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The ecology of sleep in non-avian reptiles

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ABSTRACT

Sleep is ubiquitous in the animal kingdom and yet displays considerable variation in its extent and form in the wild. Ecological factors, such as predation, competition, and microclimate, therefore are likely to play a strong role in shaping characteristics of sleep. Despite the potential for ecological factors to influence various aspects of sleep, the ecological context of sleep in non-avian reptiles remains understudied and without systematic direction. In this review, we examine multiple aspects of reptilian sleep, including (*i*) habitat selection (sleep sites and their spatio-temporal distribution), (*ii*) individual-level traits, such as behaviour (sleep postures), morphology (limb morphometrics and body colour), and physiology (sleep architecture), as well as (*iii*) inter-individual interactions (intra- and inter-specific). Throughout, we discuss the evidence of predation, competition, and thermoregulation in influencing sleep traits and the possible evolutionary consequences of these sleep traits for reptile sociality, morphological specialisation, and habitat partitioning. We also review the ways in which sleep ecology interacts with urbanisation, biological invasions, and climate change. Overall, we not only provide a systematic evaluation of the conceptual and taxonomic biases in the existing literature on reptilian sleep, but also use this opportunity to organise the various ecological hypotheses for sleep characteristics. By highlighting the gaps and providing a prospectus of research directions, our review sets the stage for understanding sleep ecology in the natural world.

Key words: sleep ecology, sleep ecophysiology, roost, retreat, refuge, inactivity, anti-predator, thermoregulation, evolution, Squamata

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I. INTRODUCTION

As one of the most fundamental and ubiquitous behaviours, sleep is shaped by ecological processes over evolutionary timescales. Sleep or sleep-like behaviour occurs throughout the animal kingdom, in organisms ranging from jellyfish (Nath *et al.*, 2017) and bees (Klein *et al.*, 2010), to sharks (Kelly *et al.*, 2021) and monkeys (Nunn & Samson, 2018). It is associated with several characteristics: behavioural quiescence, typical postures, increased stimulus thresholds for arousal, rapid reversibility to wakefulness, and homeostatic regulation (Piéron, 1912; Flanigan, 1973; Tobler, 1995). In many species, sleep conforms to a circadian rhythm, due to its evolution under the natural light–dark cycle (e.g. van Hasselt *et al.*, 2020). The prevalence of sleep in the animal kingdom, along with its homeostatic maintenance, has been ascribed to an ancient origin (even prior to the evolution of the brain; Lesku *et al.*, 2019) and suggests a role in essential functions such as energy allocation, neural reorganisation, memory consolidation, and cognition (see Schmidt, 2014). Predator avoidance, through immobility, has also been hypothesised as a function of sleep (Meddis, 1975). Despite sleep being ubiquitous in the natural world, the influence of ecological factors, such as predation, competition, and climate, on sleep remains underexplored.

Research on sleep has well-known conceptual, taxonomic, and contextual biases. A major focus of sleep research is on its possible functions. Indeed, sleep is considered to be an enigma in biology as an animal enters a dormant state, exposing itself to predation risk and preventing it from executing fitness-relevant functions (Schmidt, 2014). To understand better the possible functions of sleep, evolutionary comparisons have been particularly informative (Anafi, Kayser & Raizen, 2019), especially those that focus on the composition and duration of sleep across taxa (Lesku *et al.*, 2009). Composition of sleep is evaluated by the duration an animal spends in sleep states, such as rapid eye movement (REM) and non-REM (NREM), which are associated with distinct patterns of electrophysiological signals that differ from signals during wakefulness. Typically, NREM sleep is characterised by cortical high-amplitude, low-frequency activity or 'slow-waves' in the brain (recorded using an electroencephalogram or EEG), no change of muscle tone compared to wakefulness (electromyogram or EMG), and no or sparse eye movement (electro-oculogram or EOG), whereas REM sleep is associated with cortical low-amplitude, high-frequency activity resembling wakefulness, a reduction or loss of skeletal muscle tone, and rapid eye movements. Apart from a research bias towards the function of sleep, a strong taxonomic bias is also apparent, with the majority of data arising from studies of mammals (Campbell & Tobler, 1984; McNamara *et al.*, 2008). The surge of interest in sleep research over the last two decades now includes studies from other taxa, such as birds (Rattenborg, Martinez-Gonzalez & Lesku, 2009; Ouyang *et al.*, 2017; Rattenborg *et al.*, 2017; van Hasselt *et al.*, 2020), reptiles (Libourel & Herrel, 2016), fishes (Yoshizawa *et al.*, 2015), as well as insects (Finkbeiner, Briscoe & Reed, 2012; Tougeron & Abram, 2017). Notably, most of our understanding of sleep comes from laboratory-based studies, owing in part to technological constraints to record sleep in the wild (Rattenborg *et al.*, 2008; Aulsebrook *et al.*, 2016). Sleep observed in laboratory conditions may indeed not be representative of natural sleep, leading to calls to conduct more studies in natural settings (Aulsebrook *et al.*, 2016; Rattenborg *et al.*, 2017).

