Spatial and Thermal Factors

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Abstract

An understanding of spatial and thermal factors, two fundamentally intertwined elements, is essential to the health and welfare of captive reptiles; carers cannot address one without consideration of its influence on the other. This chapter highlights the need to recognise the many shortcomings of past practices, and urges individuals charged with keeping reptiles to become familiar and competent with new understandings revealed by research into the complex interplay of spatial and thermal factors. Essential to this issue is recognition that a 'one-size-fits-all' approach is never a good option. However, despite advances in our understanding of the spatio-thermal requirements of both wild and captive reptiles, there remains opportunity for abuse, exemplified by the highly restrictive rack system for housing snakes. In terms of spatio-thermal requirements, the modern, progressive reptile carer must become familiar, not only with species-specific requirements, but also the needs of individuals, taking into account the impact of seasonal and behavioural factors.

Keywords

Space · Temperature · Spatio-thermal · Home range · Enrichment · Rack system · Sociality · Behaviour · Body size · Overcrowding · Ectothermy · Hyperbasking · Welfare

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13.1 Introduction

The nature of captivity places constraints on organisms. These constraints can be multiform as the captive animal is no longer free to perform the same range of activities and behaviours that it can within the significantly less constrained environments experienced through living in the wild. These activities and behaviours include feeding, interactions with conspecifics, courtship, predator avoidance, wandering, hunting prey and, more specifically in the case of reptiles, thermoregulation. In captivity, all these expressions of a reptile's normal biology must be performed within the conditional limits as established by an artificially designed environment. In other words, every environmental need of the enclosed reptile must be met by the captor and, thus, the onus is on the captor to be familiar with all the species-specific requirements of the species held captive. This consideration is particularly notable in the case of zoos where the opportunity to educate exists and where some visitors not only appreciate a well-informed exhibition, but also the opportunity to ask questions of a keeper (Tribe and Booth 2003; Packer and Ballantyne 2010; Saunders 2013; Woods 1998; Yilmaz et al. 2017). In the case of reptiles and any other groups of animals that are similarly confined, species-specific knowledge may be lacking, thus knowing what is normal or abnormal can itself be a challenge. Also, fundamentally, conditions of captivity are such that expression of a normal or natural repertoire of behaviours probably becomes impossible; captive environments simply lack both the space and the stimuli present in nature (Burghardt 2013). There is a myriad of requirements that must be provided within any 'cage', but an enclosure ultimately serves to confine and in broad terms, this means a restriction of spatial requirements (Gillingham 1995; Greenberg 1995; Warwick and Steedman 1995; Gillingham and Clark 2023; Warwick 2023; Mendyk and Augustine 2023; Warwick and Steedman 2023).

As ectotherms, reptiles will orientate their bodies or move around the spatial environment to optimise the use of a heterothermic environment and thus achieve their thermal requirements (Lillywhite 2023). Thermal environmental variation itself requires space; one cannot have much temperature variation in a small area or in an area that lacks topography. Accordingly, spatial and thermal factors are, for the most part, inextricably linked to the needs of reptiles to fulfil their activity (and inactivity) demands so that they may select body temperatures that enable expression of a 'normal' repertoire of behaviours (Gillingham 1995). The present chapter explores spatio-thermal considerations of reptiles, highlighting both the importance of providing or failure in providing adequate space and temperatures for captive individuals.

13.2 Historical Approaches

Historically, determination of spatial needs and associated cage sizes largely was based on the requirements of the most recognised repositories of exotic species—zoological gardens. It was believed that the most effective way to maintain an 'intimate' relationship between the visitor and the animal being exhibited was to limit cage size and simulate key aspects of natural habitat (Bacon and Hallett 1981). Thus, the development of early animal exhibits incorporated major input from graphic designers in order to present an illusion of space and to satisfy the exhibitory plans of the institution, as well as the convenience of the keeper. Some of these early displays may have appeared grandiose, but in fact still provided relatively small areas for the animals they contained. Nevertheless, such 'diorama' displays were quite successful and became the standard approach in the design of enclosures at many zoological (and museum) exhibiting worldwide (Bacon and Hallett 1981; Insley 2007; Holmes 2009; Carter et al. 2015; Reiss 2015).

In those zoos, the size of enclosures provided to the exhibited species was also determined or influenced by the need to prevent injury or death in wild animals that were intent on escaping (Hediger 1950). For example, ungulate mammals would frequently charge against cage boundaries with dire consequences and, according to Hediger (1950), '*A practical step to avoid this is to keep such animals in cages so small that they are quite unable to develop sufficient dynamic energy for fatal fractures.*' The approach was employed for varying periods that were considered long enough to enable the animals to 'adapt' to imposed physical boundaries. Following this period of adjustment, the animal could be moved to a more spacious enclosure. However, reptiles have a long history of confinement in enclosures (vivaria) that severely limit normal behaviours from the moment they are wild-captured or captive-born (see Gillingham 1995). In regard to zoological exhibitions, an early aim was to house the greatest diversity of reptile species possible, largely in an effort to highlight variation in the animal kingdom (Benbow 2000, 2004). There was certainly little notion of the role future zoos would play in conservation and nature education (Hoage and Deiss 1996; Reid and Moore 2014; Minteer et al. 2018). Zoo cage size continued to be restrictive—reptile houses or exhibits would have deviated substantially from the norm were they to contain just a few individuals in a few extensive enclosures. That said, spatial conditions and related environmental thermal variation for privately held reptiles typically will be inferior to that of the professional zoo. Arguably, throughout the history of reptile-keeping, evidence-based welfare requirements have characteristically been secondary to practical housing and spatio-thermal considerations—a situation exemplified by the inappropriate housing commonly provided for snakes (Warwick et al. 2019; see also Mendyk and Warwick 2023).

However, today, more is known of the spatio-thermal requirements of reptiles. As Warwick (1995) noted in the first edition of this volume, satisfying the spatial requirements of reptiles involves more than just increasing the physical dimensions of an enclosure. In the 25 years since this statement, additional research has explored the complex interplay between spatial requirements and various aspects of a reptile's life history such as behaviour (including social interactions and play) and thermal requirements (e.g. Huey 1991; Lillywhite and Gatten 1995; Burghardt 2013; Noble et al. 2014; Rose et al. 2017; Lillywhite 2023; Gillingham and Clark 2023).

