal and Bolten 1990). Passage rates of food through the gut vary greatly. Some snakes and lizards will produce faeces within hours or days of feeding, whereas some viperid snakes may retain digestive excreta for months. Passage of material is greatly assisted by warm temperatures (generally >25–35 °C) and activity, especially climbing or swimming. Retention of digested material in the lower gut for minimal periods may be a requirement for the efficient absorption of water from faeces across the lower intestine or cloaca, especially in xeric-adapted species. Stout, heavy-bodied terrestrial snakes such as vipers and pythons tend to accumulate and store faeces in the hindgut for long periods, sometimes exceeding a year (Lillywhite et al. 2002). Such conditions can cause intestinal obstruction, even in wild snakes and sometimes associated with drought or brumation (Corbit et al. 2014). Thus, once again, provision of adequate water for captive reptiles is important.

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

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

2.8 Respiration and Circulation

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

Generally, routine activities of reptiles are supported by aerobic metabolism involving generation of ATP energy by oxidative reactions requiring oxygen. However, very intense activities (e.g. sprint running, digging) may require ATP energy at rates that exceed delivery via oxidative mechanisms, and in these cases, ATP is generated very rapidly by anaerobic metabolism involving glycolytic pathways without the requirement for oxygen. This energy is additive with that from aerobic sources, but usually comprises a significantly larger proportion of the total energy used (e.g. up to about ¾ in some lizards; see discussion in Pough et al. 2016). However, intense activities enabled by anaerobic energy production are limited in duration by accumulation of lactic acid and depletion of glycogen stores in muscle. Animals become exhausted and must eventually rest whilst lactic acid buildup is dissipated and metabolised by means of aerobic processes that also replenish the stores of ATP. Keepers of reptiles should be aware of this aspect of physiology related to energetics and behaviour, although few issues are expected to arise directly related to anaerobic metabolism. Activity of reptiles tends to be intermittent, and they seldom engage in behaviours that require sustained high levels of synthesis of ATP.

2.8.1 Lung Structure and Function

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

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

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

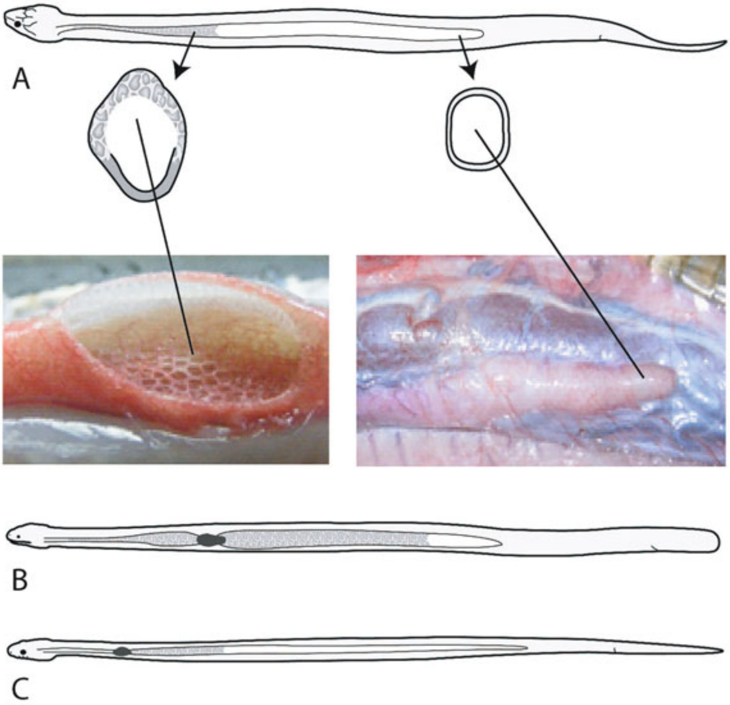

Fig. 2.7 Lung structure and heart position in snakes. (**a**) A schematic snake modeled after a Florida cottonmouth (*Agkistrodon conanti*) illustrating the extent of lung, consisting of a 'tracheal' vascularised segment (gray fill) and posterior 'saccular' lung (no fill). Cross sections below each lung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

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

Lung ventilation is powered by muscular expansion and contraction of the thoraco-abdominal space; and, in some species of turtles and squamates, pulmonary smooth muscle may contribute to air movements within the lung spaces. Both the depth and frequency of lung ventilations vary greatly, even within a species or in individual animals. Therefore, changes in ventilatory behaviour (aside from extreme alterations such as panting) are not usually reliable indicators of serious changes in health. Numerous factors such as changes of temperature, excitement, activity, diving, and skin shedding can produce marked changes in lung ventilation.

The skin, pharyngeal lining, and cloacal bursae of aquatic snakes and turtles may serve as accessory respiratory surfaces (Graham 1974; Feder and Burggren 1985; Gordos et al. 2006). However, the majority of species exchange virtually all O_2 and most CO_2 across the lung. Except for hibernating turtles, most aquatic reptiles depend on lung breathing and require periodic access to air. For reptiles that are kept in underground burrow systems, precaution should be taken to provide adequate ventilation that prevents accumulation of high levels of CO_2 (Ultsch and Anderson 1986). Reptiles that burrow in sand, soils, or leaf litter behaviourally achieve adequate O_2 uptake and CO_2 release (Pough 1969a, b). If reptiles become hypoxic, they tend to seek lower temperatures when choices are available (Hicks and Wood 1985; Wood 1991).

2.8.2 Blood Circulation

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

As in most vertebrates (and all ‘higher’ taxa), fluid, respiratory gases and other metabolically important molecules are exchanged between blood and tissues at the level of fine capillary networks. The capillary interface with interstitial fluids appears to be comparatively ‘leaky’ and fluids shift readily between the vascular and extravascular compartments, subject to physiological controls. Partly because of these attributes, reptiles can regulate blood (plasma) volume quite well (Lillywhite and Smith 1981; Smits and Kozubowski 1985). On the other hand, animals may be subject to oedema owing to excess capillary filtration when capillary pressures are high because of arterial hypertension or gravity stress. Large snakes should not be held in vertical positions for long periods (>2–3 min) because gravitational pooling of blood and oedema in dependent tissues compromise adequate blood circulation (Lillywhite 1988; Lillywhite and Smits 1992).

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

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

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

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

2.9 Pain and Stress

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

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

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

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

2.10 Animal Welfare Considerations

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

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

This chapter has provided a general overview of reptilian physiology and discuss those aspects of structure and function that are most relevant to the care and well-being of captive reptiles. The subject matter is broad and interrelated with many aspects of behaviour, life history, and veterinary care. In cases where the limitations of space curtail adequate discussion of topics, the reader has been provided with relevant references to literature wherein further information can be found. This information will hopefully provide both a perspective and roadmap that are useful to future research, synthesis, and understanding of the requirements of reptiles that are necessary for health and vigour whilst in captivity or subjected to experimental investigation.

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