It has long been acknowledged that sleep is likely influenced by many biotic and abiotic factors in the wild (Amlaner & Ball, 1983; Anderson, 1984). Given the relatively intense stimulus required to wake a sleeping animal, most researchers consider sleep a vulnerable state, with predation being a strong force in shaping the ecology of sleep (Lima *et al.*, 2005). According to this view, a species must maximise safety by optimising its duration, composition (e.g. proportions of NREM and REM), and time of sleep, collectively termed 'sleep architecture' (Lima *et al.*, 2005). For example, under the risk of predation, duration of sleep or individual states (especially REM) is known to reduce in mammals (Lesku *et al.*, 2006; Capellini *et al.*, 2008*a*) and in birds (Roth *et al.*, 2006), both across and within species (e.g. Tisdale *et al.*, 2018*b*). REM sleep could be considered a risky state because of phasic twitches in the sleeping individual and an increased arousal stimulus threshold (Tisdale *et al.*, 2018*b*). Predation risk can also influence timing of sleep, without altering sleep duration (Voirin *et al.*, 2014). Conversely, sleeping itself is considered an anti-predatory strategy as immobility could help lower detection by predators (Meddis, 1975; Siegel, 2009). Unihemispheric slow-wave sleep accompanied by unilateral eye closure has also been posited to be an anti-predator response, as one hemisphere remains active and alert to potential threats (Rattenborg, Amlaner & Lima, 2000). Other ecological factors and behaviours that could influence sleep architecture include locomotion (Rattenborg *et al.*, 2016), trophic position (Capellini *et al.*, 2008*a*), parasitism (Preston *et al.*, 2009), and climatic conditions (e.g. temperature; Dewasmes *et al.*, 2001). Apart from its obvious consequences for survival in a dangerous world, sleep can have a bearing on other aspects of individual fitness, such as reproduction; for example, male Pectoral sandpipers *Calidris melanotos* that slept substantially less during the breeding season sired more offspring (Lesku *et al.*, 2012). Additionally, the quality of sleep an individual experiences could influence attention and cognitive performance during active hours (Scullin & Bliwise, 2015), mediated by potential sleep functions such as energy allocation for immune functions, clearance of metabolic waste, neural reorganisation, and memory consolidation (see Schmidt, 2014). Thus, the ultimate and proximate dimensions of *where*, *how*, and *when* animals sleep in the wild merit attention.

Apart from sleep architecture, a range of other characteristics related to sleep, such as habitat selection, behaviour, morphology, physiology, and inter-individual interactions are also influenced by ecological conditions. These characteristics are relatively better documented in mammals (Anderson, 1998) and birds (Amlaner & Ball, 1983). Primates, in particular, are well studied (Reinhardt, 2020) and are known to select specific trees that not only accord them safety while they sleep (Anderson, 1998; Svensson *et al.*, 2018; Hernandez-Aguilar & Reitan, 2020) but also comfort and stability in terms of structural (e.g. Samson & Hunt, 2014) and thermal properties (Ellison *et al.*, 2019). Similarly, some birds prefer safer sites to sleep (e.g. higher perches, Tisdale *et al.*, 2018*b*), but are known to alter sleep posture in ways that trade safety for thermoregulation (Ferretti *et al.*, 2019, 2020*a*). Spatio-temporal use of sleep sites in primates are also driven by disease prevalence, and resources such as availability of food (Markham, Alberts & Altmann, 2015). For species that are not solitary, intra-specific aggregations during sleep suggest a role for thermoregulation, social bonding, and anti-predatory vigilance or dilution (Takahashi, 1997; Beauchamp, 1999; Ramakrishnan & Coss, 2001).