13.3 Space Utilisation, Exploration, and Enrichment

Utilisation of space by reptiles is variable according to habits, ecological niche, and biological need. Food search, prey biology, reproductive drive, reproductive status, genetic transient behaviour, social pressure, climate, season, habitat state, environmental neophilia (enthusiasm for novelty), and other factors influence when and how much an animal needs or 'wants' to move around (Warwick 1990a, b; Kerr and Bull 2006; Warwick et al. 2013; Arena et al. 2014; Cunningham et al. 2016). In contrast to mobile activities are 'immobile' activities such as, rest, sleep, brooding, hiding from predators, sit-and-wait ambush tactics, aestivation, brumation, hibernation, injury- or disease-related energy conservation, and other factors (Huey 1982; Warwick and Steedman 1995; Hayes et al. 1998; Barten 2006; Funk 2006; Rossi 2006; Brasfield et al. 2008; Fleming and Skurski 2014; Wilkinson 2015). These activity profiles may not be reliably determined or set other than by the animal itself; thus, as expected, a human keeper can only make assessments and assumptions regarding how much space an animal needs or when it needs it based on their level of knowledge and understanding. Of course, such a situation is true of every captive animal scenario. However, one must also consider that the effects of spatially related stresses are regularly observed in captive reptiles, should one be sufficiently minded and informed to look for them (Warwick et al. 2013; Warwick 2023).

In general, very few studies have investigated the influence of captivity on any group of vertebrates, particularly in terms of behaviour, and it is only largely within the past decade or so that more detailed attention has been applied to examining the impact of captivity on the behaviour of, for example, mammals, when Ross et al. (2009) investigated the limitations imposed by captivity on the behaviour of gorillas (*Troglodytes* sp.) and chimpanzees (*Pan* sp.). This study focused on the way a captive animal utilised its spatial environment, and how such investigations can facilitate assessment of welfare. Similarly, a study of space utilisation by African wild dogs (*Lycaon pictus*) determined that an understanding of how captive animals use space can reduce the occurrence of stereotypic behaviour in captivity (Hunter et al. 2014). These studies are based on the premise that in order to most effectively address the impact of captivity on the welfare of individuals, one must first examine how the occupant utilises the space of its enclosure. This concept of effective usability was explored further by Browning and Maple (2019) who developed an approach ('metric') for assessing the quality of zoo animal (pygmy marmoset, *Cebuella pygmaea*) enclosures in three dimensions. Again, emphasis was placed on providing enough space to enable the occupant to have a high degree of choice in its proximity to conspecifics and resources such as furnishings—preferences that may be quite variable (Browning and Maple 2019). A study of habitat selection in the Panamanian grass anole (*Anolis auratus*) demonstrated the value of conspecific association in habitat selection whereby anoles of one species chose to associate with others of the same species rather than individuals of a related species. This behaviour highlighted the value of conspecifics as 'cues' in the selection of suitable habitat (Kiester 1979).

Recent years have seen an increase in the number of investigations of the way reptiles utilise their spatial environment in captivity, and how this can be altered through provision of adequate space, increased opportunities for exploration, and other forms of enrichment (e.g. Case et al. 2005; Bashaw et al. 2016; Spain et al. 2020). In terms of enrichment in captivity, this can be defined as providing opportunities for an animal to express its natural behaviour in a naturalistic environment (Claxton 2011). Enrichment may include alterations to enclosure design and various stimuli, and presentation of novel objects (Brent and Belik 1997; Wells 2009). In order to quantify the impact of enrichment and consequently, the welfare of the captive animal, the presence (and absence) of specific behaviours is often used. However, again, in reptiles, until recently, this area had been rarely explored (see Warwick et al. 2013). Paucity of reptile-related research, with particular emphasis on the lack of enriched stimulating and novel environments was recognised by Burghardt (2013), who described such conditions as ‘controlled deprivation’ (Burghardt 1996; see also Mendyk and Augustine 2023). However, few recent studies, have noted that species-specific enrichment requirements of some reptiles may vary considerably (Rosier and Langkilde 2011). For example, Wheler and Fa (1995) investigated enclosure utilisation by Round Island day geckos (*Phelsuma guentheri*) and found that individual lizards utilised the environment in their enclosures in specific ways, preferring cage furnishings and hides and avoiding vertical glass walls. Lizard preference for specific areas within their enclosures was also influenced by the size of individuals (Wheler and Fa 1995). A study of captive corn snakes (*Pantherophis guttatus*) and chuckwallas (*Sauromalus ater*) determined that structural and thermal heterogeneity was vital if the captive individual was to express a normal range of behaviours (Rose et al. 2014).

Elements of enrichment can range from variable substrates to opportunities to explore, climb, and play (see Mendelson III et al. 2019; Mendyk and Augustine 2023; Warwick and Steedman 2023). Enclosure enrichment led to an improvement in the welfare (expression of positive behavioural indicators) among leopard geckoes (*Eublepharis macularius*) (Bashaw et al. 2016). Interestingly, in this study, greater levels of engagement were elicited with forms of enrichment that were linked to normal biological requirements (such as ‘thermal’ and ‘feeding’ enrichment), rather than to forms of enrichment based on novelty such as toys. This implied that the animals prioritised their behaviours, preferring forms of enrichment that addressed their physiological and behavioural needs (Bashaw et al. 2016). In a study of play, thick-toed geckos (*Chondrodactylus turneri*) were observed to engage in variable manipulation of objects in a weightless environment (Barabanov et al. 2015). Spatial memory and learning were recorded in the side-blotched lizard (*Uta stansburiana*) (LaDage et al. 2012) and the eastern water skink (*Eulamprus quoyii*) (Qui et al. 2018), whilst complex cognitive capabilities such as problem-solving were demonstrated in the anole (*Anolis evermanni*) (Leal and Powell 2012) implying that squamates have the capability to use spatial memory when performing everyday tasks such as defending territories and food acquisition. Studies such as these are beginning to highlight the complexity of reptilian behaviour and decision-making, and thus provide insight into their response to captivity and, by extrapolation, the need for greater investigation and understanding of the spatial requirements of captive animals. However, again, few such investigations exist although significant approaches to enrichment in reptile enclosures may be more prevalent than reported in the scientific literature (Eagan 2019). In addition, due to the paucity of data for reptiles, the mammalian response to captivity continues to inform (see Wolfensohn et al. 2018) and be applied to the reptilian condition despite largely different sets of physiological, behavioural, and spatial needs. At a minimum, what such research shows is that the welfare of captive reptiles extends beyond providing 'adequate' space to infer the furnishing of space that promotes opportunities for interaction and exploration.

