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Exotic Animal Research

Spatial considerations for captive snakes

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ABSTRACT

Captive environments for snakes commonly involve small enclosures with dimensions that prevent occupants from adopting straight line body postures. In particular, the commercial, hobby, and pet sectors routinely utilize small vivaria and racking systems, although zoos and other facilities also commonly maintain at least some snakes under broadly similar conditions. Captive snakes may be the only vertebrates where management policy commonly involves deprivation of the ability and probable welfare need to freely extend the body to its natural full length. In this report, we present background information concerning some relevant physical and behavioral characteristics of snakes, discuss pervading beliefs or folklore husbandry and its implications for animal welfare as well as factors concerning stress, its manifestations and measurement, and provide criteria for the assessment of captive snake welfare. As part of this review, we also conducted an observational component involving captive snakes and report that during 60-minute observation periods of 65 snakes, 24 (37%) adopted rectilinear or near rectilinear postures (stationary 42%; mobile 37%). Of the 31 snake species observed, 14 (45%) adopted rectilinear or near rectilinear postures. Ectomorphological associations, normal behavior, and innate drive states infer that snakes, even so-called sedentary species, utilize significant space as part of their normal lifestyles. We conclude that future policies for snake husbandry require a paradigm shift away from an erroneous belief system and toward recognizing the greater spatial needs of these reptiles.

Introduction

Snakes are commonly kept in captivity in various situations and conditions, including as pets, zoological exhibits, and research animals. Data on numbers of snakes kept across these sectors are not fully available. However, figures indicate that, for example, approximately 200,000 snakes are kept as pets in private homes in the United Kingdom (PFMA, 2018) and 1,150,000 in the United States (AVMA, 2012), and approximately 8,000 snakes are kept in American Zoological Association collections (AZA, 2018).

Historical and current information and beliefs regarding spatial considerations and needs for snakes in captivity vary widely. The commercial, hobby, and pet sectors frequently recommend and utilize vivaria and racking systems for snakes that involve small and highly restrictive enclosures with dimensions that prevent occupants from adopting straight line body postures, that is, extending their bodies to full and unrestricted natural length (for example, McCurley, 2005; Mader, 2006; Gartersnake info, 2013; Hollander, 2018), and many zoos (Nash, 2016; Mendyk, 2018) and other facilities also maintain at least some snakes under similar conditions.

Some nonscientific governmental guidance also broadly claims that enclosures less than the total length of the snake are consistent with their welfare (for example, NSW, 2013; Defra, 2018). Other guidance suggests that certain "active" snakes require enclosures longer than their full body length, whereas more "sedentary" species do not (for example, Kaplan, 2014; Divers, 2018).

In contrast, there exist numerous behavioral research investigations and several scientific and other guidance reports that emphasize that snakes demand as much space as possible as they actively seek and require the ability to fully straighten their bodies as an essential requirement to satisfy the need for behavioral normality, exercise, avoidance of stress and disease, alleviation of physical discomfort, and achievement of physical comfort, among others, and these factors are significant contributors to welfare in

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captivity (Astley & Jayne, 2007; BVZS, 2014; Cannon & Johnson, 2012; Hedley, 2014; Hu et al., 2009; Jepson, 2015; RSPCA, 2018; RVC, 2018a,b; Scott, 2016; Warwick, 1990a,b, 1995; Warwick et al., 2013; Wilkinson, 2015; Warwick, et al., 2018a).

In this report, we present background information concerning some relevant physical and behavioral characteristics of snakes, discuss pervading beliefs or folklore husbandry and its implications for animal welfare as well as factors concerning stress, its manifestations and measurement, provide criteria for the assessment of captive snake welfare, report results of an observational component involving rectilinear or near-rectilinear posturing in captive snakes, and make recommendations regarding minimum housing standards for snakes.

Background

Snakes are universally identifiable elongate-bodied animals that are often observed adopting coiled and straight line or near straight line postures, both during locomotion and at rest (Warwick, 1995). Several types of locomotion have been described in snakes, for example, *rectilinear motion* or *creeping motion* is a caterpillar-like locomotor style commonly adopted by snakes when moving close to straight objects such as fallen trees and rock faces, when stealthily hunting, or where there exists little environmental purchase (Hu et al., 2009; Newman & Jayne, 2017); *concertina locomotion* is a snake locomotor style commonly associated with movement in arboreal habitats where animals are challenged by cylindrical branches or other narrow items or in tunnels where lateral movement is highly limited (Astley & Jayne, 2007; Hu et al., 2009); *sliding behavior* is also used by snakes in arboreal habitats where they must negotiate sharp descents (Astley & Jayne, 2007); *serpentine lateral undulation* is a locomotor style typically adopted by snakes when moving through most habitats (for example, grasslands or bush) that offers good purchase or contact irregularities or when swimming (Shine & Shetty, 2001); *sidewinding* characteristically involves snakes that move diagonally and quickly, usually on hot desert surfaces (Secor et al., 1992). During all of these locomotor styles, the body of the snake commonly approaches a significantly or entirely straightened form, and with respect to rectilinear/creeping motion, concertina motion and sliding behavior, straight line posturing is particularly common. Figures 1-4 provide examples of rectilinear or near rectilinear posturing (n/RLP) (straight line or near straight line/stretched out positioning) as well as attempted n/RLP in captive snakes.

