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Abstract

Captive animal welfare has benefited from various new technologies and a new generation of welfare-minded and better-informed individuals adopting more welfare-oriented practices. However, for captive reptiles, there remain many aspects that are grounded in and reflect a long history of arbitrary or folklore husbandry and advice, and reptile-keeping continues to be compromised by practices that benefit the keeper rather than the animal that is kept. This second edition of *Health and Welfare of Captive Reptiles*, like the first volume, contains a diversity of primary classical subjects, each hopefully constituting an advancement in our understanding of reptilian biology and meeting the associated needs

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of these animals in captivity. Some subjects, comprise miscellaneous considerations that, directly or indirectly, will have a significant bearing on reptile health and welfare. It is these factors that form the basis of this chapter. It is hoped that, at the very least, their inclusion may create or stimulate an awareness of other potential issues that may affect the well-being of captive reptiles.

Keywords

Animal welfare · Reptile husbandry · Stress · Pain · Sensitivity · Environment · Euthanasia · Killing · Ethics

19.1 Introduction

Research into captive animal welfare has benefited from various new technologies and a new generation of welfare-minded and better-informed individuals adopting more welfare-oriented practices. However, in regards to captive reptiles, there remain many aspects that are grounded in and reflect a long history of folklore husbandry and advice (see Mendyk and Warwick 2023). In addition, the welfare of captive reptiles continues to be compromised by practices that benefit the keeper rather than the animal that is kept. It is thus not unexpected that with the adoption of any new approach to housing reptiles, particularly those that contradict basic principles of reptile biology, for example, snake rack systems (see Arena and Warwick 2023), we will also continue to face new challenges in addressing their health and welfare. Furthermore, as the original version of this chapter described, there will always remain a number of miscellaneous considerations that, directly or indirectly, will have a significant bearing on reptile health and welfare. It is these factors, some of which have been addressed within the first edition of this volume (and other chapters within this current volume), that form the basis of this chapter. It is hoped that, at the very least, their inclusion may create or stimulate an awareness of other issues that may affect the well-being of captive reptiles.

19.2 Stress, Pain and Sensitivity

The very nature of conditions of captivity and the necessity to display reptiles to the public in an educational setting imposes risks of maladaptation and injury. Furthermore, the very fact of confinement creates a variable degree of stress, which often leads to behavioural alterations with serious consequences (Frye 1991a, b, 2015; Divers and Stahl 2019). For many years, reptiles have been maintained in captivity for display, research, culinary, fashion, curio and pet purposes. The consideration of these vertebrates in both nature and captivity has suffered from two basic undesirable attributes. First, until recently, they have had little intrinsic appeal to the public and researchers alike; and second, certain anatomical and physiological differences between reptiles and, for example, mammals, have inclined them to be distanced

from the more popular and well-studied endothermic vertebrates. With respect to both of these points, a factor most often misunderstood and neglected is the reptilian response to the multi-faceted stresses that are imposed by conditions of captivity. Non-scientific herpetologists and pet keepers in particular too often associate perceived 'stoicism' in reptiles as indicative of a low sensitivity/high tolerance to abnormal conditions, stress and pain. Such misconceptions have often resulted in reptiles being mismanaged, neglected and abused.

19.2.1 Stress

The stress response and associated distress can be divided into several key categories: acute, chronic, psychological (including emotional) and physiological. Inevitably there is overlap between and complex associations within these divisions. Also, although some associations may be relatively straightforward, in that a predatory threat stressor may initiate a psychological-physiological stress sequence, other less obvious considerations also arise. For example, whilst acute and chronic stress may sometimes manifest as independent phenomena, the two can occur simultaneously, such as when a chronically stressed animal is captured and handled and where acute stress episodes cumulatively flow into chronic stress situations. The assessment and proper management of stress in captive reptiles, as for other captive animals, is essential for optimal health and welfare (Martínez-Silvestre 2014). However, the entire stress issue is by no means straightforward. In this section, we will explore additional, and perhaps less tangible, concepts that may contribute significantly to the issue of stress in wild and captive reptiles.

19.2.2 Natural Versus Captivity-Related Stressors and Stress

Acute and chronic stressors that, in nature, might present essential exercise for an organism's biological attributes, include physiological response mechanisms and these are part of experiential learning for survival. In captivity, acute and chronic stressors can be negative and highly destructive. Thus, in nature, stressors and stress may constitute a normal part of an evolved holistic system, whereas in captivity, stressors and stress likely occupy dysfunctional roles. At what point potentially valuable stress becomes a totally negative experience is difficult to define. Being able to determine the level at which a noxious influence loses any natural value and becomes adverse, has obvious welfare implications. Psychological consequences of acute stress may occur for periods of some seconds to several minutes (it is also conceivable that residual effects may last for some hours or longer) and it is worth bearing in mind that even a single acute stress occurrence, whether physical (e.g. thermal), psychological (e.g. perceived threat) or physiological (e.g. adrenal response), may have long-term adverse consequences (see Gangloff and Greenberg 2023; Greenberg 2023). Furthermore, social stress (demonstrated in rodents to be the most potent stressor—Koolhass 1997) is remembered via individual recognition for

up to a week in the lizard *Anolis carolinensis*, but not for 10 days (see Forster et al. 2005; Korzan et al. 2007).

Various forms of chronic stressor exist in nature. Drought, climate extremes, hibernation, aestivation, food deprivation, and other factors certainly contribute to long-term pressures with possibly fatal consequences. However, these factors are in natural concert with the normal psychological and physiological coping mechanisms of the individual. Such stressors challenge the individual or population, but within parameters for which they have evolved.

19.2.3 Stressors and Stress in Nature and in Captivity

There is at least one fundamental difference between, in particular, chronic stress in nature and chronic stress in captivity. Nature provides various stimuli that contribute continually to an animal's awareness of its surroundings. These stimuli are not necessarily stressful in a negative manner and include essential factors such as inter- and intraspecific interaction, food and shelter searches and predator avoidance. In addition, there exists a multitude of chaotic influences that may be very subtle. It is probable that these activities and stimuli are significantly positive, even if they serve merely to occupy animals as they endeavour to survive. Thus, natural conditions offer greater holistic stimulation of a reptile's perceptive capabilities than conditions presented by artificial, relatively sparse, sealed and inactive (biologically and climatically) enclosures of captivity. Also, in nature, animals have a variety of choices to escape from stressors, whereas in captivity, these options are denied; thus, certain situations can result in quite varied responses even when the same stressor is faced in either setting (Wielebnowski 2003). For example, in the wild, male-to-male combat behaviour during breeding seasons, which is frequently described among lizards and snakes, has a valuable role in mate selection and success; and unwilling combatants and losers can easily avoid confrontation with their victors. However, in captivity, unwilling combatants cannot avoid others, and losers and victors must co-mingle, which may result in social stress.

Bearing this in mind, a reptile that has encountered a stressor in nature may be psychologically better able to contend with the situation than a stressed captive reptile that is presented with little option but to be enveloped by its stressor. Also, despite the occurrence of sometimes severe pressures (for example, drought and starvation), the natural environment possesses a degree of non-stressing normality and familiarity (such as the diverse stimuli mentioned previously) that provides an important component of security to an animal. A major stressor in nature, regardless of intensity, may be viewed as a single aberrant event in an otherwise stable scheme, which is arguably very different from a captive environment where the various inputs may be completely inadequate, incorrect and essentially intolerable. In other words, in the wild, enough of life is 'going right' to keep stressors in context and to alleviate distress. An important exception involves anthropogenic invasion of natural environments, which can impose extraneous stressors into otherwise normal

systems, including those where animals are bound by specific resources and thus cannot relocate.