The greater the knowledge base regarding the welfare of reptiles in captivity, the more obvious it becomes that spatio-thermal requirements are not being adequately met. Stress responses are often expressed as abnormal behaviours such as hypoactivity, hyperactivity, and interactions with transparent boundaries (Warwick 1995; Warwick et al. 2013; Rose et al. 2017; Gangloff and Greenberg 2023; Warwick 2023; Arena et al. 2023). Key investigations to propose the use of behavioural responses to assess the welfare of captive reptiles listed over 30 behaviour-related signs of stress, over half of which were attributed to deficient and inappropriate environments, highlighting the potential impact of restricted spatio-thermal environments (Warwick 1990a, 1995; Warwick et al. 2013).

13.3.1 Home Ranges

It is virtually impossible to provide an enclosure that replicates an animal's natural habitat (Zwart 2001; Mendyk and Augustine 2023) or fully satisfies the innate (hard-wired) psychological and behavioural requirements of a wild animal, but if captivity is to be considered acceptable, then the appropriate size of an enclosure is one where the desire or tendency to escape no longer exists (Warwick 1995, 2023). In reality, this may never be attainable because captivity in and of itself (as stated earlier) implies confinement and restriction. Furthermore, many species regularly include naturally long-distance wanderers and others include individual population transients whose home ranges may vary by size, habitat, sex, and reproductive status (such as males wandering in search of females) and energy requirements (Kiester et al. 1982; Rose 1982; Perry and Garland 2002; Sillero and Gonçalves-Seco 2014). Here, 'home range' refers to the area through which an animal moves in order to satisfy its normal requirements such as acquiring food, mates, and shelter (Powell and Mitchell 2012). Even strategic sedentary sit and wait or ambush species, such as alligator snapping turtles (*Macrochelys temminckii*) and viperid snakes that employ caudal-luring (e.g. *Cerastes vipera*) are known to occupy large home ranges (Riedle et al. 2006; Subach et al. 2009). Furthermore, seasonal wandering and significant home range extension occur in many species in the search for mammalian prey or mates (Gardiner et al. 2013; Mata-Silva et al. 2018), whilst proximity to den sites is a crucial factor influencing home ranges and the distances that northern latitude snakes will travel (Edkins et al. 2018; Shonfield et al. 2019).

Under natural conditions, reptiles occupy space in terms of regularly traversed home ranges. These are areas that an animal regularly roams in order to fulfil its requirements for foraging, hunting, reproduction, basking, and other behaviours. In the case of arboreal, semi-aquatic, aquatic, or fossorial species that climb, swim, or burrow, respectively, such environments can be measured in three fuller dimensions. Contrary to statements such as 'herpetofauna' do not move frequently (Row and Blouin-Demers 2006), field studies indicate that reptile home ranges are commonly extensive, and many animals regularly travel large distances (e.g. up to several kilometres) in search of prey, mates, and shelter (Baeckens et al. 2017). Furthermore, even these estimates of home range size are quite miniscule compared to the transoceanic migratory behaviour of, for example, loggerhead sea turtles (*Caretta caretta*) (Polovina et al. 2004; Boyle et al. 2009) and male estuarine crocodiles (*Crocodylus porosus*), which are known to travel many kilometres in a single day (Campbell et al. 2013). Table 13.1 provides examples of home range estimates for reptiles from representative orders as determined by minimum convex polygon method in relation to average snout to vent length.

As indicated in Table 13.1, the home ranges of even comparatively small reptiles vastly extend beyond the dimensions of enclosures typically used to house them and even though more modern institutions may provide enclosures that far exceed previously acceptable norms, spatial provisions in such institutions commonly equate to a fraction of natural home ranges. Merely providing basic presumed environmental, physiological, behavioural, and psychological elements within an enclosure does not negate innate, hard-wired, drivers for greater space (Warwick 1990a, 1995; Warwick et al. 2013; Warwick 2023).

A common view among reptile keepers is that because an animal's essential needs are met (as perceived by its caregiver), then this reduces or eliminates requirements for them to engage in an array of normal behaviours common to their wild counterparts. This perspective, at its roots and within a spatio-thermal context, follows the thinking that an animal in nature essentially roams large areas because 'it has to' in order to secure what it needs. Some studies have shown that spatial need is influenced by habitat quality—what the environment provides (Christian and Waldschmidt 1984; Perry and Garland 2002; Verwaijen and Van Damme 2008; Stellatelli et al. 2016; Patterson 2018); thus, home ranges may be larger within poorer habitats (Perry and Garland 2002). Theoretically, this argument suggests that if captivity has provided all relevant requirements, corresponding drive states become redundant, and the animal does not need and does not 'miss' the natural world.

If correct, an animal contained within a high-quality enclosure—i.e. one that is abundant in terms of, for example, provisions regarding thermal range, food, water, habitat diversity, opportunities for key normal positive behaviours, social conspecifics where relevant, and general enrichment, ought not attempt to escape nor even harbour a drive to do so. However, if this were true, then there would be absolutely no need to utilise restrictive boundaries in an artificial environment, because the occupant would simply have no interest in exploring beyond the immediate provisions. This perception is essentially discounted by numerous observational and other evaluations concluding that, for example, many animals with

Table 13.1 Examples of home range estimates for reptiles from representative orders as determined by minimum convex polygon method in relation to average snout to vent length (SVL)