Home range studies demonstrate that while some snakes exhibit relatively sedentary behavior at times, activity levels even in such species may, for example, manifest a four-fold increase at other times (Brito, 2003). As such, even the more sedentary snakes manifestly use significant amounts space when there are appropriate opportunities to do so. Although snake home ranges may be dynamic and are often measured using different field techniques, Table 1 provides examples of the extensive areas occupied by these reptiles.

It is inarguable that both free-living and captive snakes utilize large areas of space and diverse habitat where available and also adopt straight line, rectilinear, stretched-out posturing at will in sufficiently spacious environments, and this may be performed regularly.

Discussion

Folklore husbandry and mythology

Folklore husbandry is a phenomenon referring to a belief system based on typically unscientific, often anecdotal, information communicated via keeper-to-keeper, hobbyist forums and magazines, trade and amateur herpetological groups, and "care sheets" developed by vested interests (Arbuckle, 2010, 2013; Mendyk, 2018; Warwick, 1995; Warwick, et al., 2013). Furthermore, practices that are reported as successful may represent results of individualized husbander goals and not be generally applicable (Mendyk, 2018). Particularly problematic is the issue that scientific evidence and high-level objective data and opinion are frequently overlooked, disfavored, or disregarded by commercial and private snake keepers where it is inconsistent with folklore husbandry (Arbuckle, 2010, 2013; Mendyk, 2018). Although challenging to eradicate, there are current efforts by the scientific herpetological community aimed at replacing folklore husbandry with evidence-based practice (Arbuckle, 2010, 2013; Mendyk, 2018).

Common justifications for spatially minimalistic enclosures and husbandry practices involving snakes in general are based on a number of beliefs, including that snakes are sedentary, insecure in large environments, do not use space, suffer from agoraphobia (anxiety related to open spaces) and anorexia, and further that snakes thrive in small spaces, and feed, grow, and reproduce well (for example, Bartlett & Bartlett, 1999; Engler, 2010; Iherp, 2011; McCurley, 2005; Pets4Homes, 2018; Reddit, 2015; TBC, 2018). However, these views are not universal among herpetologists, herpetoculturalists, and other snake keepers (for example, Mendyk, 2018; Rose et al., 2014; Silvestre, 2014).

Figure 1. Aquatic rectilinear motion: python (*Python* sp.) in zoological conditions. (Image credit: C. Warwick).

Figure 2. Terrestrial near rectilinear motion: milk snake (*Lampropeltis* sp.) in hobbyist/private conditions. (Image credit: C. Warwick).

Claims regarding sedentarism and spatial insecurity are poorly considered by many keepers. For example, in highly exposed areas, many species will naturally utilize local cover during locomotion or seclude themselves in small or tight refuges at rest, but such behavior constitutes only part of overall activity budgets (Gillinghan, 1995; Mendyk, 2018). Agoraphobia is a human anxiety condition and not recognized in snakes (Warwick, et al., 2013). Extensive natural home ranges, as outlined previously, dismiss notions that snakes do not use space. Indeed, were snakes truly both sedentary and agoraphobic then keepers would require no vivaria frontage or lids and could open all enclosures confident that snakes would not leave the proposed security of their cages. However, snakes will freely leave their enclosures when permitted to do so and they are known for their abilities to escape captive environments.

Established captivity-stress–related behaviors are also commonly associated with snakes in small enclosures (Warwick, 1990a,b, 1995; Warwick et al., 2013); thus claims that these animals are thriving lack balance. In contrast, snakes are known to function more successfully in larger, naturalistic environments (Warwick, et al., 1995; Wilkinson, 2015).

Regular feeding and breeding is frequently also reported in association with captivity-stress where energy may be redirected toward basic biological functions (Warwick, 1990a,b, 1995; Broom & Johnson, 1993; Moore & Jessop, 2003), which may result in

Figure 3. Concertina motion: kingsnake (*Lampropeltis* sp.) in hobbyist/private conditions. (Image credit: C. Warwick).

Figure 4. Attempted rectilinear motion: python (*Python* sp.) in pet 'fair', 'expo' 'market' conditions. (Image credit: ProWildlife/Animal Protection Agency).

reproductive exhaustion or obesity, and thus these factors are not reliable indicators of good welfare.

It is arguable that highly restrictive enclosures in some respects may offer limited prevention against certain potentially welfare-negative situations. For example, ease of cleaning associated with the minimalistic conditions of racking systems (McCormack, 2015; Warwick, 2015) may prevent accumulation of particular potentially pathogenic wastes and microbes. In addition, nontransparent opaque plastic or wood boundaries prevent the highly problematic behavior known as interaction with transparent boundaries (Warwick, 1990a), and thermal burns are avoided where no direct heating sources are used (Mendyk, 2018). However, diminutive enclosures and racking systems are also known to be associated with their own suite of particular management, observation, and hygiene problems, as well as stressors and diseases (McCormack, 2015; Warwick, 1990a,b, 1995; Warwick et al., 2013; Warwick, 2015) (see also Tables 2 and 3). Therefore, it is also arguable that the potential benefits of minimal housing are artificial and ingenuine.