Non-avian reptiles have been considered to be a key group to understand the ecological and evolutionary context underlying sleep characteristics (Libourel & Herrel, 2016). Although behavioural indicators of sleep are widespread in reptiles, electrophysiological evidence is variable, and thus far restricted to less than 0.2% of all reptiles (Libourel & Herrel, 2016). New research on reptilian sleep has found evidence for the presence of a REM-like state in lizards (Shein-Idelson *et al.*, 2016), but high inter-specific variation indicates

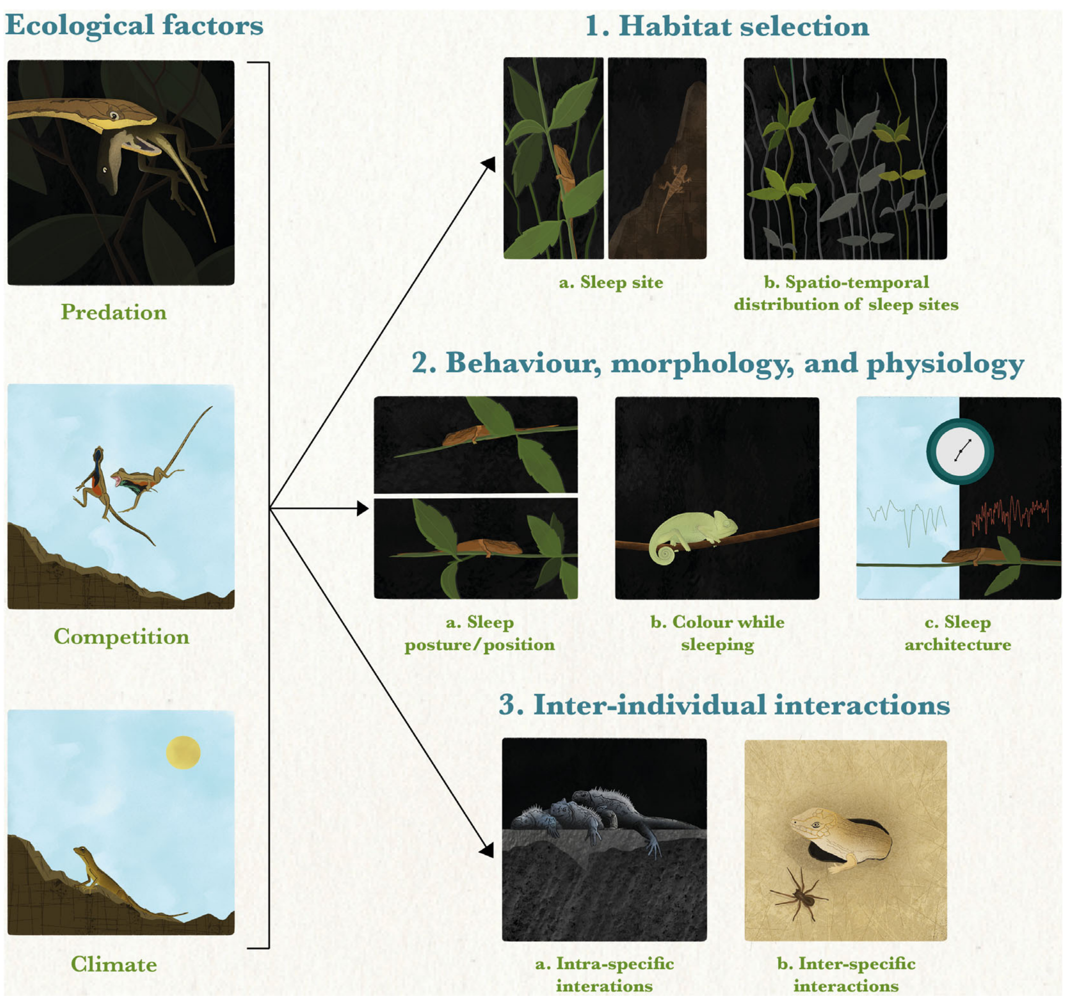

Fig. 1. Ecological factors (left) that drive sleep traits (right) in reptiles. Sleep traits include, (1) habitat selection, such as (a) sleep site selection on varying substrates, including unstable vegetation and warm rocks, and (b) spatio-temporal distribution of sleep sites, including high site fidelity to some sites (in grey) of the many available sites (in green), (2) Behavioural, morphological, and physiological traits of sleep include (a) posture and position, such as facing away from the main trunk, (b) colour state, such as dorsal lightening, and (c) sleep architecture (e.g. time, duration, and composition of sleep), and (3) inter-individual interactions that can be (a) intra-specific, such as sociality during sleep, or (b) inter-specific, such as sleeping in burrows engineered by other animals. Illustrations: Pooja Gupta.

that the evolution of sleep states is likely more complex (Libourel *et al.*, 2018; Libourel & Barrillot, 2020). Notably, the ecological context of sleep in reptiles remains unexplored (Libourel & Herrel, 2016). Although natural-history observations of sleep in reptiles have long been recorded (Kennedy, 1958), there is still a lack of systematic knowledge on how predation, competition, and thermoregulation, amongst other factors, may drive variation in aspects of reptilian sleep ecology.