Order	Common name	Scientific name	SVL (average)	Home range estimate	Source
Testudines	Green turtle	*Chelonia mydas*	90 cm	1662 ha	Seminoff et al. (2002)
	Red-eared slider	*Trachemys scripta*	21 cm	23.35 ha	Slavenko et al. (2016)
	Gopher tortoise	*Gopherus polyphemus*	28 cm	3.2 ha (m)[a]1.24 ha (f)[a]	Castellon et al. (2018)
Crocodylia	Nile crocodile	*Crocodylus niloticus*	410 cm	2200.7 ha (m)	Calverley and Downs (2015)
	Estuarine crocodile	*Crocodylus porosus*	700 cm	[b]23.9 ha (m) 5.9 ha (f)	Brien et al. (2008)
Lacertilia	Round Island day gecko	*Phelsuma guentheri*	12 cm	73 m^2 (m) 31 m^2 (f)	Gerner (2008)
	Australian sleepy lizard	*Tiliqua rugosa*	35 cm	4 ha	Bull and Freake (1999)
	Black-headed monitor	*Varanus tristis*	70 cm	40.3 ha (m) 3.7 ha (f)	Thompson et al. (1999)
	Komodo dragon	*Varanus komodoensis*	300 cm	278–530 ha	Ciofi et al. (2007)
Serpentes	Stephens' banded snake	*Hoplocephalus stephensii*	100 cm	20.2 ha (m) 5.4 ha (f)	Fitzgerald et al. (2002)
	Milk snake	*Lampropeltis triangulum*	150 cm	24 ha	Row and Blouin-Demers (2006)
	Eastern indigo snake	*Drymarchon couperi*	220 cm	201.7 (m) 75.6 (f)	Breininger et al. (2011)
	South western carpet python	*Morelia spilota imbricata*	230 cm	17.6 ha	Pearson et al. (2005)

m male, *f* female
[a]Data for scrub habitat
[b]Data for late dry/mid-wet season

naturally large home ranges are less able to adapt to zoo environments, resulting in compromised welfare, often expressed as stereotyped behaviours such as pacing (Clubb and Mason 2003).

As indicated earlier, almost all captive scenarios, from reptiles kept as pets in private homes to those in the highest-quality zoological facilities, typically rely on barriers to forcibly confine animals to the human perceived 'all-providing' conditions. Therefore, a simple test could be applied to ascertain the degree of acceptability of enclosures to reptiles, which would be to remove all limiting barriers from captive situations—open the cages 24/7. Of course, opening such barriers would likely result in most, if not all, of the occupants exiting the areas. Accordingly, there is more to the issue of spatio-environmental needs than meets the eye of the caregiver's belief that basic provisions negate need for space. Indeed, as previously stated, it is a common phenomenon among animals that activity patterns and home range use are significantly influenced by hard-wired drive states (whether for additional space, novel territory, reproduction, and other factors), as well as the biological need to control their own space (Dawkins 1990; Broom 1991; Owen et al. 2005; Ross 2006; Morgan and Tromborg 2007; Alligood and Leighty 2015; Kroshko et al. 2016; see also Warwick 2023), and these influences are not eliminated by 'abundant' captive provisions.

The evidence regarding home ranges stands contrary to the over-simplified assumptions by many (in particular hobbyist) herpetologists who wrongly claim (and frequently report in online reptile-keeping forums) that reptiles are stressed or 'agoraphobic' in open spaces on the basis that they may seek shelter or cover (see Mendyk and Warwick 2023). Indeed, the belief that agoraphobia (which is a human anxiety disorder) exists in reptiles is used as frequent justification for overly and severely restrictive enclosures (Warwick et al. 2013). Few studies have examined the impact of confinement on the welfare of reptiles. However, one such investigation of ball pythons (*Python regius*) found a significant rise in plasma corticosterone (i.e. a stress response) when animals were confined to a narrow container (a PVC—polyvinyl chloride) tube that prevented the snake from turning around) (Kreger and Mench 1993). Similarly, reptiles that are restrained in collection bags show increases in corticosterone levels (Tyrell 1998; Mathies et al. 2001). Although these are extreme examples of reduced space, they demonstrate that an elevated stress response is likely if a confined reptile (or likely, any other animal) is restricted to the extent that it is unable to express normal behaviours and exercise control over its environment.

In snakes, vindication for the approach of adopting highly restrictive enclosures is partly fueled by a long held erroneous belief that snakes do not need to stretch out, making them the only captive vertebrates denied by flawed information the ability to straighten their bodies at will (Warwick et al. 2019; Mendyk and Warwick 2023). Moreover, snakes regularly adopt near rectilinear postures during daily activity and this need to fully stretch should be a prime consideration in both the design and enrichment of enclosures (Warwick 1995; Warwick et al. 2018a, 2019). In the case of semi-arboreal and arboreal species, this requirement applies to both horizontal and vertical dimensions. The need to wander, explore, and problem solve are no longer traits of endothermic vertebrates alone (see Warwick 2023). It would perhaps be more honest of reptile keepers to acknowledge that typical vivaria are designed for human convenience rather than for the welfare of their charges.

13.3.2 Rack Systems

Considerations (and the lack thereof) regarding the spatio-thermal requirements of reptiles are arguably exemplified in reference to the rack systems used to house large numbers of reptiles (commonly snakes) within a limited area (Warwick et al. 2019; Cadenas and Martínez-Silvestre 2020). Rack systems, which effectively disregard basic principles of reptile biology and responsible husbandry, typically involve individual drawers or tubs, each commonly containing an individual snake. In many cases, a single rack of uniformly sized containers will house snakes of different sizes, indicative of the application of a naïve standardisation of care in regard to species-specific or indeed ontogenetic variation in needs.

The extreme spatial restriction of rack systems results in a myriad of basic husbandry deficiencies. Opportunities for important and effective thermal selection by individuals according to variable physiological need simply do not exist. Instead, occupants are subjected to a largely uniform temperature that is governed and influenced by the physical design of the system, the position of the tub, and the estimates of the manager (Davis 2008). In many cases, the complete rack system is maintained at or close to the ambient temperature of the room with little variation; and both tropical and temperate species may be housed in the same room and subject to the same thermal regime (Davis 2008). Constant temperatures across all enclosures within a single facility or room are not only poor practice, but may result in stress with both short- and long-term welfare issues (Warwick et al. 2018a; Gillingham and Clark 2023). Although localised heating in the form of heat pads, tapes, wires, or probes may be installed, spatial restriction simply does not provide the animals with opportunities to willfully and diversely thermoregulate in order to match normal physiological variation or requirements (Arena and Warwick 1995; Gillingham 1995; Mendyk 2018).