The scientific community generally accepts that snakes require the provision of enriched captive environments (Burghardt, 2013; Funk, 2006; Vosjoli, 1999; Warwick, 1990a,b, 1995; Warwick & Steedman, 1995; Warwick et al., 2013; Wilkinson, 2015). In contrast, the minimalistic enclosures, as used by numerous commercial snake breeders and some private collectors, impose no or extremely limited enrichment on their occupants, resulting in controlled deprivation (Burghardt, 2013) and negative health implications (Mendyk, 2015, 2018; Morgan and Tromberg, 2007; Warwick et al., 2013). The accepted scientific and rational view that snakes require enriched lives and the view that those kept without enrichment also experience good welfare, constitute mutually exclusive perspectives.

Evolutionary considerations

As with all organisms, the principle of form follows function through the process of evolution explains the elongate morphology of snakes—they are the way they are because it is necessary. Ectomorphological associations (i.e., morphology and behavior in the environment) are also inextricably linked, thus the evolutionary biology of snakes requires that their bodies are able to do what is normal. Furthermore, because snakes, like all reptiles, are greatly governed by innateness, behaviors and needs are substantially hard wired or preset, regardless of whether an animal is free-living or captive-bred (Arbuckle, 2013; Burghardt 2013; Warwick, 1990, 1995; Warwick et al., 2013). In addition, being ectothermic, environmental temperatures and behaviors are fundamentally linked, and where imposed thermal regimes and gradients are insufficiently complex or fail to satisfy basic thermoregulatory needs, behavioral expression, including activity patterns, is constrained (Rose et al., 2014; Wilms et al., 2011) (for example, providing a false indicator of sedentarism).

It is valid to argue that normal behavior includes offensive and defensive activities, and that these are not necessarily desirable, and indeed often disfavored, in captivity because of their association with stressors and injuries among co-occupants (Homer, 2006; Warwick, 1990a,b, 1995; Warwick et al., 2013; Wilkinson, 2015). Relatedly, some may consider that straight line posturing is also unnecessary in captivity, despite being normal behavior.

However, in nature, offensive and defensive behaviors are fundamental survival and reproduction features (including prey acquisition, predator avoidance, courtship, territorial, or group hierarchies), involving extreme elevated physiological and physical responses consistent with occasional acute challenges or stress (Gillinghan, 1995), whereas straight-line posturing is typically part of a quiescent behavioral repertoire as experienced by snakes in a regular daily context (Warwick, 1990a, 1995). Importantly, in nature, almost limitless space allows opportunities for withdrawal or escape in many situations (Gillinghan, 1995; Silvestre, 2014). In captivity, major spatial limitations dramatically alter the encounter-avoidance possibilities thereby effectively intensifying the dynamic of potentially harmful consequences and raising the undesirability of offensive and defensive behaviors, making otherwise natural

Table 1
Example home range occupations for snakes

Species	Home range	Source
Lataste's viper (*Vipera latastei*)	0.24 ha-1.52 ha	Brito (2003)
Northern pine snake (*Pituophis melanoleucus melanoleucus*)	59.9 ha with core areas averaging 7.9 ha, snakes traveled 273 m per move	Gerald et al. (2006)
Great Plains rat snake (*Elaphe guttata emoryi*)	3.98 ha-26.95 ha (average of 10.17 ha)	Sperry & Taylor (2008)
Black pine snake (*Pituophis melanoleucus lodingi*)	92-396 ha, with single movement events of 338m	Baxley and Qualis (2009)
Timber rattlesnake (*Crotalus horridus*)	21.1 ha-39 ha	Hamilton (2009)
Florida pine snake (*Pituophis melanoleucus mugitus*)	59.2 ± 50.8 ha	Miller et al. (2012)
Indigo snake (*Drymarchon corais*)	33 ha and 1,528 ha	Hyslop et al. (2013)
Indigo snake (*Drymarchon couperi*)	44 ha-76 ha and 156 ha-202 ha for males and females, respectively	Breininger et al. (2011)
Burmese python (*Python molurus bivittatus*)	22.5 km^2	Hart et al. (2015)

Table 2
Behavioral signs of captivity-stress associated with confinement of snakes in overly restrictive enclosures