19.2.4 Stress and Natural Rhythms

Reptilian life in nature, as with all animals, is strongly influenced by solar, lunar and other environmental cycles. It is conceivable that there exists particular sensitivities in the context of a circadian rhythm that are of special importance in the issue of stressors and stress in nature and in captivity. In nature, an animal may experience a number of acute stressors; for example, a predatory conflict or occasional fall during the course of its daily activity pattern (Oliveira et al. 2010). Indeed, several such events could occur in a single day. In these situations, exposure to individual stressors probably lasts only a few seconds or minutes. In predatory encounters, the victim either is killed or escapes and, in serious falls, an animal either soon dies of its injuries or may be met by scavengers. The chances are, though, that one way or another, an acute stress experience will cease within a day. Where stressors (or perhaps just certain types of stressor) and stresses persist over much longer time periods, then the factor arguably becomes an extra-routine pressure, and potentially it is biologically perceived by the organism that the challenge is more involved than a daily problem and so has inherently different demands. Some activities, such as seasonal male-to-male combat, may incorporate prolonged, repeated stressors. However, associated stress, being largely part of voluntary actions, presumably occupies a contextual position, i.e. subject to hormonal-related drives that balance favourably against pressures of combat.

No matter how stressful, the end of an animal's day is usually concluded with a period of necessary quiescence and sleep, and the individual probably moves into the next day in a more or less unstressed state. Sleep (and rest) may be a major part of such stabilisation (Warwick 2023) and to date, the relatively few studies of sleep in reptiles indicate that these animals do indeed sleep (Libourel and Herrell 2015; Shein-Idelson et al. 2016). However, in captivity, it is conceivable that disturbance of rest and sleep may compound the already compromising effects of captivity-related stressors (Mancera and Phillips 2023; Warwick 2023).

In captivity, diverse stressors are present that simply do not fit in with either acute or chronic stressor patterns occurring in nature. For example, a victim of a predatory encounter will not be held captive in highly restrictive conditions for days; whereas for transportation, storage, sometimes display, and even prior to research processing, captive reptiles are often confined in cloth bags or small containers, and the stressful episode may be drawn out beyond a daily rhythm. These sorts of stressors are very common and present a worrying problem in the captive environment. Apart from facing artificial, multi-faceted and possibly abnormally severe stressors in captivity, the cage environment usually lacks opportunities for normal interactions that, in nature, may reduce potential impacts of stressors and stress.

It could be argued that animals which, for example, sustain painful injuries from a predatory encounter but nevertheless escape may suffer negative physical or

psychological effects lasting more than a day. However, either the consequences will quickly be fatal or the victim will be able to return to normality because its environment remains viable for normal interaction. There are some situations in nature where an acute stress problem exceeds beyond the day and prevents animals from returning to their normal patterns (e.g. shelter places, feeding routines and so on). An animal that falls into a crevice or trap may face this situation. Studies of such unfortunate problems appear elusive, but from personal observations and some anecdotal accounts of captive animals, trapped reptiles often battle for extended periods of time trying to free themselves. This comparison and analogy may offer a perspective on the searching behaviour seen in caged reptiles—animals that are literally trapped and confined, behaving as they might had they fallen into a ditch except that, instead of either escaping or deteriorating and dying due to dehydration or starvation, in captivity, they are caught half-way between the two.

Consequently, it is possible that periods of stress that persist beyond one day may dramatically affect the way in which stressors are perceived by animals and impact accordingly on stress effects. Extra-circadian stress may form a marker between acute and chronic stress and pose a particularly significant threat to wild or captive reptiles. Of course, circadian rhythms in captivity are not usually compatible with those in nature. The issue has various connotations in husbandry, but in this stress context, it obviously interferes greatly with estimating the start and finish of a reptile's normal day, and so the establishment of any pattern of extra-circadian stress.

19.2.5 Stress Measurement Through Disease and Mortality Data

There are various ways of recognising and assessing stressors and stress. These may be physiological (see Gangloff and Greenberg 2023; Greenberg 2023) or behavioural (for example, Warwick 1990a; Martínez-Silvestre 2014; Mendyk and Augustine 2023; Warwick 2023). However, whilst observations and evaluations of stressors and stress are possible using these approaches, analyses of historically collated data are generally not possible because records of, for example, abnormal captivity-stress-related behaviours are not regularly gathered. More routine collations of data are maintained in veterinary documentation associated in particular with formal zoological and laboratory facilities. These data might add a useful, although not necessarily comprehensive, measurement for maladaptation and stress in animals based on the type and frequency of disease outbreaks.

Abnormally high incidence of disease, pathological conditions associated with normally innocuous sources, and non-specific degenerative manifestations may be related to captivity stresses and a compromised immune response. This would seem to be the case with crocodylians (P.C. Arena, pers. obs.). Indeed, this perspective is related to Cowan's (1980) evaluation of 1200 captive reptile mortalities. Other studies have been conducted that collate results of necropsies in captive reptiles and examine the aetiologies of mortalities. For example, Bosch and Frank (1983) analysed post-mortem data for 6591 reptiles (and 583 amphibians) and concluded

that significant pathological changes were found in the liver and intestine in reptiles other than snakes. In snakes, the intestinal tract was most frequently affected. Bacteria were important direct or indirect contributors to disease and fatalities. Parasites played a less significant role, but were present in 30–50% of cases. Although a large number of the instances of disease and death were probably attributable to particularly poor husbandry, many were implied as occurring in reputable establishments. Scheinert et al. (1992) analysed 307 reptile cases and concluded that the most common causes of mortality were pneumonia, parasites and overall poor husbandry. Interestingly an investigation of the intestinal microbiota of farmed Australian saltwater crocodiles (*Crocodylus porosus*) detected high levels of pathogenic bacteria that had no apparent impact on the host's health, although the authors concluded that this required further investigation (Willson et al. 2019). Whilst it is not possible to draw stringent conclusions from these data, which are based on diverse and often highly specific histories, findings of these studies are largely consistent with opportunistic microorganism and parasite infections, and therefore, suppressed immune competence is implicated.

19.2.6 Emotional Stress

Some methods of stress assessment offer strong indicators of a particular state—for example, measurement of the adrenal response in a physiological approach, hyperactivity in a behavioural approach, or by examining physical condition and growth. It is also worth considering that animals showing neither physiological nor behavioural indicators of stress and normal growth may still be experiencing distress (see Gangloff and Greenberg 2023; Greenberg 2023; Warwick 2023). Numerous studies have shown that the reptilian neuroendocrine system is essentially similar to mechanisms within other vertebrates (see Gangloff and Greenberg 2023; Greenberg 2023), and indeed, behavioural indicators of stress in reptiles often appear to approximate signs in mammals and birds (see Gangloff and Greenberg 2023; Greenberg 2023; Warwick 2023).

To these examples one could add a human dimension because we share familiar categories of stress response and distress. In anthropomorphic terms, most of us probably realise that humans may endure chronic stress related to poor environments and unsatisfactory lifestyles for much of their existence, and similarly so, where incarcerated in prisons. It might be appropriate to regard such states as also involving emotional stress. Despite such unfortunate states, people feed regularly, grow well, interact diversely, and often apparently normally and, where relevant, reproduce successfully, activities that are frequently perceived as signs of an absence of significant stressors, and often the mere presence of one of these signs is thought a significant indicator that all is well. However, in reality, this is routinely far from the case and it is reasonable to assume that, whilst the variable may be difficult to trace, reptiles also suffer emotional stress, an indicator of which is acutely elevated body temperature, manifested through basking behaviour (Cabanac and Gosseli, 1993;

Kreger 1993; Cabanac and Bernieri, 2000). Among current tools proposed to assess such scenarios is Benn et al.'s (2019) 'Welfare Quality® Protocol'.

19.3 Pain Perception and Assessment Sensitivity

Reptiles have the capability to detect and respond to painful stimuli and appear to possess established mechanisms by which this may be achieved (Loew 1987; Liang and Terashima 1993; Crowe-Riddell and Lillywhite 2023; Lillywhite 2023). In humans, pain assessment can be aided by verbal communication. However, because this is not possible in most animals, it is their behavioural reactions to pain that must be used (Carstens 1987). Pain-related behaviour is often easily recognised in domesticated animals, but subtle pain-related signs may become increasingly difficult to recognise and routinely evaluate as one examines non-domesticated animals related more distantly to mammals. With this in mind, it is even more crucial to practise preventive care, in particular through observational vigilance for genuinely normal behaviour and physical condition, because it may be unclear when an animal is experiencing harmful and potentially damaging conditions. Although this approach is common sense, too often it is not common practice.