Regardless of how heat is provided for the rack system, the result is thermal entrapment, which likely serves to compromise physiological processes within the individual. A recent study concerning the spatial requirements of snakes itemised 24 signs of captivity-stress (including interactions with transparent boundaries, open mouth breathing and co-occupant aggression), and 22 signs of clinical illness (including rostral abrasions, dystocia, and ventral contact dermatitis) associated with snakes confined to small environments (Warwick et al. 2019).

13.3.3 Space Utilisation: Sociality and Size

For many vertebrates (including fishes) the carrying capacity (stocking density) of the enclosure is often determined by its size or volume. However, as we have discussed, the physical dimensions of an enclosure do not necessarily imply holistic utilisation of every surface or furnishing by the occupant. In addition to satisfying the various aspects of a reptile's biology, meeting the spatial requirements of captive reptiles demands an understanding that these requirements may change as investigations reveal more of the complex nature of reptilian life histories. One such factor is sociality and the housing of individuals with conspecifics (see Doody 2023).

Members of the genus *Egernia* (Family, Scincidae) include highly social species of lizards that regularly form aggregations such as family groups (Duffield and Bull 2002; Chapple 2003; Masters and Shine 2003; Gardner et al. 2007). In some species such as Cunningham's skink (*Egernia cunninghami*), which occupies rocky habitat, family groups are common and individual lizards will selectively choose specific sites where they defaecate (Chapple 2003). These latrines are not utilised for any other purpose, but specifically as sites for 'scat piles', which may act as spatial boundaries or social markers. For example, the pygmy blue-tongued skink (*Tiliqua adelaidensis*) also uses scat placement as a form of chemosensory marker or social signal (Bull et al. 1999, 2000; Fenner and Bull 2010) whilst scat placement by the related Australian sleepy lizard (*Tiliqua rugosa*) appears to have little social value (Fenner et al. 2015). In captivity, although the skink (*E. cunninghami*) may be kept in groups in order to emulate their natural social aggregations, whenever enclosure dimensions are provided, they are rarely of a dimension sufficient for latrines. For example, guidelines provided by Walker (2016) suggested that four adult skinks (*E. cunninghami*) can be maintained in an indoor enclosure with a floor area of approximately 1 m^2; dramatically little space for a reptile that regularly utilises rocky outcrops and crevices and with recorded movements of individuals in the wild of up to approximately 70 m (Barwick 1965; Stow et al. 2001).

As such, severe spatial constraints may result in a form of social dissonance where animals are unable to interpret chemosensory cues or are not provided with enough room to exercise appropriate behavioural responses. Bernheim et al. (2020) found that restrictive captive conditions had a negative impact on reproductive behaviours of spur-thighed tortoises (*Testudo graeca*), proposing that female tortoises failed to emit the chemical cues necessary for initiation of precopulatory behaviour in males. At the very least, a more spacious, semi-natural enclosure was necessary for normal reproductive behaviour in this species (Bernheim et al. 2020). Furthermore, Mancera et al. (2017) showed that blue-tongued skinks (*Tiliqua scincoides*) would try to escape environmental stressors such as noise and cold and, again, smaller enclosures would restrict expression of appropriate stress avoidance behaviour.

It would be erroneous to assume that smaller species and individuals do not always require as much space as larger occupants (Warwick 1995). Smaller individuals may be regularly more active during hunting because of their highly mobile invertebrate prey as well as the exploratory behaviour necessary to locate them; also, smaller individuals feed more frequently and engage in greater predator avoidance and conspecific interactions (see Warwick 1995, 2023). Accordingly, the spatial needs of smaller species and individuals may be underestimated.

It is possible that larger species and individuals must overcome constraints of body size (such as frictional forces) when they are required to hunt or escape. Indeed, it may be energetically costly to accelerate a larger body mass (Higham 2019). However, one must be cautious when attempting to apply generalisations regarding the influence of size on the physiological performance and spatial demands across and within taxonomic groups. For example, within the genus *Varanus* (family Varanidae) (that includes species that vary in size of almost four orders of magnitude), larger species tend to be foragers whilst smaller species tend to adopt a sit-and-wait feeding strategy (Clemente 2006; Clemente et al. 2009). Heavier individuals were also found to have the fastest speed and acceleration although both factors were related to the topography with faster species occurring within open habitat. The form of substrate may also have an influence on performance. For example, Glasheen and McMahon (1996) found that smaller individual basilisks (*Basiliscus basiliscus*) were able to generate greater relative forces that enable them to more effectively run across water than larger conspecifics. In a similar fashion, hatchling green iguanas (*Iguana iguana*) have been observed to 'run bipedally' across water, whereas adults swim (Burghardt et al. 1977). Similar reasoning applies when a lizard is moving quickly across a surface such as soft sand—larger individuals cannot generate the force required to oppose the greater gravitational forces and move themselves efficiently over these surfaces. However, again, within the varanids, substrate type was shown to have no effect on either speed or acceleration (Clemente 2006).

Accordingly, the impact of body size on spatially associated behaviour may be quite complex and is also influenced by foraging mode; for example, a sit and wait predator may not have to move far to acquire prey. Thus, in principle, some sit and wait predators can afford appropriate increases in body size and reproductive state (in most cases, pregnant or gravid females are less active than non-gravid individuals; see Schuett et al. 2013). Therefore, appropriate and adequate space may in fact, be of proportionately greater importance for smaller species and individuals if they are to be permitted to express a 'normal' repertoire of locomotor behaviours.

13.3.4 Overcrowding

Overcrowding may manifest overtly or covertly. Overt overcrowding relates to the plain physically excessive numbers of animals in a given space (Warwick et al. 2013, 2018a; Arena et al. 2014). Overt overcrowding is relatively easy to identify and may result in, for example, crushing injuries, asphyxiation, co-occupant aggression, and competition for food and basking sites. Covert (or crypto) overcrowding may not be as apparent and relates to the inability of all animals in an enclosure to access any one of its features at any one time (Warwick et al. 2013, 2018a; Arena et al. 2014). For example, larger, less populated, enclosures may not appear overcrowded, but may not allow free access for all occupants to use a water container or basking site at one time (i.e. too few or disproportionately small provisions for the number of animals); causing an enclosure to be covertly overcrowded. Both overt and covert overcrowding are often seen at intensive farming facilities of sea turtles (Arena et al. 2014) and most likely to occur in the freshwater turtle farming schemes of China where large quantities of turtles are raised in a multibillion dollar industry, supplying food, medicinal products, and the pet trade (Haitao et al. 2008) and crocodiles (Tosun 2013), when the carrying capacity of an enclosure results in reptiles scrambling or perching on top of each other to access a radiant heat source in order to satisfy thermoregulatory requirements. However, the problem is also observed in zoos (see Almazan et al. 2005), laboratories, the pet trade, and private homes where multiple animals share single poorly conceived environments. As a final point here, when housing more than a single animal, keepers must be familiar with life history traits of captive species, in particular, with managing sex ratios.