Issue	Possible cause	Sign
Interaction with transparent boundaries (ITB)	Related to exploratory and escape activity. Self-compounding and destructive. Inherent psychological organization and adaptational constraints result in failure to recognize abstract invisible barriers.	Persistent (up to 100 percent activity period) attempts to push against, crawl up, dig under or round the transparent barriers of enclosure.
Hyperactivity	Often associated with ITB. Overcrowding. Self-compounding and destructive. Common in overly restrictive, deficient, and inappropriate environments.	Abnormal high-level physical activity, surplus, or redundant activity.
Hypoactivity	Too low temperature, infection/organic dysfunction, falling, dropping, co-occupant attack, transport trauma, occupant harassment.	Hypothermia, disease, injury, pain, co-occupant harassment.
Anorexia	Too low temperature, infection/organic dysfunction, falling, dropping, co-occupant attack, transport trauma, occupant harassment.	Hypothermia, disease, injury, pain, co-occupant harassment.
Hyperalertness	Often related to fear/stress, defense, and escape behavior. Common in overly restrictive, and exposed, deficient, and inappropriate environments.	Abnormal high level of alertness "nervousness" to environmental stimuli.
Rapid body movement	Often related to fear/stress, defense, and escape behavior. Common in overly restrictive, and exposed, deficient, and inappropriate environments.	Abnormal "jerky" locomotor or jumping action.
Flattened body posture	Often related to fear/stress, defense, and escape behavior. Common in overly restrictive, and exposed, deficient and inappropriate environments.	Flattening of body against a surface often combined with hyperalertness.
Head-hiding	Often related to fear/stress or ambient light/photo stress behavior. Common in overly restrictive and exposed (including excessive ambient light for nocturnal species), deficient, and inappropriate environments.	Deliberate seclusion of head including under objects or substrate.
Inflation of the body	Often related to fear/stress, defense, and escape behavior. Common in overly restrictive and exposed (including light for nocturnal species), deficient and, inappropriate environments.	Deliberate (often repeated) inflation and deflation of the body. May or may not be associated with "hissing" sound.
Hissing	Often related to fear/stress, defense, and escape behavior. Common in overly restrictive and exposed (including excessive ambient light for nocturnal species), deficient, and inappropriate environments.	Hissing sound, accompanied with deliberate repeated inflation and deflation of the body.
Co-occupant aggression	Often related to courtship routines, inability to avoid cage-mates when required, overly restrictive, and exposed deficient and inappropriate environments. Hunger.	Aggressive or defensive displays, biting, chasing cage mates.
Human-directed aggression	Often related to fear/stress, defense, and escape behavior. Common in overly restrictive and exposed (including excessive ambient light for nocturnal species), deficient, and inappropriate environments.	Mock/real strikes.
Clutching	Often related to fear, stress, or ambient light/photo stress behavior. Common in overly restrictive and exposed (including light for nocturnal species), deficient, and inappropriate environments.	Snake tightly grasps human or object.
Death-feigning	Often related to fear/stress.	Animal (commonly snake) appears limp, upside-down, unconscious.
Loop pushing	Often related to fear, stress, or ambient light/photo stress behavior. Common in overly restrictive and exposed (including light for nocturnal species), deficient, and inappropriate environments.	Snake uses "arch" of body to resist/deflect physical contact from cage-mate or human.
Freezing	Often related to fear, stress, or ambient light/photo stress behavior. Common in overly restrictive, deficient, and inappropriate environments.	Eye contact with or general presence of observer results in freezing posture/tense immobility.
Hesitant mobility	Often related to fear/stress. Common in overly restrictive, inappropriate environments.	Animal uncharacteristically moves in "fits and starts".
Wincing	Often related to fear/stress. Common in overly restrictive, inappropriate environments. Pain, disease.	Hypersensitivity to minor stimuli causing retraction of head, limbs, or tail.
Open mouth breathing	Hyperthermia, infection/organic dysfunction/disease, major head/neck injury, falling, dropping, co-occupant attack, transport trauma.	Sporadic, usually slow, open-mouth respiration or gasping
Cloacal evacuations when handled	Often related to fear/stress.	Urination, defecation, excretion of malodorous substance from cloaca.
Projection of penis or hemi-pene	Often related to fear/stress.	Projection of penis or hemi-pene associated with human presence or contact.
Voluntary regurgitation of food	Often related to fear/stress.	Regurgitation of food associated with human presence or contact.
Venom spitting	Often related to fear/stress.	Venomous snakes ejecting venom associated with human presence or contact.
Atypical locations	Often related to disease, injury, discomfort, co-occupant aggression, hyperthermia, hypothermia.	Reptile occupies an atypical location for an unusual amount of time or other unusual context (eg, an arboreal snake on cage floor).

(Adapted and modified from: Warwick, C., Arena, P.C., Lindley, S., Jessop, M. and Steedman, C. [2013] Assessing reptile welfare using behavioral criteria, *In Practice*, 35:3 123-131doi:10.1136/inp.f1197)

behavior a problem in captivity, caused by captivity (Howell & Bennett, 2017; Silvestre, 2014; Warwick, 1990; Warwick et al., 2013). Nevertheless, some captive snakes deprived of live food have been reported to redirect aggression toward co-occupants and human keepers, indicating that pursuit of prey may in some situations be an ethological need (Burghardt & Denny, 1983; Warwick, 1990a,b, 1995).

Nocturnality is an important issue associated with welfare assessment (Warwick et al., 2018a). Being commonly nocturnal, snakes are typically at rest and relatively inactive when observed by their keepers. Nocturnality in species raises important welfare concerns in that the contrasting activity patterns with humans may have negative influences on rest cycles and also implies that normal monitoring for problematic behavioral signs are, as a consequence, regularly confounded (Warwick, et al., 2018a).

Behavioral versus physiological assessments of captivity stress

Behavioral observation of snakes monitors normal or abnormal activities and their contexts. Numerous behavioral signs are

Table 3
Reported clinical and physical problematic issues and signs associated with confinement of snakes in overly restrictive enclosures (in particular = less than 1 x snake straight line length and "racking" systems)