In this review, we synthesise literature on the sleep ecology of reptiles and identify broad patterns across multiple aspects of sleep (Fig. 1). In particular, we examine patterns in sleep traits that fall broadly within three categories, (*i*) habitat selection, (*ii*) behaviour, morphology and physiology, and (*iii*) inter-individual interactions (Fig. 1). We then outline the underlying evolutionary processes that likely govern these aspects and provide insights into the possible evolutionary consequences of these sleep traits. Given the rapid changes in ecological and environmental conditions in the Anthropocene, we also consider the ways in which sleep ecology of reptiles interacts with the applied research fields of restoration ecology, biological invasions, and urbanisation. Thus, in this review, we present a systematic assessment of the existing literature, thereby identifying conceptual and taxonomic biases, and provide insights into the way forward with new research directions in this exciting field.

II. METHODS

We searched the *Web of Science Core Collection* (on 23rd December 2019) with the key words: Topic = (sleep* OR roost* OR inactiv* OR rest OR refug* OR retreat*) AND Topic = (reptil* OR turtle* OR tortoise* OR lizard* OR herpetofauna OR crocod* OR testudin* OR ophidia OR sauria OR squamat* OR snake*) NOT TOPIC: (resting OR inactivation). The search (modified from van Wilgen *et al.*, 2018) spanned 1945–2019, covering all reptilian taxa. We used broad search terms to characterise 'sleep', including synonyms in the literature (e.g. roost) and indirect evidence (e.g. prolonged inactivity). We did not include aspects related to hibernation, aestivation, or torpor in our review (Kilduff *et al.*, 1993). This search resulted in 2470 papers, to which we added 145 papers (from citations therein); these were scrutinised for relevance to the topic of sleep in reptiles (see online Supporting Information, Fig. S1 for PRISMA flow diagram; Moher *et al.*, 2010).

We read the abstract and title, and where necessary the main text of the paper, to judge relevance. As sleep ecology is not a well-defined branch of research, we are aware that information could be contained in studies with other primary aims. To this end, we examined in detail natural-history notes, species descriptions, and habitat use or activity studies (e.g. telemetry). Our criteria to define sleep was intentionally broad; we included previously defined behavioural and electrophysiological indicators (see Libourel & Herrel, 2016), as well as observations of prolonged inactivity in a circadian cycle. Observations during known inactive periods of the day (e.g. nocturnal records of diurnal reptiles) were only included if there was supporting information that individuals were indeed inactive in that phase. We are aware that sleep may not be monophasic in many reptiles and therefore we excluded studies where we could not confirm inactivity during the phase of observation (e.g. Romijn, Nelson & Monks, 2014). We acknowledge that the classification of sleep based only on behavioural observations recorded in papers used in this review may not represent actual sleep, but may include states of rest, and should be verified by robust electrophysiological evidence and assessment of arousal thresholds. But given the extreme paucity of such evidence for reptiles (available for less than 0.2% species; Libourel & Herrel, 2016), we avoid excluding papers solely on this criterion.

To assess patterns of conceptual and taxonomic biases, we extracted information on the species evaluated (each as an individual row in our database) and the aspect of sleep examined. Sleep aspect included 'site' – type and characteristics of sleep site, 'posture and position' – orientation and head direction, 'spatio-temporal distribution' – spatio-temporal distribution of sleep sites (e.g. site fidelity), 'architecture' – duration and time of sleep/sleep state, 'interaction' – intra- or inter-specific interactions related to sleep (including intra-specific aggregations), and 'applied' – sleep in relation to conservation (e.g. restoration), biological invasions, climate change and urbanisation. Since information on 'sleep' was not the main focus of many of these studies, we acknowledge that our review may not be exhaustive in terms of capturing all published ecological information of sleep characteristics across reptiles. To assess taxonomic bias in the existing literature on sleep ecology, we calculated the number of species at two taxonomic levels (order and family) from the selected literature and compared these to the total number of known reptilian species for these levels (Uetz, Freed & Hošek, 2020) based on a random expectation generated using the hypergeometric distribution (van Wilgen *et al.*, 2018) in the statistical software R (version 3.5.3; R Core Team, 2019). Taxa outside the 95% confidence intervals were considered to be either over- or under-represented in the existing sleep literature.