Male reptiles, for example, copperhead snakes (*Agkistrodon contortrix*) in the wild may seasonally engage in agonistic rivalry behaviours towards other males (Schuett 1996; see also Doody 2023), and should not be housed together in captivity (Whiting and Miles 2019). This principle also applies to females that may display aggression towards other females (Oonincx and van Leeuwen 2017; Whiting and Miles 2019).

13.3.5 How Much Space Is Enough Space?

It is probable that captive reptiles do not and cannot have enough space to meet their inherently natural and normal needs. Although space is often emphasised as a requirement (e.g. in the housing of tortoises (*Gopherus* spp., *Testudo* spp., *Agronemys* spp., *Centrochelys* spp. and box turtles *Terrapene* spp.)—see Boyer and Boyer 2019), spatial considerations for housing reptiles (particularly indoors) are likely to be governed by keeper convenience rather than species-specific behaviour. Reptiles are commonly maintained in overly restrictive permanent enclosures, but many species are often sold as novelty items along with small housing kits that, whilst satisfying market appeal, impose a severely restrictive environment for the occupant (Warwick et al. 2018b). Of course, there are situations when a small enclosure may be acceptable and indeed, unavoidable. This includes short-term confinement of reptiles, such as for essential clinical, quarantine, or transportation purposes (Warwick 1990a, b; Warwick and Steedman 1995; Warwick et al. 2019), assuming such confinement is for the benefit of the animal. Minimally, space should provide opportunities for expression of an appropriate range of normal behaviours; access to an adequate range of thermal zones; ability to fully extend bodies and travel in any dimension; ability to accelerate, decelerate, and stop without injuriously impacting boundaries; ability to make rapid descents without injury and conditions where spatially related physical injuries and diseases or psycho-behavioural stress signs are absent.

Where appropriate, enrichment and hiding sites should be provided so that an alarmed or otherwise stressed animal may take refuge without the need to resort to uncontrolled flight. An observational study of the spatial requirements of 65 species of snakes found 31 species regularly stretched to full length and adopted rectilinear or near rectilinear postures (Warwick et al. 2019). Thus, snakes, which have long been wrongly assigned especially diminutive enclosures, should, as an absolute minimum, be able to fully extend their bodies within an enclosure when they choose to do so.

Warwick et al. (2018a) proposed a method of determining absolute minimal spatial provision for captive animal (including reptile) enclosure sizes in commercial situations. This process involves visualising the animal in a coiled or rolled ‘ball like’ state and multiplying this estimated dimension by a factor of 10. For arboreal or semi-arboreal species, this same principle would apply to the vertical enclosure dimension. For small species or individuals, a proposed minimum primary dimension was 100 cm with all other dimensions no less than 40% of this (Warwick et al. 2018a). However, this algorithm is intended to indicate absolute minimum enclosure dimension primarily for commercial establishments in order to improve commonly overly minimalistic approaches utilised by those sectors. It should not be confused with aspirational and progressive approaches to accommodation including requirements previously discussed in this chapter.

Providing meaningful space infers more than marginally expanding small quarters; it implies allowing substantial room, in association with naturalistic (or natural) conditions, so that in most cases, the desire or attempt to escape is not created. The spatial requirements of some reptiles (for example, those that exhibit migratory tendencies) may never be fulfilled, even with areas measured in hectares or kilometres. Nevertheless, if allowing sufficient room to cater for animal well-being seems impossible, then it is their very presence in captivity that requires review.

13.4 Thermal Considerations

It could be argued that no organism is entirely independent of ambient temperatures, and as stated earlier in this chapter, for ectotherms, ambient temperature and individual thermoregulation are key factors defining and governing the lives of reptiles (Fernandez et al. 2011; de Andrade 2016; Nowakowski et al. 2018; Taylor et al. 2020). Accordingly, the need for reptiles to express thermal choices is fundamental to their health and welfare (Heatwole and Taylor 1987; Arena and Warwick 1995; Lillywhite and Gatten 1995; Lillywhite 2023). For the majority of reptiles, temperature is regulated primarily through behavioural means, such as shuttling between warmer and cooler areas and to a minor extent, through physiological processes (Sears et al. 2016).

Within this general scheme of ectothermy, most reptiles may be classified as either heliotherms (their prime source of heat being derived from sun-basking) or thigmotherms (their prime source of heat is derived from direct conduction with warm surfaces) (Carter et al. 2012; Garcia-Porta et al. 2019; Lillywhite 2023). However, reptiles, at least diurnal species, likely utilise a combination of these approaches to satisfy their thermoregulatory requirements (Fei et al. 2012), selecting a range of temperatures at any point in their activity cycles in response to specific needs whether on land or, in the case of aquatic and semi-aquatic species, in water. For example, some species of freshwater turtles are able to maintain relatively stable body temperatures via semi-aquatic basking (exposing the carapace to the air whilst submerged) or by aquatic basking (altering their position in response to the vertical temperature stratification within water bodies) (Chessman 2019).

In a similar fashion, sea snakes thermoregulate by ‘tracking’ appropriate temperatures within the water column, whilst the latter, when on land, utilise strategies such as basking and kleptothermy (stealing heat) by sharing burrows with seabirds (Brischoux et al. 2009; Heatwole et al. 2012). The latter behaviour has also been recorded for the tuatara (*Sphenodon punctatus*) (Corkery et al. 2018). In terms of habitat selection, a study of the thermoregulatory behaviour of three species of sympatric Mediterranean lizards (*Podarcis* spp.) found that individuals were able to maintain their preferred body temperatures within narrow limits by moving between microhabitats (patches) of variable thermal quality (Sagonas et al. 2017). Sears et al. (2016) also highlighted the importance of the spatial distribution of 'thermal microclimates' in the regulation of body temperature in spiny-tailed lizards (*Sceloporus jarrovi*).