Issue	Possible cause	Sign
Rostral abrasions	Friction associated with repeated attempts at escape.	Inflamed or necrotized lesion on tip of snout, systemic disease.
Ventral contact dermatitis	Insufficient ground space and accumulation of excessive substrate moisture.	Inflamed or otherwise discolored ventral or ventro-lateral skin, systemic disease.
Over feeding	Understimulation, insufficient exercise, excessive food.	Obesity, disease.
Dystocia	Physiological deficiencies, improper thermal, humidity and nesting facilities, overcrowding.	Egg or fetal retention and associated behaviors, disease.
Opportunistic infections	Immune suppression.	Disease.
Respiratory issues, disease	Poor ventilation, inappropriate humidity, low air-lung clearance, immune suppression.	Infection.
Set constant or minimally varied thermal conditions or insufficient thermal gradients	Inability to thermoregulate.	Hypoactivity, hyperactivity, other stress-related behaviors, disease.
Suboptimal lighting and	Inability to maintain normal activity patterns.	Hypoactivity, hyperactivity, other stress-related behaviors, disease.
UV deficiency	Inability to convert UV influences to vitamin D.	Disease, hypovitaminosis D.
Excessive reproduction	Understimulation.	Atypically frequent clutches/neonates.
Reproductive underperformance/sterility	Multiple stressors.	Atypically infrequent clutches/neonates.
Parasitic infestations	Close contact housing.	Parasite presence, disease.
Contagion risk	Close contact housing.	Epidemiological outbreaks.
Bite injuries	Feeding live food in minimalistic space.	Injury lesions.
Inappropriate substrata	Substrate ingestion.	Distension of gut, obstipation, constipation, anorexia, sudden loss of condition.
Insufficient volume of substratum.	Inability to "burrow" to depth appropriate for species.	Hyperactivity, hypoactivity, inappetence; decline in general condition; gastro-intestinal disorders.
Insufficient enclosure height	Inability to climb.	Hyperactivity, hypoactivity, and/or attempts to hide.
Inadequate and/or inappropriate cage furnishings, including excessively small cages.	Physical and psychological understimulation.	Hyperactivity, hypoactivity anorexia, absence of mating activity, excessive mating activity.
Potential issues of additional concern		
Bowel constipation and obstipation risk	Inability to properly uncoil and defecate.	Defecation infrequency.
Glandular overfilling and dysfunction	Underactivity and reduced mobility.	Disease.
Cloacal and hemipenis disorders or urinary tract disease	Underactivity and reduced mobility.	Disease.
Musculoskeletal disorders, compromised spinal articulation, and degenerative joint disease of the spinal joints	Underactivity and reduced mobility.	Disease.

(Derived from: Warwick, et al., 1995; Jepson, 2015; McCormack, 2015; Wilkinson, 2015; Oonincx & van Leeuwen, 2017; Warwick et al., 2018a; and consultation with expert clinicians.)

commonly associated with negative acute and chronic states, including injury, disease, disturbance, co-occupant aggression, as well as those defined by attempts to avoid or escape captive conditions (Arena et al., 2012; Chiszar et al., 1995; Gillinghan, 1995; Greenberg, 1995; Guillette et al., 1995; Mancera et al., 2017a; Warwick, 1990a,b, 1995; Warwick et al., 2013; Warwick et al., 2018a) (see also Tables 2 and 3). As discussed elsewhere in this report, fundamental underlying causes of stress are highly variable and present accordingly, whether due to factors including malnutrition, poor thermal regimes, or spatially overly restrictive environments. Behavioral indicators of captivity stress typically and significantly resolve with alteration of captive provisions to include more naturalistic environments and greater space, confirming the importance of behavioral indicators as stress markers (Warwick, 1990a,b, 1995). In addition, behavioral observations, rather than physiological assessments, of stress are typically noninvasive and allow for more objective investigation.

Physiological monitoring involves obtaining blood, fecal, and other physical samples to test for stress-related levels of relevant hormones, notably corticosterone (Guillette et al., 1995; Moore & Jessop, 2003; Silvestre, 2014; Warwick et al., 2013). Under controlled experimental conditions as well as targeted clinical veterinary assessment, physiological parameters can provide important indicators of certain stressors and particular health states in reptiles (Dupoué et al., 2018; Frye, 1991; Mancera et al., 2017a).

It has been suggested that physiological measurements are a useful alternative to behavioral observation for assessing stress in snakes, while also recognizing significant interpretational limitations with the physiological approach (van Waeyenberge et al., 2018). Impacts from physiological monitoring on snakes vary, for example, blood sampling is invasive because of handling and needle extraction and may itself elevate blood corticosterone values, whereas fecal sampling is noninvasive because of collection of organic detritus (Moore & Jessop, 2003; Silvestre, 2014; van Waeyenberge et al., 2018; Warwick et al., 2013).

Sampling physiological parameters under natural conditions may occur against a background of noncontext-specific scenarios and multifactorial or nondetermined histories (Silvestre, 2014). For example, all physical sampling may be affected by seasonality, age, sex, body condition, or reproductive state (among other factors), fecal values may be affected by diet, and ecdysis samples may reflect medium- and not recent-term histories (Angelier and Wingfield, 2013; Moore & Jessop, 2003; Silvestre, 2014; van Waeyenberge et al., 2018; Warwick et al., 2013). Thus, these various sampling factors may potentially impact on normally important scientific controls and affect relevance for extrapolation to snakes under abnormal and artificial situations.

Comparing acute or chronic stress under natural versus artificial conditions may be mutually incongruent for important contextual reasons. In nature, stressors manifest transiently within evolved frameworks, and thus occur against a background of generalized normality (Gentsch et al., 2018; Warwick, 1995). In captivity, stressors are often consistent with maladaptation and inconsistent with evolved coping mechanisms as well as a lack of normalizing recovery opportunities (Warwick, 1995).