19.3.1 Stress-Induced Analgesia

Stress-induced analgesia may function to reduce pain sensation and motor responses in injured animals that use behavioural strategies such as tonic immobility or death feigning (voluntary thanatosis) (Purkayastha and Das 2010; Sannolo et al. 2014; Castro-Exposito et al. 2017) to escape predators. It may also function to prevent further damage during recovery from injury (Carstens 1987). During predator/prey or aggressive conspecific interactions, stress-induced analgesia may be employed to reduce pain from injury and thus allow the animal to recover and act to continue or engage in appropriate attack, defence or escape behaviour (Butler and Finn 2009; Madin and Madin 2011; Breuning 2018; Gentsch et al. 2018; Van Waeyenberge et al. 2018; Warwick 2019a, b). This issue has been demonstrated in rats (*Rattus* spp.) and, given the similarity in neurogenic response, other vertebrates, including reptiles may have the ability to self-induce analgesia in the presence of noxious stimuli. However, the possibility of self-induced pain suppression should not be readily interpreted as a product of conscious convenience in the animal; rather, it is most likely a complex and variable holistic response. Whilst it is believed that some behaviours (e.g. maladaptive stereotypies and related forms) may occur as moderators of stress and pain (Hediger 1964; Broom 1991; Garner 2005), there are no confirmed cases of such stereotypies in reptiles (see Warwick 2023). Furthermore, manifestation of (theoretically) stress-moderating stereotypies should anyway be regarded as biologically desperate responses to human-generated environmental deficiencies that constitute a grave sign of poor husbandry.

19.4 Thermal Factors, Thermoregulation and Light

Temperature is one of the most important factors governing the biology of reptiles (Heatwole and Taylor 1987) (see also Arena and Warwick 2023; Gillingham and Clark 2023; Lillywhite 2023). Although this issue has long been recognised as crucial to the maintenance of reptiles in captivity, it is surprisingly poorly understood. Unlike the thermoregulatory opportunities afforded free-ranging animals, captive reptiles are presented with a narrow and often inadequate range of thermal parameters based very largely on human-estimated requirements. This almost certainly results in reptiles adopting considerable modifications in behavioural routines to attempt to satisfy their thermal needs. Consequently, provision of thermal environments should be appropriately compatible with those in nature to accommodate physiological and behavioural aspects. Inadequacies in artificial temperature regimes probably present significant adaptational problems and undesirable demands on an animal. Here we outline some of the key considerations.

19.4.1 Captive Reptiles and the Thermal Environment

Too often, reptile keepers have not considered the natural thermal behaviour of reptiles when designing artificial conditions and, just as importantly, the thermal properties of the natural environment itself (Avery 1991; Cabanac and Gosselin 1993). Data are needed regarding the type, thermal attributes and position of heat sources in captive situations (see also Arena and Warwick 2023). In artificial conditions, a form of ‘thermal confusion’ may arise because environments rarely provide the diversity and range of micro-climates and microhabitats required for adequate site selection and temperature exchange. Although numerous heat sources are available nowadays, these are almost certainly incompatible with the natural thermal environment and provide only elementary temperature variation. Small enclosures present particularly poor thermal ranges, and it seems reasonable that artificial environments that are incapable of allowing proper thermal gradation should not be used, even for short-term instances. Furthermore, species-specific seasonal changes in thermoregulatory requirements are rarely taken into consideration, particularly with captive individuals that are perpetually on display to satisfy exhibitory requirements. These seasonal requirements should also take into account the provision of adequate cover and substrate depth, because many heliothermic lizards (e.g. *Tiliqua* spp.) will regularly seek shelters or burrows in response to varying ambient temperatures and activity levels (Kerr et al. 2003; Kerr and Bull 2004; Mendyk and Warwick 2023).

Also, in the case of heliotherms in particular, the common thermal gradient design may have to be replaced by cages of a greater magnitude with heat sources that will allow the entire body to be bathed by heat (directly via radiation and reflection and also via conduction and convection) and additional cooler areas for shuttling between, including between land and water (Terpin et al. 1979), and between surface and shelter (exposed and unexposed) (see also Arena and Warwick 2023). Thermal

matters are complicated further because there may not be a clear distinction between the various thermal requirements of reptiles, and they may utilise a combination of methods of regulating heat depending on a variety of factors. For example, it has been shown that large reptiles depend primarily on radiant sources of heat for thermoregulation, whereas smaller species tend to rely on convective ones (Porter and Gates 1969; Terpin et al. 1979). In addition, larger individuals and species can take advantage of greater thermal inertia, which consequently can have a major impact on heating and cooling rates. The impact of body size on thermoregulatory requirements has been investigated further in some of the largest reptiles (crocodiles), where large size tends to render typical reptilian shuttling behaviour ineffective as a means of making rapid changes in body temperature (Grigg et al. 1998). Instead, certainly in *Crocodylus porosus*, daily temperature variability decreased with increasing body mass (Grigg et al. 1998; Seebacher et al. 1999).

Basking periods may be important indicators of thermal provisions; if an animal remains in a heating or cooling phase for prolonged periods, this may indicate difficulties in thermoregulation and maintaining a preferred temperature. Furthermore, thermal extremes or sudden temperature changes (even a single event) may be deleterious to health, although adverse consequences may not become apparent until perhaps days or weeks after its occurrence (Lance 1992). This thermal shock factor has very important implications for reptiles that are transported in the cargo holds of aircraft and indeed, many storage, transport and other situations where species-specific temperature requirements may not be met precisely.

In conclusion, the subtleties of natural thermal factors and thermoregulation have great implications and consequences for reptile husbandry, not only for long-term captives in zoos and elsewhere, but also for animals under short- and medium-term conditions where naturalistic ranges of temperature and corresponding behaviours are not available or permitted.

19.4.2 Thermal Burns

An example of apparent, but almost certainly misunderstood, physical insensitivity and poor thermal environments concerns thermal burns, which are common in captive reptiles (Gartrell et al. 2019), and which occur when animals come into direct contact with heat sources whilst attempting to raise their body temperature to preferred levels. The general problem may be exacerbated somewhat by ambient temperatures that are too low, and which result in animals being forced to raise their body temperature through extreme proximity to heat sources (J.B. Murphy, pers. comm.). Thermal burns may also result from inappropriate heat sources or exposure to high-intensity/inappropriate wavelengths of ultraviolet radiation (Hellebuyck et al. 2012).

Damage from thermal burns ranges from minor lesions and scarring of the skin to extensive injury such as fusion of the eyelids or burns that extend deep into the body tissues (Frye 1991a). In addition, thermal burns may result in erythema, necrosis, delayed healing, and may become secondarily infected with pathogenic bacteria or

fungi (Gardiner et al. 2009; Baines 2010; Hellebuyck et al. 2012). The first report of damage to the eyes of captive reptiles linked the appearance of lesions on the eye spectacles of gold-striped geckos (*Woodworthia chrysosiretica*) with the placement of ceramic heating bulbs (Gartrell et al. 2019). In this study, the integrity of the spectacles was damaged in terms of ulceration, perforation and mycotic dermatitis (the latter possibly due to inadequate maintenance of temperature and humidity) (Frye 1991a; Warwick et al. 2013; Gartrell et al. 2019; Hollwarth 2019).

These injuries and their resulting complications may lead to permanent defacement, disability or death. In addition, although light and heat sources are available that approximate the range of spectra present in solar radiation, the mere proximity of the source to the reptile may be damaging to ocular tissue, particularly in the case of fossorial, crepuscular and nocturnal species (which are likely to be thigmotherms—see Arena and Warwick 2023). Indeed, ultraviolet b (UV-B) lamps of inappropriate wavelengths have been associated with major eye and skin damage and even death in reptiles (Gardiner et al. 2009). These lamps are commonly employed to raise level of vitamin D3 and stimulate metabolism and reproduction in reptiles (Burger et al. 2007), yet there exists little empirical data on the natural UV exposure of reptiles and consequently, guidance on adequate provision of UV requirements in captivity are sparse (Baines et al. 2016). However, a recent study determined that UV-B lamps are hazardous for reptiles and ineffective in achieving plasma levels of vitamin D comparable to free-living bearded dragons (*Python molurus bivittatus*) (Diehl et al. 2018). On the other hand, Bos et al. (2018) used UV-B radiation to raise levels of plasma vitamin D in Burmese pythons (*Python molurus bivittatus*), but stated that further investigations are required in order to determine whether these raised levels have health benefits to these and other species of snake.