Key to determinations of this thermal heterogeneity has been the use of physical models in establishing operative temperatures—the temperature to which a non-metabolising object would equilibrate in a particular environment (Bakken and Gates 1975). To determine operative body temperature, various physical models are used to approximate the size, shape, and reflectivity of live animals (Shine and Kearney 2001; Seebacher et al. 2003; Tracy et al. 2007). These predictions take into account heat exchange involving radiation, conduction, and convection (Shine and Kearney 2001).

In captivity, spatial limitations certainly act to reduce this thermal 'landscape' and thus compromise the ability to effectively thermoregulate. As mentioned earlier, the spatial and thermal environments are inextricably linked, and one cannot have much temperature variation if there is little space and reduced structural heterogeneity. In nature, the thermal requirements of a basking reptile in the wild (e.g. heliothermic lizard) are achieved through a combination of modes of heat transfer, all of which would be influenced, not only by the nature and temperature of the primary heat source, but also by the physical nature of the surrounding environment, which acts to provide secondary sources of heat (Angilletta 2009; Kearney et al. 2009; Battles and Kolbe 2018; Battles et al. 2018).

13.4.1 Thermal Gradients and Zones

Contrary to popular claims or aspirations (as evident through current practices in reptile-keeping and fueled by arbitrary husbandry practices; see Mendyk and Warwick 2023; Warwick et al. 2017), it is practically impossible in most captive situations to provide thermal heterogeneity that even approximately matches natural thermal conditions, especially within small enclosures. Even where larger environments are involved, misinterpretation or misjudgement of space versus thermal heterogeneity often arises from presumptions that total linear length (extreme point-to-point within an enclosure) temperature variation provides meaningful variation, whereas total variation in some larger enclosures may register temperature differences of, for example, 15 °C (which may theoretically suit some species), actual usable thermal options (the important feature of gradation) may be diminutive or practically non-existent. Thermal gradation zones (i.e. thermally distinct and behaviourally relevant useable areas of space) infer that each zone is of adequate size to enable one or all of the occupants, at any single time of their choosing, to occupy that zone. Each zone must, therefore, offer a temperature relative to the next higher or lower temperature zone. Thus, a gradient variation of 15 °C may actually include micro-zones of incremental changes that singly are too small to physically accommodate an individual for optimal thermoregulation.

Accordingly, multi-zone thermal environments provide for animals to occupy an entire region of an enclosure that offers important thermal variation, and all zones ought to be of sufficient size and enrichment complexity to accommodate normal behaviour, indeed to encourage normal behaviour. This zonal gradation requires significant space—for example, as proposed here, five thermal gradation zones may require at least five square metres of ground area, which may provide essential thermal conditions for smaller individuals less than 1 m in length (as determined by the range of desired temperatures and intensity/form of the heat source).

Numerous studies have demonstrated the complexity of temperature selection in reptiles. For example, ring-necked snakes (*Diadophis punctatus*) will select temperatures 3 °C higher than their usual preferred temperature when they share sites in aggregations of conspecifics, whereas solitary snakes prefer sites where the temperature is similar to their usual preferred body temperature (Cox et al. 2018). Some species of python are able to metabolically raise their body temperature during incubation of eggs (facultative thermogenesis) (Harlow and Grigg 1984; Stahlschmidt et al. 2011; Brashears and DeNardo 2015), and other reptiles, for example, leatherback turtles (*Dermochelys coriacea*) (Bostrom et al. 2010) and tegu lizards (*Salvator merianae*) (Tattersall et al. 2016), possess limited but distinct endothermal capacity. Also, reproductive state can influence thermal preferences in reptiles, and reproductive success can be dependent on temperature. For example, oviparous species such as the spiny lizard (*Tropidurus spinulosus)* will select higher temperatures when gravid (López et al. 2018). The intensity of courtship in male red-sided garter snakes (*Thamnophis sirtalis parietalis*) has been shown to be directly related to the length of cold temperature dormancy periods (Krohmer 2004).

Finally, it is well known that temperature has a profound effect on reptilian digestion (Plasman et al. 2019) and reptiles will select higher body temperatures when fed than when unfed (Regal 1966; Lang 1979; Sievert 1989). Studies such as these have clear implications for captive animals and require due to consideration of whether animals are housed individually or with conspecifics in addition to the provision of appropriate retreats, refugia, and basking sites (these may include appropriate semi-aquatic sites and sandbanks in the case of turtles and crocodiles).

Despite recognition of the importance of temperature as a key factor governing the lives of reptiles, in captivity, major transgressions of this basic principle occur, leading to failure to identify suboptimal or even detrimental conditions. For example, one phenomenon seen in captive reptiles involves ‘hyperbasking’, which is a state where individual reptiles spend excessive portions of their daily activity budgets basking (Warwick 1995; Warwick et al. 2013). Essentially, hyperbasking typically occurs in several situations, the most common being when a heat source does not provide sufficient heat for an animal to elevate its body temperature to a desired level (Warwick et al. 2013; Benn et al. 2019). Another scenario concerns large individuals in environments where heat sources do not adequately radiate over the animal’s body. In nature, radiant sources (such as the sun) are general and thus can, where required, heat the whole animal. In captivity, heat sources (such as lamps) often can warm only part of an (especially large) animal causing it to prolong basking in an endeavour to elevate the temperature of its entire body. However, not uncommonly in nature, reptiles will partially expose themselves to sunlight, i.e. not their entire bodies (Heath 1964; Seebacher 1999; Gibson et al. 2015; Black et al. 2019).

The logical conclusion from this behaviour is that thermal zones in captive situations should include both areas where the animal can exposure its entire body to heat resources within the thermal zone as well as areas where heat within the zone is more patchy—a 'thermal mosaic', enabling selective heating of particular areas of the body. A further scenario is when an entire thermal zone represents the only acceptable (even if suboptimal) environmental temperature in an enclosure, thus the animal occupies that zone for prolonged periods (Warwick 1990a, 1995). Reptiles may also manifest behavioural fever (elevation of body temperature due to stress or disease) (Kluger 1979; Frye 1991; Cabanac and Gosselin 1993; Cabanac and Bernieri 2000; Warwick et al. 2013; Rakus et al. 2017).