III. SUMMARY OF SLEEP LITERATURE

The literature survey of sleep traits in reptiles that we conducted here yielded information from 343 species (Table S1), the majority of which belonged to Sauria (80.17%). Given the number of known species across reptilian orders, we found Sauria and Testudines to be over-represented, whereas Serpentes was under-represented (Fig. 2A). At the family level, large groups (>100 species) such as chamaeleonids and anoles were over-represented whereas agamids, lacertids, colubrids, gymnophthalmids, and gekkonids were under-represented (Fig. 2B; see Fig. S2). Interestingly, some of the taxonomic over-representation arises from the way researchers sample for animals. For example, the prevalence of studies on sleeping chameleons is due to the fact that nocturnal sampling is typically employed by most researchers since chameleons are more easily visible at night (see Section IV.2*b*). Most of the information available on sleep is limited to sleep sites across Sauria, Serpentes, and Testudines (Fig. 3). The dominance of sleep site information is probably due to the relative ease of observing and reporting, as compared to other sleep aspects. Finally, we also found a high number of studies on inter-individual interactions at sleep sites in Sauria (Fig. 3A) and on sleep architecture in Testudines (Fig. 3C). In sleep research, crocodilians have been almost exclusively studied in the context of sleep architecture. Despite the gaps (e.g. information on the spatio-temporal distribution of sleep sites), our current knowledge base is at a suitable stage for overall synthesis, enabling us to investigate patterns in the ecology of sleep traits in reptiles.

IV. SLEEP TRAITS

(1) Habitat selection

(*a*) *Sleep sites*

Where an animal sleeps is at the core of its sleep behaviour (Lima *et al.*, 2005). Sleeping reptiles require safety from predators as well as a conducive thermal environment. Therefore, sleep sites are likely to be selected for and specialised in terms of structural and/or thermal properties. These constraining requirements could therefore lead to sleep sites being different from those used during active phases, even at the microhabitat level.

Many semi-arboreal and arboreal reptiles sleep on narrow-girthed, unstable substrates. This is particularly common for diurnal lizards and snakes that sleep on vegetation at night (Clark & Gillingham, 1990; Martins, 1993). The majority of anoles (family Dactyloidae) sleep on narrow vegetation (e.g. saplings), in stark contrast to the wider perches (e.g. tree trunks) used for displaying and foraging during the day (Shew *et al.*, 2002; Vitt *et al.*, 2002; Poche, Powell & Henderson, 2005; Singhal, Johnson & Ladner, 2007; Cabrera-Guzmán & Reynoso, 2010; McCranie & Köhler, 2015). Many arboreal agamids (family Agamidae) also conform to this sleep site pattern, including species of the genus *Acanthocercus* (Reaney & Whiting, 2003), *Coryphophylax* (Mohanty, Harikrishnan & Vasudevan, 2016), *Monilesaurus* (Bors, Mohanty & Shankar, 2020) and *Calotes* (N.P.M., unpublished data). Forest-floor anoles (e.g. *A. tropidonotus* and *A. quaggulus*) could be exceptions to this pattern as they have been documented to sleep on leaf litter (McCranie & Köhler, 2015), although a systematic assessment across a larger number of species is required.

Similarly, sleep sites of chameleons (family Chamaeleonidae) tend to be located on unstable perches, either narrow-