The point of particular interest here is that when it comes to thermal burns, individuals may appear to be oblivious to gross trauma during the period of damaging injury, and in fact, insensitive to pain. One current view is that these burns arise after an animal has rested against an inactive heat source, which is then activated and heats up rapidly, causing tissue and presumably local neural damage (Frye 1991a). Anecdotal accounts suggest that reptiles also settle on already active heat sources and then suffer burns. We propose that a major reason for this behaviour is threefold. First, a large reptile may not be able to attain an optimal body temperature from a small intense heat source such as a lamp. Second, thermal provisions in captivity fail to simulate adequately the thermal diversity of the natural environment. Finally, a contributory factor may be the variation in the thermal perception of different areas of the reptile body. For example, recent investigations of nociception capabilities in reptiles using thermal stimuli demonstrated that the dorsal integument was less sensitive to temperature detection than the ventral surfaces of the feet and that reptiles may vary in their responses between thermal and other noxious stimuli (Sladky et al. 2009; Couture et al. 2017).

In nature, the thermal requirements of, for example, heliotherms are satisfied by a radiant solar source, which bathes the entire animal with heat. However, the efficiency with which a body absorbs warmth depends on not only its own properties,

but also other factors, including the intensity of the heat source, the position of the body with respect to the heat source and the proximity and properties of other reflective surfaces (Geiger 1959). Thus, a thermally receptive body is subject to thermal inputs of a multidimensional and heterogeneous nature. Different regions of a reptile's body have different absorbency spectra and thus different heating rates (Heatwole and Taylor 1987). In captivity, often the only source of heat available is one or two small, and usually intense, heat lamps or floor heaters. In order to raise their body temperature, reptiles move toward a heat source and bask. Especially where large reptile species and individuals are involved, with associated slower blood circulation (Coulson and Coulson 1986), and thus heat dispersal, these animals must attempt to raise the temperature of the entire body using primarily diminutive heat sources. Thermal absorption is attempted whilst continually losing warmth from body surfaces that are not exposed to the heat source and that may, indeed, be in contact with cooler surfaces that conduct heat away from the animal (see also Arena and Warwick 2023).

Compensatory behaviour may include moving closer to the heat source, whereupon the peripheral nerve endings are damaged and desensitised. Once this occurs, the reptile moves closer still and eventually contacts the heat source in an attempt to raise its body temperature to an optimal level, a point it may never achieve. Thus, an unnatural thermal environment and related 'biological confusion' (analogous to an ecological trap, whereby the reptile's natural ability to assess the quality of its environment become compromised by novel conditions [Dwernychuk and Boag 1972]) may result in thermal burns. Clearly, more data are needed to clarify the reasons behind this aberrant behaviour, especially in consideration of body size and the associated heating requirements of reptiles. If this hypothesis were supported, heliotherms of a small body size in particular, would be less likely to suffer thermal burns because a heat lamp is, to them, a relatively expansive source that may more effectively saturate their bodies entirely. Related considerations include the fact that large lizards are more reflective of solar radiation than smaller individuals (Norris 1967), and that they heat and cool at a slower rate as a result of a low ratio of surface area to volume. Snakes, by the very nature of their morphology, may be compromised by inadequate thermal provision.

Of key interest is that thermal burns in snakes are commonly seen in immunosuppressed pythons (A. Martínez-Silvestre, pers. obs.). An interesting clue is that the ventral skin may be contaminated with the animal's own faeces, which consequentially causes infection, with or without high temperatures. Such immunosuppression can be related to poor husbandry, including high temperatures that—although insufficient to burn the skin—may leave the skin at greater exposure to infection. Thus, in these cases, although the skin may bear the appearance of a thermal burn, the sign may actually be an indicator of husbandry-associated stress.

19.4.3 Light and Photo-Invasive Environments

Because photoperiods are integral cyclic influences on the biological responses of an animal these, to an extent, control various physiological and behavioural parameters. In many captive situations, reptiles are provided with a single combined source of heat and light. These may be operated manually or automatically set to particular light and thermal periods—which may not correspond with natural conditions. Unfortunately, in the captive environment, photoperiods are often based around convenience for keepers rather than natural patterns for the reptiles.

Apart from obvious physiological and behavioural disruptions brought about by unnatural photo and thermal periods, it is also suggested that incompatible periods, and especially prolonged exposures to light, are probably a significant stressor for captive reptiles (Warwick et al. 2018a). Photo-invasive environments may also be highly disruptive on rest and sleep quality (see Arena and Warwick 2023; Mancera and Phillips 2023). Consequently, it is imperative that animals are always provided with suitable hiding places where individuals may avoid light at any time, as well as ensuring normal periods of light and dark.

19.5 Circadian Rhythms and Nocturnalism

Circadian rhythms are highly conserved biological phenomena with a circa-24-hour period. These phenomena allow organisms to adapt to the 24-hour light-dark cycle on earth and control a variety of physiological and biochemical processes in life forms as diverse as vertebrates, plants and cyanobacteria (Sun et al. 2019). There are broad similarities between the circadian clocks of vertebrate classes, and the genes regulating this process are remarkably conserved (Sun et al. 2019). Reptiles exhibit circadian rhythms of feeding, metabolism, egg hatching, sleep and thermoregulation, as well as locomotor and burrowing behaviour (Norris and Kavanau 1966; Heckrotte 1975; Blem and Killeen 1993, Lutterschmidt et al. 2002; Roe et al. 2004; Nash et al. 2015; Ping et al. 2016). The circadian clock of reptiles is contained within the retina, pineal and parietal eye and is multioscillatory in nature (Tosini et al. 2001). Unlike mammals, the pineal gland is a key part of the circadian system of reptiles (Tosini et al. 2001).

Although there has been little research on the effects of circadian disturbance in reptiles, there is a large body of evidence from a range of species showing that organisms undergoing experimental disruption of circadian rhythms show impaired biological functioning, increased levels of disease and decreased life spans (Martino et al. 2008; Evans and Davidson 2013). For example, mice housed on a 20 h light/dark cycle underwent changes to metabolic hormones leading to obesity, and a rearrangement of neural architecture leading to reduced executive function and cognitive flexibility (Karatsoreos et al. 2011). In humans and rodent models (where most research has been performed), circadian disruption has been implicated in deregulation of inflammatory responses, increased oxidative stress, immune

suppression, insulin resistance, cancer, mood disorders (including depression-like symptoms) and premature death (Martino et al. 2008; Evans and Davidson 2013).

Circadian disruption in captivity is likely to have a greater impact on nocturnal species whose rhythms are at odds with those of their diurnal human keepers. For example, many snake species are nocturnal, although others are able to exhibit some plasticity in their circadian systems (Degregorio et al. 2014). Nocturnal reptiles, in particular, are often subjected to shifts or reversals in circadian rhythms in captive environments (see also Warwick 2023; Arena and Warwick 2023). Most zoos use reverse light schedules for the exhibition of nocturnal animals, but the effects of this on the physiology, welfare and long-term health of the animals is unknown because virtually no literature exists. However, such practices are likely to be detrimental (McWilliams and Atkinson 1999). As well as a physiologically appropriate light/dark schedule, animals need a gradual shift from light to dark analogous with dawn and dusk to allow physiological processes to adapt; this is also missing even in many interior zoo enclosures (McWilliams and Atkinson 1999). In pet shops and private collections, the lighting schedule is likely to be arranged primarily for the convenience of the keepers, meaning nocturnal reptiles are probably disturbed during the daytime for cleaning and feeding purposes, as well as transfer between enclosures. Very little is known about the effects of circadian disruption and reverse light/dark cycles on reptiles, and, given the prevalence of nocturnal reptiles such as snakes kept in zoos and other collections, this is an area that warrants urgent investigation.