'Hyperbasking' may also occur where an animal unsuccessfully attempts to achieve a higher target temperature, which could incur important reductions in immune competence and homeostasis. Hyperbasking is extremely common in poor conditions of captivity, and seems largely unrecognised by keepers. Many may take for granted seeing reptiles basking for long periods—perhaps on the false presumption that such behaviour is always normal or healthy. However, hyperbasking is now recognised as abnormal and a form of maladaptation, rather than normal thermoregulatory behaviour (Warwick et al. 2013; Mendyk 2018; Warwick 2023). Accordingly, all forms of hyperbasking may be considered as negative thermoregulatory compensation behaviours (Warwick et al. 2013; Warwick 2023).

Thermal needs not only vary in response to physiological requirements (e.g. post feeding), but also seasonally. Here, knowledge of behaviour in the wild becomes crucial to understanding the requirements of reptiles in captivity. Many reptiles will experience seasonal periods of reduced activity, in response to fewer natural resources and metabolic conservatism or as part of their reproductive strategy (e.g. post mating, when there is no longer a need to seek out potential mates) (Bull et al. 1991; Christian et al. 1999; Seebacher 2005; Berg et al. 2017). At these times, provision must be made to enable the captive individual to meet its thermoregulatory requirements. Therefore, adequate space is needed so that thermal inputs can be adjusted—there must be enough room provided to enable the individual to escape heat if required, and this may include the provision of sufficient and appropriate substrate to enable an animal to bury itself or seek other suitable seclusion.

13.4.2 Subtle Thermal Changes May Be Critical

It is widely accepted that subtle differences in thermal conditions can influence a variety of physiological and developmental phenomena in reptiles. For example, immune competence is closely linked to temperature and physiological state, which can result in protective behavioural fever (e.g. Kluger 1979; Frye 1991) or alternatively, disease-associated voluntary hypothermia (Warwick 1991). Also, in species that exhibit temperature-dependent sex-determination, ambient temperature variation of a few degrees can have a pivotal influence on the sex of offspring (Mitchell and Janzen 2010, 2019; Singh et al. 2020). Therefore, thermal environments require gross and subtle variations in order to provide reptiles with essential temperatures for normal life. Furthermore, the conceptual landscape and horizon for these gross and subtle variations are extensive and arguably ought to include relevance to species-specificity, season, physiological state, size, stressors, and diet—each of which requires multiple considerations. These issues highlight the need for a detailed understanding of spatio-thermal requirements of reptiles and for the necessary provision of a wide range of temperatures and multiple thermal zones extending beyond the commonly narrow limits based on presumed preferred body temperatures.

13.5 Animal Welfare Conclusions

Despite growing interest in the welfare of captive reptiles, spatial and thermal considerations for these animals continue to fail to meet biological norms. Whilst there may appear to be progressive provision of recommended standards and guidelines for husbandry, in practical terms, much of this information is not evidence-based, and cannot satisfy all spatio-thermal criteria. Relevantly, when one drills-down into the rationale and 'evidence-base' for both claims and common practices that promote or result in reptiles being confined to their typical spatially minimal vivaria, one quickly discovers a paradigm devoid of scientific merit.

Furthermore, regardless of increasing understanding of spatio-thermal requirements for reptiles, the multimodal influence of space and temperature (and indeed, water—Kearney et al. 2018), and the value of enrichment in improving the welfare of captive reptiles (Londoño et al. 2018), there remains an ongoing tendency among some to disregard important welfare biology—perhaps exemplified by the impoverished constraints of the snake rack system (see Warwick et al. 2019; Cadenas and Martínez-Silvestre 2020). In whatever form, smaller spaces offer fewer opportunities to provide the habitat variation and essential features important to overall health and welfare, and likely directly impose specific stressors (Martínez-Silvestre 2014). Thus, a paradigm shift towards consistently providing larger environments should be a benchmark of best practice. Larger, well-designed enclosures with known thermal gradient mosaics may also offer greater opportunities for understanding species-specific spatio-thermal requirements. For an ectothermic vertebrate, spatial provisions and the physical nature of an enclosure must aspire to allow the animal to manifest its daily and seasonal cycles of preferred body temperatures across a diversity of relevant contexts.

Reptiles may be nocturnal, diurnal, or crepuscular; tropical or temperate; fossorial or arboreal; terrestrial, semi-aquatic, or aquatic with preference for habitats from the topographically very barren to structurally complex with an abundance of retreats. Meeting the spatio-thermal requirements for this highly variable class of animals is particularly difficult given that the biological needs of a large number of species from this group remain poorly understood or investigated (Oonincx and van

Leeuwen 2017). Without this knowledge, it is impossible to confidently provide for spatio-thermal issues in the context of the health and welfare of captive reptiles. However, home range studies demonstrate that reptiles are considerably, often dramatically, more active than frequently presupposed, and there are no good reasons to believe that the wide spaces of nature are not relevant to captive reptile welfare. Furthermore, even with the promise of enrichment, natural behavioural responses cannot be expressed if spatio-thermal requirements are not adequately addressed, and moreover we can be confident that there are many more important spatio-thermal needs than we currently understand.

Regardless of normal sedentary or nomadic traits, animals in nature move around expansive habitats in search and location of appealing environments, and this activity may be regular. Within captivity, the environment is typically predetermined and set, not by climate or natural features, but by characteristics perceived relevant by human custodians. Realistically, the chances are remote that conditions being imposed would match the gross and subtle influences driven by nature. As a result, captive reptiles are forcibly confined and restricted to environments that they would unlikely freely select.

Captivity may be most aptly considered as a situation where animals are effectively trapped, rather than accommodated. Options for an individual animal to select its normal preferences for self-maintenance and well-being are largely removed by its presence in captivity. As captives isolated from normal contextualised regulatory activities, reptiles are fundamentally dependent on the knowledge and practices of their keepers. Accordingly, keepers have an overriding obligation to address all of their charge's positive needs regardless of inconvenience to the manager or to refrain from holding reptiles in captivity.

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