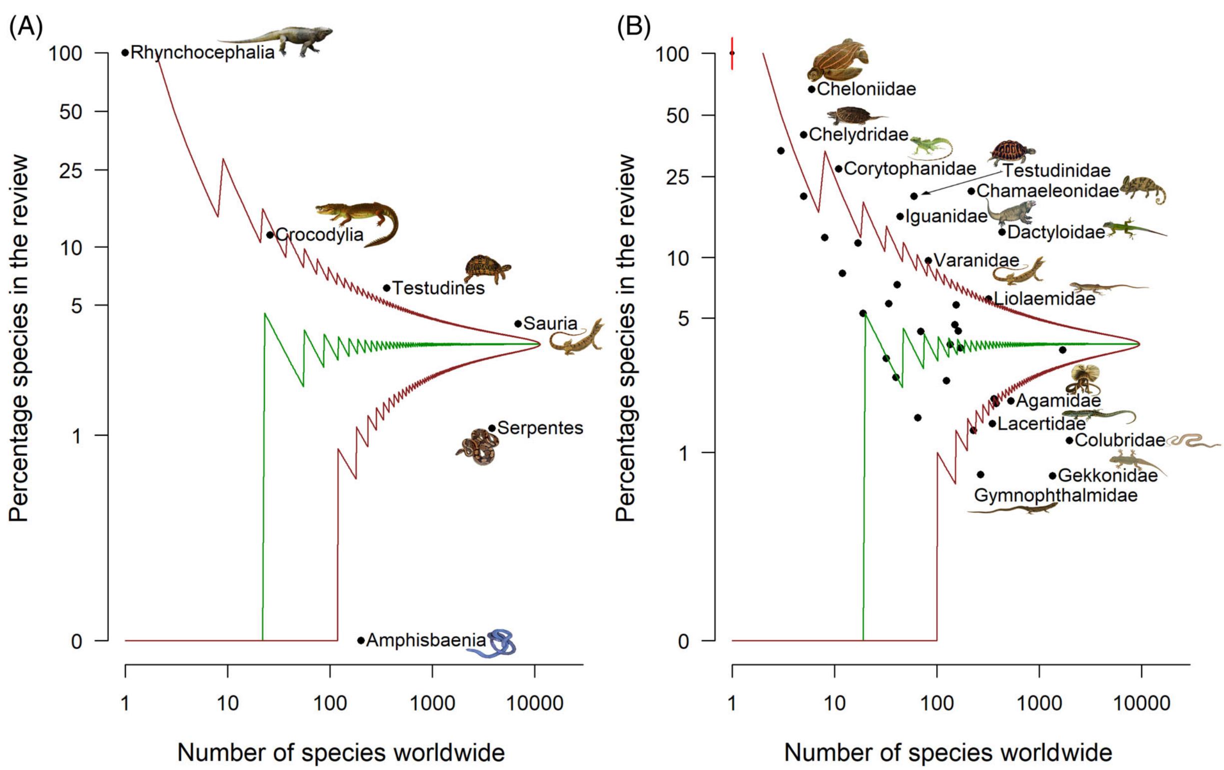

Fig. 2. Taxonomic patterns at the level of reptilian (A) order and (B) family observed in the literature on sleep. The median (green line) and 95% confidence intervals (brown lines above and below), adjusted for multiple comparisons, were estimated from a hypergeometric distribution. Those labelled taxa that fall above the 95% confidence intervals are over-represented and those below are under-represented in our data set on reptilian sleep.

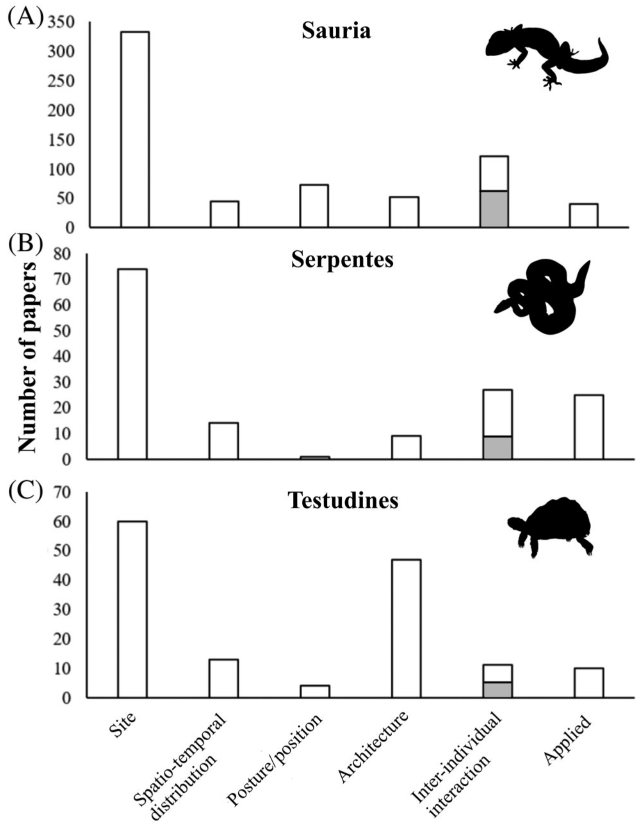

Fig. 3. Studies on the ecological aspects of sleep that focus on (*i*) sleep site, (*ii*) spatio-temporal distribution of sleep sites, (*iii*) sleep posture and position, (*iv*) sleep architecture, (*v*) inter-individual interactions (including intra-specific aggregations in grey) and (*vi*) applied sleep ecology, in (A) Sauria (lizards), (B) Serpentes (snakes), and (C) Testudines (turtles)