19.6 Growth

Growth often is regarded as a definite indicator of good physical and mental health. However, although a popular perception among many amateur and some professional herpetologists, growth as a positive health sign per se is a gross over-interpretation of condition and overlooks important biological aspects. Often, estimates of optimal growth are based on continuous, fast development. However, optimal growth rates should mean normal growth rates, compatible with conspecifics in nature that have access to appropriate sustenance in the context of evolved energetic considerations. Normal growth may, therefore, be slow and erratic and very different from patterns in captive animals (see Gangloff and Greenberg 2023; Greenberg 2023; Warwick 2023). Indeed, what many keepers view to be good growth may actually be excessive and create pathological conditions (Frye 1991a, b; Mendyk and Warwick 2023; Warwick 2023). Thus, a growing animal may be promulgating disease because of its growth rate.

Even reptiles that do appear to be exhibiting reasonably normal growth rates develop and harbour a diversity of diseases (Frye 1991a). Further, behavioural signs of psychological stress are often identified in reptiles showing apparently normal growth (Warwick 1990a, 2023), and studies involving domesticated animals have drawn similar conclusions (Fox 1984; Broom 1986, 1988; Broom and Johnson 1993). Consequently, the absence of good growth or the presence of abnormal growth may offer reasonable indication of physical and psychological problems,

but, importantly, the presence of even normal growth rates does not confirm an absence of psychological or physical distress. Growth rates, like other potential indicators of condition, should be considered in association with a variety of physical and behavioural signs and not as an independent indicator of holistic health.

19.7 Electromagnetism in the Artificial Environment

Environmental electromagnetism (EEM) is occasionally suggested as a potential interference with an organism's own electromagnetic field (EMF). Mostly, this relates to popular concerns regarding perceived human health hazards from powerful electricity sources such as overhead mains cables, but sometimes reference is also made to domestic convenience facilities. Despite the widespread nature of electromagnetism, data appear to be in short supply and inconclusive, but the issue has attracted some scientific interest and there is now growing evidence of the impact of EEM on wildlife and various ecosystems (Balmori 2009, 2010; Sun et al. 2019).

Reptiles (particularly in the case of intensive collections) are often housed in close proximity to a myriad of electrical maintenance devices, including air, substrata and aquatic radiators, heat lamps, cables, tapes, pumps, filters and other electrical and electronic equipment. Furthermore, since the first edition of this volume, there has been a dramatic increase in the adoption of mobile and wireless technologies, not only for the purposes of mobile communications, but for various forms of temperature and humidity sensors. The impact of EEM on human health still remains contested and controversial (D'Angelo et al. 2015). However, there is a growing body of evidence relating to the effects of EEM on animal tissues from nematodes (Sun et al. 2019) to rats (EL-Naggar et al. 2019). Long-term exposure to EEM has also been linked to the variation in abundance of bird populations adjacent to EEM emitting base stations (Everaert and Bauwens 2007). In addition, Nishimura et al. (2010) found that the agamid lizard *Pogona vitticeps* displayed behavioural changes in response to extremely low-frequency electromagnetic fields (ELF). Individual lizards exposed to ELF for extended periods raised their tails significantly more than individuals in a control group. Because tail-lifting in lizards has been linked to predator defence postures, and intraspecific agonistic behaviours (Cooper 2001; Sherbrooke and Middendorf 2004), the study by Nishimura et al. provided evidence that reptiles may be sensitive to electromagnetic fields.

Interestingly Everaert and Bauwen (2007) proposed that because EEM may also have an impact on invertebrate species, this, indirectly, may lead to reduced numbers in bird species that feed on insects. If this interaction was valid and there is growing evidence that various species of insects are negatively affected by EEM (Balmori 2009), then it can be extrapolated that many wireless emitting repellent devices used in homes and other facilities that house reptiles may have an impact beyond the control of invertebrate pests. Information regarding potential impact of EEM on wildlife is still in its infancy. However, given the evidence to date, and the increasing adoption of, at times, intensive housing conditions of reptiles, there is a need to

investigate the true impact of EEM on the welfare of captive reptiles (see also Mancera and Phillips 2023).

19.8 Reintroductions to Nature

Occasionally, captive reptiles are released or considered for release into nature following either short-term studies, wherein wild animals are held temporarily captive, or where a few formal zoological establishments work toward reintroducing reptiles as a measure to populate an area for perceived conservation purposes. Deliberate releases of, for example, unwanted pets also occur, as do accidental escapes from formal and private collections; a case in point is the Burmese python (*Python molurus bivittatus*), which has successfully invaded ecosystems in the southern US (Engeman et al. 2011). Because the latter of these introductions are already discouraged or guarded against, little further needs to be said here apart from reiterating the importance of minimising wherever possible the chances of such events occurring. In the former categories, and especially zoological establishment projects, species reintroductions have become increasingly popular as a prospect for formal facilities to demonstrate some practical application to conservation endeavours. Whilst protection of biodiversity is not of direct relevance to this volume, the actual and potential impact of captive animal release projects has relevance for the welfare of both of those set free and of those animals in nature with which introduced individuals may come into contact. Thus, not only is the concept of a reintroduction idea of direct significance to the welfare of animals, but also the welfare and success of those released is of direct significance to the validity and success of reintroduction ventures.

Several aspects require consideration in the reintroduction issue. These can be categorised as ontogenetic modification, the consequences of artificial selection, pathological threats and inheritance of acquired characteristics. Associations between these matters, welfare and the integrity of natural populations may be obvious in some cases, and highly obscure in others, but all are important academic, practical, scientific, and ethical considerations. Ontogenetic modification and artificial selection, and related matters of individual competence and potential impacts on nature, have received attention elsewhere in this volume (see also Chiszar et al. 1993; Burghardt and Layne-Colon 2023; Warwick 2023). Some interest is at last being directed towards wider education concerning potential variables in the evaluation of animal competence and minimising the risks of introducing potentially pathogenic microorganisms and parasites into free-living populations (Burke 1991; Dodd and Seigel 1991; Chiszar et al. 1993; Jacobson 1993, 1994; Lepeigneul et al. 2014; Ferrell 2019; Martínez-Silvestre and Franklin 2019). However, we feel that pathological threats are worth re-emphasising here and that the possibility of inheritance of acquired characteristics, whilst often controversial and seldom discussed, merits attention.

The concept of releasing reptiles maintained previously in captive conditions, may involve either ‘soft releases’—where acclimation is provided via in situ

enclosures, or ‘hard releases’ without acclimation, directly into the target habitat. Soft releases, perhaps due to low-stress conditions, have resulted in greater survival and site fidelity than hard releases. However, one study found no difference in survival between soft release and hard release in terrestrial tortoises (Radzio et al. 2019). Another release strategy, known as ‘head-starting’, is designed to accelerate growth rate, increase body size and eventually improve survival of individuals from species with an otherwise high juvenile mortality. However, in pursuing these objectives, individuals may be subjected to: *first*, chronic stress during the first months of life (e.g. unnatural diets, absence of brumation period, clinical husbandry conditions); and *second*, acute stress at the time of release (e.g. deprivation of shelter, problems locating water supplies, incorrect identification of conspecifics, the establishment of atypical hierarchies, difficulty identifying prey or predators). Therefore, techniques should be performed according to perceived pros and cons that may beneficially affect the survival of the released reptiles.

Stress under natural conditions can also have evolutionary consequences. For example, the symmetry of turtle shells can develop in ways that allow individuals to self-right more easily if turned upside-down, as has been observed in Herman’s tortoises (*Testudo hermanni*) with right-side directional asymmetry (Parés-Casanova et al. 2019). Applied consideration of such developmental factors, for example, through selective breeding for known favourable morphologies, could theoretically increase the survival chances of individuals in release programmes.