Relatedly, there exists a dearth of baseline physiological data, especially for the large diversity of species involved, implying that meaningful normal and abnormal physiological values can be difficult to ascertain or apply (Moore & Jessop, 2003; Silvestre, 2014; van Waeyenberge et al., 2018; Warwick et al., 2013). In humans, for example, where vast data are known for physiological states, studies reveal that although cortisol may be mediated by factors including agitation-related stimuli, other states including generalized stress, anxiety, and depression may not increase cortisol (van Eck et al., 1996). Studies concerning the effects of noise on mice found that stress resulted in reduced corticosterone, while behavioral stereotypes increased indicating that stress had already created a behavioral "coping mechanism" to reduce physiological activation (Mancera et al., 2017b).

In our view, physiological complexity, impracticality as a regular means of assessment, baseline data reference deficiencies, evolutionary relevance, problematic contextualization and interpretation, invasiveness for some procedures, and situation- and temporal-specific sampling biases undermine generalized physiological monitoring of stress in snakes. In contrast, behavioral assessment constitutes the primary objective method for evaluation of stress and welfare of snakes in captivity and may help to avoid underascertainment of captivity stress (Moore & Jessop, 2003; Silvestre, 2014; Warwick et al., 2013).

Confinement, captivity-stress, injury, and disease

Snakes are known to manifest a wide range of behavioral and morbidity problems related to their captive conditions and husbandry, many of which are very common and persistent (Frye, 1991, 2016; Homer, 2006; Mader, 2006; Oonincx & van Leeuwen, 2017; Pilny, 2015; Warwick, et al., 1995; Whitehead, 2018; Wilkinson, 2015). Objective scientific studies reveal high mortality rates among captive reptiles (including snakes), for example, 41% at 10 days relating to the commercial sector (Ashley et al., 2014) and 75% annually in the private home (Toland et al., 2012). Prevalence and specificity of behavioral and physical problems, morbidities, and mortalities related to overly restrictive enclosures are generally unavailable in documented form. For many if not most commercial and other breeders or producers of snakes, documentation of serious welfare issues or captivity-related disease, injury or death may both equate to an admission of management failure and also

Figure 5. Example of a racking system in which many snakes are commonly confined. (Photo credit: PETA).

Figure 6. Close view of a racking system enclosure showing a Royal (`ball') python (*Python regius*) under minimalistic spatial and other provisions. (Photo credit: PETA).

attract legal consequences (Warwick et al., 2017). Therefore, between possible misinterpretation of numerous behavioral and physical signs and particular transparency concerns, it may be appropriate to regard overly positive anecdotal reports relating to snake welfare in diminutive enclosures and racking systems with a degree of circumspection. Accordingly, the lack of reliable information from the commercial and private sectors may represent serious under-reporting of minor and major problematic issues associated with truth telling surrounding sensitive topics (Moorhouse et al., 2017; Warwick et al., 2017). Figures 5–7 provide examples of a racking system.

Behavioral and clinical considerations

Table 2 provides a list of primarily behavioral signs of captivity-stress associated with confinement of snakes in overly restrictive environments. Table 3 provides a list of primarily clinical signs associated with confinement of snakes in overly restrictive enclosures. Although the problematic issues listed in Table 3 manifest in both larger and smaller captive conditions, these issues most likely increase with decreased space (Rose et al., 2014).

Temporary, transient, and permanent conditions

It is generally recognized that snakes, as for many other animals, may be held under temporary conditions that would not be acceptable for longer-term accommodation (Warwick, 1990b; Warwick & Steedman, 1995). Acceptable conditions include clinical situations where snakes may be undergoing veterinary observation or treatment, some quarantine protocols, efficient transportation, and in some experimental field and laboratory situations (Warwick, 1990b; Warwick & Steedman, 1995). Reasonably acceptable periods for temporary conditions may be said to involve durations of hours or days. Some exceptional scenarios, such as long-term quarantine for purposes of biosecurity, are justifiable transient accommodation, and in such situations, animals should be afforded permanent style environments where feasible (Miller, 1996; NRC, 2011; Pough, 1991; Warwick, et al., 2018a). Examples of unacceptable temporary conditions include days, weeks, or months during storage at commercial wildlife collection, export, import, wholesale and retail sites, and itinerant events known as pet fairs, expos, or markets (Arena et al., 2012).

Figure 7. Inside of a racking system enclosure showing a Royal (`ball') python (*Python regius*) under minimalistic spatial and other provisions. (Photo credit: PETA).

Table 4
Rectilinear or near rectilinear posturing (n/RLP) in captive snakes during approximately 60 minutes diurnal observation periods

Location	No. of enclosures capable of accommodating snake rectilinear or near rectilinear posturing	No. of snakes displaying rectilinear or near rectilinear posturing	Snake stationary = *s*; snake mobile = *m*; not recorded = -
Facility 1	7	2	*s x 2*
Facility 2	9	5	-
Facility 3	15	8	*m x 5/s x 3*
Facility 4	14	3	*s x 3*
Facility 5	7	3	*m x 2/s x 1*
Facility 6	9	2	*m x 2*
Facility 7	1	1	*s x 1*
Facility 8	3	0	
Total 8	Total 65	Total 24 (37%)	Total *s* = 10 (42%) Total *m* = 9 (37%) Total - = 5 (21%)

Observational component

As part of this report, we conducted an observational component to assess prevalence of rectilinear or near-rectilinear posturing (n/RLP) among captive snakes.