girthed plants or thin perches on trees (e.g. terminal branches; Carpenter, 2003; Da Silva & Tolley, 2013; Measey, Raselimanana & Herrel, 2014), as documented for several species of the genus *Bradypodion*, *Calumma*, *Chamaeleo*, *Furcifer*, *Rhampholeon* (Burrage, 1972; Akani, Ogbalu & Luiselli, 2001; Keren-Rotem, Bouskila & Geffen, 2006; Reisinger, Stuart-Fox & Erasmus, 2006). A complete shift in the microhabitat is observed in chameleons of the genus *Brookesia*, which are typically terrestrial and found on leaf litter during the day, but invariably sleep on unstable perches such as shrubs, saplings, or dead twigs at night (Raxworthy & Nussbaum, 1995; Carpenter, 2003; Razafimahatratra, Mori & Hasegawa, 2008; Miller, 2017). Similarly, several species of diurnal snakes and geckos also sleep exclusively on thin vegetation at night (Martins, 1993; Montgomery, Lips & Ray, 2011; Ikeuchi, Hasegawa & Mori, 2012). Additionally, many of these species sleep on higher perches than those used for general activity (Singhal, Johnson & Ladner, 2007; Montgomery, Lips & Ray, 2011; Ikeuchi, Hasegawa & Mori, 2012; Mohanty, Harikrishnan & Vasudevan, 2016). Individuals of a species can also use multiple substrate types while sleeping, as long as the sleep perch is relatively narrow and unstable (e.g. Rand, 1967; Bors, Mohanty & Shankar, 2020). This strategy is even apparent in lizards that utilise artificial substrates (e.g. fence wire that is narrow and flexible) while sleeping (Hirth, 1963*b*).

The specialisation of sleeping on unstable perches could act as an 'early warning system' to detect approaching predators (Anderson, 1998; Table 1) and minimise predation risk. Firstly, narrow-girthed plants may preclude many predators, especially large-bodied species, from climbing. If a predator indeed climbs the perch plant, thin perches ensure that tactile cues reach the sleeping animal and enable timely arousal and escape. This argument is further supported by divergent perch use between sleeping prey and foraging predators (Chandler & Tolson, 1990). Examples of successful predation on sleeping lizards by snake predators approaching from adjacent plants (Yorks *et al*., 2003) and unsuccessful attempts when approaching from the same perch plant (Mohanty, Harikrishnan & Vasudevan, 2016), are in line with this predator-avoidance strategy. The co-evolution of predation strategy on sleeping prey is likely as prevalent as the strategy of prey sleeping on an unstable substrate.

Another unique predator-avoidance strategy appears to be the use of plants with thorns in some species. For example, Australian gecko and agamid species are found sleeping on or within thorny *Spinifex* sp. plants in arid regions (Julia L. Riley, personal communication). Similarly, snakes of the genera *Boiga* and *Oxybelis* have been observed to sleep on spiny plants such as *Pandanus* sp. and *Mimosa* sp., respectively (Henderson, 1974; Hetherington *et al*., 2008; Mesquita *et al*., 2012).

In many saxicolous reptiles, sleep sites (or 'retreat sites') in rock crevices are specialised in terms of both structural and thermal properties (Webb, Pringle & Shine, 2004). A preference for relatively warm rocks compared to all available rocks has been documented in both nocturnal and diurnal species of gekkonids, iguanids, colubrids and elapids (Huey *et al*., 1989; Sabo, 2003; Croak *et al*., 2008*a*). With respect to structural properties, diurnal geckos of the genus *Amalosia* select narrow crevices in rocks with large surface areas but thin in depth (Schlesinger & Shine, 1994*a*,*b*). The choice of crevice structure could further involve crevice position and its three-dimensional structure (e.g. number of openings; Croak *et al*., 2008*a*). These requirements of sleep sites are matched, at least partially, in geckos of the genera *Tarentola* (Penado *et al*., 2015; Pereira *et al*., 2019), *Homonota* (Aguilar & Cruz, 2010), and *Nephrurus* (Shah *et al*., 2004). Elapid snakes of the genera *Hoplocephalus* and *Cryptophis* exhibit similar site selection to *Amalosia* (Webb, Pringle & Shine, 2004; Webb, Pringle & Shine, 2009), but chosen rocks could differ in surface area (Croak *et al*., 2008*a*). Macrohabitat features, such as canopy cover and consequently sun exposure, on the other hand, are particularly important in determining the thermal environment of these rocks (Pringle, Webb & Shine, 2003; Webb, Shine & Pringle, 2005).