Pathological threats to wildlife from organisms carried by former captives present a prospect so serious that we find it incomprehensible that release programmes, without appropriate screening (see below), can be contemplated, let alone considered scientifically and ethically justifiable. Not only is the system through which potentially pathogenic organisms in captivity may infect natural populations well understood, but there already exist cases where captive releases are implicated in wildlife disease (Frye 1991a; Jacobson et al. 1991; Viggers et al. 1993; Cunningham 1996; Kuehler et al. 1996; Martínez-Silvestre and Franklin 2019). Further, it is known that whilst it is technologically possible to screen captive animals for several suspected potential pathogens and possibly their identification, it may not be possible either to establish the presence of latent target organisms and particles or to examine comprehensively for non-target organisms and particles that might be present.

The effect that stress plays on the appearance of diseases in released reptiles after periods of captivity is important; stress and immune status may affect the presence of pathogens in rehabilitated reptiles. Under stressful conditions, shedding of pathogens, including zoonotic agents, may be enhanced (Martínez-Silvestre and Franklin 2019). Applying diagnostic techniques for isolation or detection of specific microorganisms is important and useful prior to considering the release of a reptile. These techniques may include bacterial and fungal cultures, polymerase-chain-reaction (PCR) testing, and antibody testing for reptilian pathogens such as *Mycoplasma* sp., *Mycobacterium*, *Brucella*, *Salmonella* and viruses including ranaviruses, picornavirus, herpesvirus, or paramyxoviruses.

Consequently, it may or may not be possible to establish the presence of some potential pathogens, but it is not possible to conclude that pathogens are absent.

Therefore, any animal released into nature is a potential vector for infection of natural populations. Indeed, there is a worrying chance of introducing non-indigenous (captive-related) morbidities and it is conceivable that the development of microorganism infection and parasitic infestation in screened animals may be prompted by possible physical stress and/or trauma associated with the captivity-wild relocation process itself. Considering the number of actually and potentially pathogenic organisms and particles known to be in circulation among captive reptiles, and the frequency with which animals are exchanged between collections, countries and continents, the risks of infecting wildlife is particularly disturbing. Finally, there is the issue of zoos performing these releases where they are obliged by law to conduct conservation-related activities, but the institution may not actually know how to do this nor have the required budget to conduct appropriate screening (Stagegaard et al. 2018).

19.9 Euthanasia and Killing

Reptiles are euthanised and killed for various reasons, including commercial, research, education and humane issues. From a welfare perspective, considerations for improved quality of life among captivity animals should not overlook the quality of death. Paradoxically, although we have mentioned elsewhere similarities in (for example) neural responses among vertebrates, reptiles possess anatomical, physiological, and behavioural attributes that can make the establishment of consciousness or death difficult, and render some of the typical methods of killing inhumane.

19.9.1 Problems in Establishing Signs of Life and Death

From anecdotal accounts and personal experiences with these animals, attempts to ascertain the point of death by, for example, observations of pupillary responses seem to have variable results. Blink reflexes (corneal and palpebral) are often unreliable indicators of death or even unconsciousness; Warwick has observed situations where freshwater turtles, following partial drownings, showed no pupillary or blink reflexes, but were otherwise relatively well coordinated. Respiration rates are difficult to monitor due to the variability in breathing modes shown by reptiles and the ability of many animals to cease breathing for extended periods with no apparent ill effects. Although the use of electroencephalograph (EEG) or electrocardiograph (ECG) devices to monitor fundamental signs of life, and thus death, have been postulated widely, many situations (particularly commercial) often make their use impracticable. Also, such approaches must be considered guardedly. For instance, anecdotal accounts suggest that EEG devices frequently give inconclusive results in reptiles, due in part to poor electrode connections because of thick integument and bony masses, and to problems of identifying potential residual activity in the brain stem. Because reptiles often continue to show coordinated reactions and behaviours with their hearts removed (as in some live animal commercial and marketplace

settings), cardiac monitoring is clearly not an ideal option for measuring signs of life. Therefore, short of complete destruction of the central nervous system or the clear onset of post-mortem changes, it seems that no completely reliable method of assessment currently exists for determining the occurrence of death. Relatedly, a recently discovered and apparently lifeless animal presents similar considerations for establishing the presence of life or death.

19.9.2 Euthanasia and Killing Methods

It is not possible to provide here detailed recommendations on methods of euthanasia and killing. Instead, the reader is referred to Cooper et al. (1989) and OIE (2019) for a review and recommendations on this issue. However, generally speaking, the preferred chemical means of killing reptiles appear to be pentobarbitone sodium via intravenous or intracoelomic injection (with the animal maintained at an active rate body temperature). The favoured physical means seems to be complete and rapid destruction of the central nervous system. There are certain considerations relevant to this subject that do not appear to have been widely discussed and that we feel should be given particular attention.

19.9.3 Decapitation and Spinal Cord Severance

For many years, decapitation was widely recommended as a ‘humane’ physical method for killing reptiles. However, this technique has been identified as inhumane largely because coordinated signs of consciousness in severed heads often continue for long periods after decapitation (e.g. Cooper et al. 1989; Warwick 1991). This situation probably arises due to the resilience of the reptilian nervous system to conditions of hypoxia and anoxia (Belkin 1963; Cooper et al. 1989), which allows prolonged post-decapitation neural function (Cooper et al. 1989; Warwick 1990b, 1991; OIE 2019). Spinal cord severance (e.g. often used on crocodylian ranches) has also been investigated and is similarly associated with long periods of post-severance consciousness (Warwick 1990b). Thus, spinal cord severance is not considered a humane method of killing alligators (Warwick 1990b; Nevarez et al. 2014; OIE 2019).

Some commentators appear to regard decapitation preceded by anaesthesia as an acceptably humane method, based on the assumption that animals should be completely oblivious to the physical trauma. However, evidence derived from EEG evaluation of rodents (Klemm 1987) suggests that this may not be a reliable assumption because decapitated heads from pre-anaesthetised animals showed signs of regaining consciousness. It is suggested that the massive afferent bombardment resulting from the physical severance provides sufficient stimulus to overpower the effects of chemical agents. It is not unreasonable to suggest that this same situation might apply to reptiles, especially in view of the potential for long periods of post-

decapitation consciousness. Consequently, decapitation, even with pre-anaesthesia cannot be regarded as a reliably humane method of euthanasia or killing.

19.9.4 Hypothermia in Relation to Anaesthesia, Euthanasia and Killing

The issue of whether hypothermia (cooling and/or freezing) in reptiles as part or whole procedures relating to their anaesthesia, euthanasia and killing has been discussed for some considerable time. Early assessments recommended against the use of hypothermia due to raised concerns regarding lack of genuine desensitisation attributable to cold and ice-crystal formation causing pain (Cooper et al. 1989). Subsequent similar guidance has followed (e.g. AVMA 2013; OIE 2019). It has also been reasoned that hypothermia may be acceptable in some artificial situations based on its natural seasonal and apparently normal healthy occurrence among certain species (Shine et al. 2015; Lillywhite et al. 2017; Nevarez 2019). Others have reasoned that the evidence for cold endurance among certain species in nature is poorly understood and should not be regarded as broadly relevant to practices in captivity (Warwick et al. 2018b), thus recommending against hypothermia for sedation or anaesthesia. Furthermore, not only is it difficult to accurately monitor for signs of consciousness versus unconsciousness in reptiles, but this would be even more true of determinations of nociceptor function (Warwick et al. 2018b). Currently, primary guidance bodies do not recommend hypothermia for general use in reptiles (AVMA 2013; OIE 2019). Arguably, approaches to anaesthesia, euthanasia, and killing that utilise carefully targeted, natural and evolved or holistic principles theoretically offer potentially rational ways to address what are often difficult applied questions. However, it is also important that the line of relevant reasoning develops in which animal welfare resides centrally to it, and protocols do not emerge in which practical convenience overrides meticulous contextualisation of biology and welfare need.