Methods

We conducted observations for approximately 60-minute diurnal periods at eight zoological facilities in the United Kingdom and Canada to estimate the possible prevalence of n/RLP in captive conditions capable of allowing straight line behavior. Three observers used scan sampling that involved each animal being revisited within an approximately 60-second time period. A pilot test-run at two sites (facilities 1 and 2 of Table 4) was conducted to crosscheck and verify note-taking consistency, and still image cameras were used to record relevant postures among captive snakes. Although circadian observations would have been preferable, access to zoological facilities was limited to diurnal periods. Although rectilinear, concertina, and other snake postures may be categorized as separate and distinct, all can involve straight line or near straight line posturing. Thus our recording of n/RLP includes any displayed behavior resulting in straight line or near straight line posturing. To estimate whether an enclosure possessed at least one dimension capable of allowing a snake to fully extend its body or straight line posture, we assessed the primary length of all snake enclosures, visually located snakes, and then utilized the 10 X coiled body-size diameter rule (Warwick et al., 2018a) to establish an approximate length for each snake. If snakes could not be visualized sufficiently, these enclosures were not further assessed. Snakes displaying n/RLP were also recorded as being either stationary (s) or mobile (m) to acknowledge whether the animals were active or at rest, and where not recorded as (-).

Table 5
List of all species of captive snakes observed and species displaying rectilinear or near rectilinear posturing (n/RLP)

Species range observed		Species displaying rectilinear or near rectilinear posturing	
Common name	Scientific (family) name	Common name	Scientific (family) name
Amethystine python	*Morelia* sp.	Black and white rat snake	*Pantherophis* sp.
Black-headed python	*Aspidites* sp.	Black-headed python	*Aspidites* sp.
Black and white rat snake	*Pantherophis* sp.	Black mamba	*Dendroaspis* sp.
Black mamba	*Dendroaspis* sp.	Boa constrictor	*Boa* sp.
Blanchard's kingsnake	*Lampropeltis* sp.	Burmese python	*Python* sp.
Boa constrictor	*Boa* sp.	California kingsnake	*Lampropeltis* sp.
Bornean blood python	*Python* sp.	Carpet python	*Python* sp.
Bredl's carpet python	*Morelia* sp.	Green anaconda	*Eunectes* sp.
Bullsnake	*Pituophis* sp.	Green mamba	*Dendroaspis* sp.
Burmese python	*Python* sp	Monocled cobra	*Naja* sp.
Californian kingsnake	*Lampropeltis* sp.	Red tailed racer	*Gonyosoma* sp.
Carpet python	*Python* sp.	Reticulated python	*Python* sp.
Corn snake	*Pantherophis* sp.	Royal/ball python	*Python* sp.
Dumeril's boa	*Acrantophis* sp.	Western hognose snake	*Heterodon* sp.
Eastern diamond-back rattlesnake	*Crotalus* sp		
Emerald tree boa	*Morelia* sp.		
Eyelash viper	*Bothriechis* sp.		
Green anaconda	*Eunectes* sp.		
Green mamba	*Dendroaspis* sp.		
Honduran milk snake rattlesnake	*Lampropeltis* sp.		
Indigo snake	*Drymarchon* sp.		
Jamaican boa	*Epicrates* sp.		
Madagascan tree boa	*Sanzinia* sp.		
Monocled cobra	*Naja* sp.		
Puff adder	*Bitis* sp.		
Red-tailed racer	*Gonyosoma* sp.		
Reticulated python	*Python* sp.		
Royal/ball python	*Python* sp.		
Spectacled cobra	*Naja* sp.		
Thai cobra	*Naja* sp.		
Western hognose snake	*Heterodon* sp.		
Species range observed no.	**31**	**Species displaying rectilinear or near rectilinear posturing no.**	**14 (45%)**

Table 6
Summary of essential absolute minimum containment conditions for snakes

Provision	Rationale
Minimum space of 1x snake length in primary linear, and for arboreal species also vertical, dimension; no other dimension to be les than 40% of primary dimension.	Allows fundamental rectilinear behavior associated with locomotion, comfort, and avoidance of discomfort.
All facilities must recognize the crypto-overcrowding principle.	Allows for adoption of crypto-overcrowding principle = all animals must be able to use any facility/furnishing (e.g., water bowl, bathing pool, perch, hide, basking site) at any one time.
Naturalistic furnishings where relevant to species natural history.	Allows for relevant, physical, psychological and behavioral stimulation, as well as appropriate multiseclusion opportunities.
Thermal gradient range relevant to species natural history with built-in safety margins of approximately 5 °C.	Allows for normal critical regulation of body temperature according to current physiological and behavioral requirements.
Lighting periodicity relevant to species natural history.	Allows for relevant photostimulation and avoidance of photo-invasive conditions.
UV lighting.	Allows for normal physiological conversion of energy to essential nutrients and control of ectomicrobes.
Nocturnal observation for relevant species.	Allows for relevant welfare inspection during species normal activity period.
Naturalistic substrate where relevant to species natural history.	Allows for key normal environmental interaction and balanced cleanliness.
Water pool(s) of sufficient size, including depth.	Allows for drinking, bathing, or swimming for relevant species.

(Adapted and modified from: Jepson, 2015; McCormack, 2015; Warwick, et al., 1995; Mellor, 2012, 2015; Wilkinson, 2015; Warwick et al., 2018a.)

Results

The total number of snakes that were visualized in enclosures to determine their capability to adopt straight line postures by rectilinear or near rectilinear behavior was 65. The total number of snakes adopting n/RLP was 24(37%). The total number of species observed was 31. The total number of species adopting n/RLP was 14(45%). Table 4 provides a breakdown of the observation-based data. Table 5 provides a list of all species observed and species displaying rectilinear or near rectilinear posturing (n/RLP).

Given that our observations were of relatively short duration (approximately 60 minutes per location) and conducted during diurnal periods, the finding of 37% prevalence for n/RLP among snakes is significant, and we anticipate that these data are probably minimally representative of actual n/RLP prevalence. We propose that within a 24 hour period, most snakes, regardless of species, would exhibit n/RLP where housed in permissible enclosures. In addition, the presence of significant rectilinear or near rectilinear postures across a wide range of species, including those with reportedly highly sedentary lifestyles, further contradicts anecdotal claims and belief-based husbandry concerning spatial needs of snakes. The variable proportionality of total number of enclosures capable of accommodating snake straight line/rectilinear posturing versus number of snakes displaying rectilinear or near rectilinear posturing among different study locations may be explained by varied husbandry routines such as feeding times and lighting, as well as visitor-related noise and other disturbances. Both stationary and mobile n/RLP (42% and 37%, respectively) in snakes indicated that straight or near straight line posturing is important in both resting and active animals.

Conclusions

We believe that this introductory investigation may be the first of its kind to examine near-rectilinear or rectilinear behavior in captive snakes, and that future research involving circadian time budget observations may prove helpful to further evaluate n/RLP prevalence.

Ectomorphological associations, behavior, and innate drive states confirm that snakes utilize and biologically need considerable space as part of their normal lifestyles. However, captive snakes may be the only vertebrates where management policy commonly involves deprivation of the essential ability and welfare need to voluntarily straighten their bodies. Spatial deprivations routinely imposed on snakes would be unacceptable for any other vertebrate species, and while larger enclosures may represent significant inconveniences for many snake breeders and keepers, current common approaches to accommodation for many snakes are scientifically and ethically unjustifiable. Other than for short-term confinement such as clinical or essential transportation purposes snakes should not be held in enclosures with dimensions that do not permit these animals to fully extend their bodies, including both horizontally and vertically where semi-arboreal or arboreal species are involved.

Erroneous folklore husbandry has long governed snake, and other reptile, keeping practices. Although many of the best zoos and some other facilities and individuals may provide flagship housing for snakes (although these likely still represent a vast reduction in terms of spatial requirements and natural homes ranges), it remains commonplace for others, in particular the commercial, hobby, and private pet keeping sectors, to confine snakes in overly restrictive environments that are substantially inconsistent with their biological needs or the basic provisions of the Five Freedoms (FAWC, 2009; Mellor, 2012) or the Five Welfare Needs (RSPCA, 2005).

Snake-keeping practices typically demonstrate a recurring generalized animal husbandry problem that left uncorrected over time "bad practices become normal" (Silinski et al., 2016). The normalization of numerous misperceptions, beliefs, false-facts, and bad practices in snake keeping constitutes a major obstacle to good welfare. To what extent either scientific ignorance or practical convenience governs many snake-keeping habits is unclear. There is good evidence to show that uptake of objective information by exotic pet sellers and keepers is poor (Howell & Bennett, 2017; Kohler, 2010; Moorhouse et al., 2017; Pees et al., 2014; Warwick et al., 2018b).

Essentially, n/RLP posturing is integral to normal and desirable behavior and should be regarded as being as fundamental for healthy activity as other accepted essential ethological needs as well as avoidance of abnormal behavior and ill-health (Warwick, 1990a,b; Warwick et al., 2013; Scott, 2016). Captive birds are expected to be able to fully extend (stretch) their wings, and whether or not some birds elect to perform this behavior, the requirement is generally accepted, and for instance in the UK, enshrined in law (WCA, 1981). Relatedly, there is no scientific reason for failing to allow all snakes the comparable ability to straighten their bodies whenever they wish to do so, and a zero-tolerance position should be adopted toward enclosures less than the total length of the snake.

Future policies for the care of these animals require a paradigm shift away from folklore husbandry and toward recognition of the behavioral and ecological complexities of these reptiles. Given that folklore husbandry appears to be ingrained in both practice and attitude among snake keepers, it follows that targeted education of husbanders alone is unlikely to attract relevant changes in snake care. Accordingly, it may be necessary for governmental authorities to stipulate policies for minimum spatial requirements and general husbandry as outlined in this report, as well as formalize obligations within legal frameworks.

Recommendations

The authors do not suggest that snakes can be readily (indeed probably very rarely) provided with environments and lifestyles sufficiently naturalistic to be free from captivity-stress. Regardless, provision of space for snakes should be sufficient to allow them to move around without imposed bodily restriction, be stimulating and accommodate as much natural and desirable behavior as possible, including the ability to fully straighten or stretch out their bodies. Enclosures must also be large enough to accommodate essential provisions and furnishings, including appropriate thermal gradation, heaters, basking zones, lights, humidifiers, seclusion and specific retreats or hides, water vessels or pools, rocks, burrows and plant, or plant-like furnishings, where relevant to the species without cluttering the general environment or posing risk of injury to the occupant.

Table 6 provides summary guidance of essential absolute minimum containment conditions for snakes (other than for essential temporary or transient conditions, such as clinical treatment and during short-term transportation).

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Conflict of interest statement

C. Warwick and C. Steedman have acted as professional consultants to the Animal Protection Agency (APA), which had no input into design, research, data collection, analysis, or other directional role in this report.

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