19.10 Occupancy and Post-Occupancy Evaluation

Occupancy and post-occupancy evaluation (O/POE) refer to the observable forensic assessment of (in particular) an enclosure or area in which animals live, or recently occupied, in order to gain insight into relevant activities, such as visible tracks or indentations in substrate that may indicate behaviour patterns. The term stems from 'post-occupancy evaluation', which has long been used in zoos and other major facilities (Shettel-Neuber 1986; Maple and Finlay 1987; Wilson et al. 2003; Kelling and Gaalema 2011; Tingey 2012). Occupancy/post-occupancy evaluation is potentially helpful in determining what facilities in an environment are or are not being used, and generally, what levels of activity may be present when continuous observation is impractical. Therefore, O/POE can be a valuable tool in animal welfare.

In reptiles, key O/POE signs are detritus on transparent boundaries—indicating potentially problematic and stress-related interaction with transparent boundaries (ITB) behaviour; substrate depressions or disturbances adjacent to boundaries—indicating exploratory and escape attempts; substrate depressions adjacent to air vents—possibly indicating poor ventilation; substrate depressions adjacent to shaded areas—possibly indicating photo-invasive environments; excessive liberal dispersal of senescent skin or faeces—indicating poor hygiene management; absence of substrate tracks or disturbance of furnishings (e.g. foliage)—indicating disuse of provisions, sedentarism or hypoactivity; excessive markers of activity proximal to a heat source—indicating a poor thermal environment or hyperbasking and excessive markers of activity proximal to a cool area—indicating a poor thermal environment (see Arena and Warwick 2023; Warwick 2023).

19.11 Human–Animal Interactions and Relationships

Claxton (2011) suggested that all animals begin with a fear of humans, and an individual's interactions with humans can exacerbate or mitigate this fear. For livestock, gentle handling is widely considered a positive stimulus (de Passille et al. 1996; Hosey 2008), and positive human-animal relationships have been described as crucial for good welfare (Hemsworth 2002). Positive human-animal interactions have also been reported to improve the welfare of birds, as well as primates and other mammals living in zoos (for review, see Hosey 2008). However, there is less consensus that human-animal interactions are beneficial for reptiles (Warwick et al. 2011).

A few studies have revealed responses suggesting that handling interactions can be neutral for—or even improve—welfare. For example, holding and manipulating bearded dragons (*Pogona vitticeps*) resulted in decreased hiding (Cannon et al. 2002) and gentle handling of leopard geckos (*Eublepharis macularius*) increased exploration behaviours and behavioural diversity (Bashaw 2017). However, most studies find human handling of reptiles results in physiological (e.g. Bailey et al. 2009) and behavioural (e.g. Agha et al. 2015; Acaralp-Rehnberg 2020) changes indicative of stress, even for normally docile species. For example, Stockley et al. (2020) found handling of bearded dragons increased tongue-flick rate, suggesting stress. Also, it is worth bearing in mind that handling by humans is widely used as a stressor for reptiles in ecological and physiological studies (Broom and Johnson 1993; Stockley et al. 2020).

For mammals, the sex of the handler (Sorge et al. 2014), the type and consistency of handling (Gourkow and Fraser 2006), and the individual animal's previous experience with handling (Hosey 2008) can all affect the animals' perception of handling, and therefore its welfare (Waiblinger et al. 2006; Whitham and Wielebnowski 2013). Reptile handling procedures can be deconstructed into a variety of elements that may or may not be present in any particular handling protocol, including exploring a novel environment (as in Hoopes et al. 2000), enclosure in a bag or bucket (as in Lance et al. 2004), physical restraint or

immobilisation (as in Kalliokoski et al. 2012), repeated blood sampling (as in Wack et al. 2008), forced exercise (as in Trompeter and Langkilde 2011), and inversion (as in Cabanac and Bernieri 2000). Each of these elements likely has a different potential for causing a stress response. For example, inverting sheep for shearing is more aversive than shearing them whilst restrained upright (Rushen 1996). Work is underway in the laboratory of the author (MJB) to identify which elements most reliably predict stress responses and provide guidance on how to most efficiently produce or avoid handling stress in reptiles. Interactions with humans may also provoke different reactions in different individuals. Indeed, several studies (Bowers and Burghardt 1992; Mehrkam and Dorey 2014; Gibson 2015) have identified individual differences in reptiles' responses to human interactions, and Bashaw and McMillan (2018) found that some leopard geckos actively avoided opportunities for gentle handling whilst other individuals did not.

Repeated interactions with humans are an inevitable consequence of captivity. Hosey and Melfi (2014) explained how human–animal relationships develop based on the history of these interactions. The form of these relationships will depend on whether the animal perceives the interactions as positive, neutral, or negative and to what extent the animal can differentiate individual humans. As an illustration, Wielebnowski et al. (2002) found that having fewer keepers who each spent more time with clouded leopards (*Neofelis nebulosa*) was associated with lower faecal glucocorticoid hormone metabolites; they suggested the formation of relationships with keepers reduced stress. Whilst human–animal relationships have not been well studied in reptiles, Burghardt and colleagues described how captive Aldabra (*Aldabrachelys* spp.) and Galapagos (*Chelonoidis* spp.) tortoises (*Chelonoidis carbonaria*; Bowers and Burghardt 1992), green iguanas (*Iguana iguana*; Bowers and Burghardt 1992), and monitor lizards (Burghardt 2013) differentiated among individual humans, seeking interactions with familiar people and exhibiting fear-related behaviours to unfamiliar ones.

Although the World Association of Zoos and Aquariums (WAZA) places choice for animals at the top of its welfare pyramid (Mellor et al. 2015), and the opportunity to make meaningful choices is a critical contributor to welfare (Boissy et al. 2007; Whitham and Wielebnowski 2013), captive animals rarely have a choice about whether or how to engage with humans. Hosey (2008) predicted that animals who have some control over their interactions with humans are likely to perceive the interactions as more positive. For example, adding a retreat space where petting zoo mammals could escape from contact with unfamiliar people improved their welfare and reduced human-directed aggression (Anderson et al. 2002). Similarly, positive reinforcement training (PRT), where animals are given a request for a behaviour and desirable responses produce a reinforcer, has been associated with improved welfare in nonhuman primates (Bassett et al. 2003; Laule et al. 2003; Schapiro et al. 2003) and other laboratory animals (Bayne 2002). Paralleling the proliferation of PRT, captive animal facilities are also increasingly moving to 'protected contact' systems in which animals and humans interact only through a barrier and no punishment is used (Desmond and Laule 1991). These systems are perceived as desirable in part because they give the animal greater control over its interactions with humans by allowing choice of whether or not to participate in husbandry activities (Clubb and

Mason 2003; Desmond and Laule 1994). Positive reinforcement training, especially target training, is increasingly being used with reptiles and successful techniques are being shared among reptile enthusiasts through informal means (for example, in social media groups such as Facebook's 'Reptelligence'). However, to date, little published scientific research has explored the effects of PRT on reptile welfare.

19.11.1 Changing Human Behaviour to Improve Captive Welfare

Captive reptiles are, by definition, under the care of humans and are therefore wholly reliant on humans to meet their welfare needs. Whilst there has been some argument that it would be impossible to provide a captive environment that provides sufficient enrichment and stimulation to approximate a reptile's natural habitat (Warwick 2023), it is imperative that reptile handlers endeavour to meet the needs of the animals in their care. There is a wealth of evidence-based advice available on how to better manage captive reptiles, including in this book. Nonetheless, many carers, especially private individuals, may not be engaging in husbandry practices to ensure optimum feasible welfare for their animals, as evidenced by self-reported husbandry conditions (Howell and Bennett 2017; see also Jessop et al. 2023; Mendyk and Warwick 2023), and concerns by veterinarians (Loeb 2018; Whitehead 2018). Educating people by providing factual information alone can have limited success in changing longstanding behaviour (Kelly and Barker 2016; Warner and Forward 2016), so it is necessary to first consider the barriers to behaviour change, and, subsequently, ways to effectively get around them.

Previous research into captive reptile management behaviours has determined an over-reliance on arbitrary or folklore husbandry by reptile keepers (Arbuckle 2013; Mendyk 2018; Mendyk and Warwick 2023). Arbitrary or folklore husbandry is the tendency to engage in a management practice simply because 'it has always been done that way' (Mendyk and Warwick 2023). This approach is perhaps understandable in cases where scientific evidence for appropriate management does not exist, but it is problematic when available evidence suggests that existing practices are potentially harmful. When reptile keepers learn that their current management practices are lacking, and that available scientific evidence suggests changing these practices, not all keepers make these changes, thus poor husbandry persists.

So why do some keepers resist making positive changes? At times, people engage in behaviours that are not consistent with their existing beliefs and attitudes (Festinger 1962; Bennett and Perini 2003). For example, private lizard keepers indicated that taking care of their reptile was one of their highest priorities and that they felt confident in their ability to care for their lizard (Howell and Bennett 2017). In principle, therefore, they should be open to making any necessary changes that would benefit the animal. However, the extent of arbitrary or folklore husbandry present in reptile care suggests that, for some reptile carers, their beliefs and attitudes about the importance of looking after their reptile does not accord with their actual behaviours, which could be detrimental to the animal. There are several possible

reasons for this situation, such as having a lazy attitude towards behaviour change, or the inconvenience associated with learning how to manage a captive animal more appropriately. However, neither of these reasons seem likely in the case of reptile carers who claim to prioritise animal welfare and feel confident to meet their reptile's needs. Instead, other factors may be involved.

According to the theory of cognitive dissonance, when people experience a disconnect between their attitudes and their behaviour, this causes a sense of discomfort (Festinger 1962). In order to alleviate this discomfort, people can either choose to change their behaviour to bring it more in line with their attitudes and beliefs or they can try to justify their existing behaviour (Festinger 1962). When people have already engaged in a dissonant behaviour, they are more likely to justify it, rather than change, because changing would require them to acknowledge that their earlier behaviours were not ideal (Bennett and Perini 2003). In other animal contexts, this dissonance has been found in dedicated, affectionate dog breeders who engaged in painful, medically unnecessary tail-docking procedures on puppies, arguing that it reduced the likelihood of tail injuries in adult dogs (Bennett and Perini 2003). It is possible that many reptile carers who engage in potentially damaging husbandry practices simply struggle to accept that they could be doing more harm than good, especially if they consider themselves to be confident, capable carers, such as those reported in Howell and Bennett (2017).

Even though cognitive dissonance is a barrier to behaviour change, it is possible to implement programs that can effectively change behaviour. According to the theory of planned behaviour, the factors that most influence the intention to perform a behaviour are pre-existing attitudes towards the behaviour, what people believe their friends and family would think of them engaging in the behaviour (i.e. subjective norms), and how difficult they believe it would be to engage in the behaviour (Ajzen 1991). The normalisation of poor husbandry practices mentioned earlier in this chapter may be explained by the subjective norms highlighted in the theory. Perceived difficulty can also influence the intention to engage in recommended companion animal management behaviours (e.g. cat containment indoors; McLeod et al. 2015), and this may be the case for reptile keeping, which requires a great deal of equipment and resources. It is possible that some management practices are perceived as too difficult to realistically implement. For example, snake owners may agree with the requirement for minimum enclosure dimensions which posits that a snake's cage should be at least as long as the full length of the snake (Warwick et al. 2019; Arena and Warwick 2023), but they may lack the space to accommodate a larger enclosure.

The theory of planned behaviour has been used as a basis for programs designed to effect behaviour change (Coleman et al. 2000; Hemsworth et al. 2002), but its success in other animal husbandry contexts appears to depend partially on how intensively the program is managed. A successful program has been ProHand, which aims to change livestock handler behaviour in order to improve welfare outcomes for livestock, by changing the negative attitudes that often underlie negative behaviours towards livestock (Coleman et al. 2000). The program includes a 60–90 minute online or face-to-face course with facilitated discussion (Coleman et al. 2000), and

sometimes includes monthly newsletters and a follow-up visit by the researchers between 1 and 3 months after the online course (Hemsworth et al. 2002). The more intensive follow-up showed improved outcomes for stockperson behaviour, as well as livestock welfare and production (Hemsworth et al. 2002). The course without substantial follow-up showed fewer improvements over the long term, although there was a reduction in the proportion of negative behaviours towards the animals (Coleman et al. 2000).

Effecting behaviour change in reptile keepers is not impossible, but it will take more than simply supplying factual information, and may even require generational change in the case of recalcitrant carers who refuse to accept that their practices may be deficient or defective. Effective strategies should focus on improving attitudes towards evidence-based practices, and helping people understand the ways in which they can realistically implement any desired changes.

19.12 Ethical Considerations

Aside from the occasional gecko that wanders freely in to and out of someone's home, reptiles are generally forcibly confined in captivity for whatever purpose appeals to their human captors and rarely for the benefit of the animal. This somewhat blunt description of a common human-reptile relationship underscores the keeper's responsibility to ensure that the best efforts are employed to secure an animal's well-being. Keeper responsibilities also extend beyond reptile welfare to conscientiously prevent harm relating to various matters allied to keeping captive animals, including live prey food welfare, species conservation, ecological protection, invasive alien introductions, and public health and safety (Warwick 2014; Mendyk and Warwick 2023).

A concluding feature of Warwick's (2014) essay on the ethics of reptile keeping asks whether people would accept confining a dog to a vivarium in the home? Most likely, such confinement would not happen, and the captors may face prosecution were they to do so. The common position among reptile keepers that such confinement is acceptable does not reflect lesser biological and welfare needs for reptiles—whether for space, environmental or other provisions and complexities. Rather, it reflects normalisation of certain practices (Mendyk and Warwick 2023) and reflects a widespread erroneous belief that reptiles lack intelligence and emotions, highlighting an anthropomorphic perspective that has been discussed elsewhere in this book (see Doody 2023). It is arguably a most unfortunate scenario that those reptile keepers or enthusiasts and biologists who are, on the one hand, such admirers and advocates of their characteristics are, on the other hand, also their greatest deprivors of freedom and holistic well-being. Good ethics demand that people do the right thing. Therefore, it is imperative that reptile keepers (having incarcerated these animals in their restricted position) continuously question themselves about the welfare of their charges and the rightfulness of their dominion over them.

19.13 Animal Welfare Conclusions

Reptiles, as a result of their unique anatomical and physiological attributes, are one of the most popular vertebrate groups held in captivity. The fact that these vertebrates may remain alive to endure atrocious conditions of captivity, often for comparatively long periods, has led to them being diversely exploited in such phenomena as rattlesnake round-ups, crocodylian ranching, turtle ranching, culinary situations, zoos and other exhibition halls, and museums and research establishments, but perhaps most detrimentally by the pet trade.

When reptile curators and scientists fail to recognise or understand factors affecting the well-being of their charges, they seem unable to presume the benefit of any doubt in favour of animal welfare. For example, the belief that reptiles did not feel or express pain, as at one time viewed, led to them being (and remaining) poorly understood and mistreated. At least as unfortunate is the ingrained perspective, held by many proponents of animal-keeping, that their practices are justified until proven otherwise. Not only is this view imbalanced, but it is also unscientific and unethical. Those who promote matters as serious as confining life forms for their own non-essential purposes can reasonably be requested to justify their position, scientifically and ethically, ahead of their practices. Where welfare is concerned, anything less than this is unwise and unfair.

Our ability to exercise the benefit of the doubt is perhaps the most important consideration for animal health and welfare. Practically, this could mean not participating in or otherwise condoning situations wherein reptiles are kept and where any doubt exists over associated well-being. Arguably, this is not only the most ethical approach, but also the most scientific approach. Scientists, curators and others, particularly those in positions of influence and responsibility, could do far more to increase the acceptability of the individual animal's welfare as being paramount. However, rooting this philosophy in educators is largely dependent on the prospective welfare proponents themselves becoming properly motivated in the first place. We feel that it is reasonable, from both a comparative biological perspective and a necessary ethical perspective, to suggest that one of the most important steps toward greater sensitivity to reptiles and other animals is simply to focus on our many similarities rather than differences and to put ourselves in the position of the utilised subject. With our existing biological knowledge, and with the benefit of the doubt placed on the side of non-human animals, we are then qualified to ask the question: how would we like life in their position?

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