The selection of specialised sites reflects strong influences of predator-avoidance and thermoregulatory requirements while sleeping during the day, foregoing heliothermy (direct

Table 1. Hypotheses in sleep ecology, with supporting examples of reptilian taxa

Hypothesis	Description	Source	Reptile examples
Sleep site			
Early detection of approaching predators	Animals choose sleep sites that facilitate early detection of approaching predators through noise and vibration	Anderson (1998)	*Anolis*, *Coryphophylax*, *Calotes*, *Monilesaurus*, *Bradypodion*, *Calumma*, *Chamaeleo*, *Furcifer*, *Rhampholeon*, *Brookesia*, *Oxybelis*, *Erythrolamprus*, *Dipsas*, *Leptodeira*, *Chironius*, *Lygodactylus*
Thermoregulation at sleep sites	Interaction of thermodynamic and antipredator requirements determines sleep traits	Anderson (1998); Lima *et al.* (2005)	*Amalosia*, *Sceloporus*, *Intellagama*, *Homonota*, *Underwoodisaurus*, *Varanus*, *Thamnophis*, *Hoplocephalus*, *Pseudonaja*, *Cryptophis*, *Geochelone*
Comfort at sleep sites	Sleep sites are selected on the basis of physical comfort afforded (e.g. shelter from the elements, avoidance of biting insects or other disturbances)	Anderson (1984, 1998)	
Hygiene at sleep sites	Sleep sites reduce exposure to disease vectors	Anderson (1998); Shah, Hudson & Shine (2006)	*Underwoodisaurus*
Spatio-temporal distribution			
Site fidelity *vs* 'shell game'	Animals choose the same sleep site over time to reduce the perceived risk of predation. Alternatively, animals use multiple sleep sites to reduce predictability and avoid predators	Mitchell & Lima (2002); Lima *et al.* (2005)	*Anolis*, *Tympanocyptis*, *Hoplocephalus*, *Eretmochelys*
Sleep posture/position			
Visual detection of approaching predators	Animals at sleeping perches orient themselves towards the approach path of a predator to enable visual detection	Clark & Gillingham (1990); Mohanty, Harikrishnan & Vasudevan (2016)	*Anolis*, *Coryphophylax*, *Monilesaurus*
Sleep architecture			
Blackout sleep	Sleep in one short and single block is safer and increases time awake and fully vigilant to predators	Lima *et al.* (2005); Lima & Rattenborg (2007)	
Sentinel hypothesis of REM sleep	REM sleep events enable an animal to escape when attacked, and the brief arousals that precede or follow REM sleep have an anti-predatory role	Snyder (1966); Voss (2004)	
Tailoring-of-sleep	Sleep architecture can be modified according to risk perception	Voss (2004)	*Dipsosaurus*
Inter-individual interactions			
Environmental constraints on sleep sites	Limited availability of sleep sites led to the evolution of sleep-site sharing (sociality)	Leu, Kappeler & Bull (2011)	*Tiliqua*
Evolution of sociality	Sleeping associations are a precursor to sociality during active phase	Leu, Kappeler & Bull (2011)	
Sleep function			
Immobilisation	Sleep serves a protective role during times when an animal is not engaged in any other activity	Meddis (1975)	

basking; Table 1). Thigmothermy (indirect basking by touch) throughout the day necessitates appropriate substrate structure and macro-habitat to avoid both underheating and overheating (Kearney & Predavec, 2000; Pringle, Webb & Shine, 2003; Vasconcelos, Santos & Carretero, 2012). Indeed, such thermally sub-optimal sleep sites may have consequences for locomotor performance (e.g. sprint speed; Aguilar & Cruz, 2010). Crevice structure is likely to play an important role in predator avoidance, as narrow crevices preclude predators from entering (Schlesinger & Shine, 1994*a*,*b*; Webb & Whiting, 2005). However, selection of these sites is likely governed by trade-offs between optimal thermal environment and safety (Webb, Pringle & Shine, 2004). For example, *Amalosia lesueurii* prioritise the use of safe sites (i.e. without predator cues) which are thermally sub-optimal as opposed to unsafe but thermally optimal sites (Downes & Shine, 1998*a*). Such choices, however, may result in long-term fitness costs (e.g. *Lampropholis guichenoti*; Downes, 2001).

Various reptile species, including skinks, agamids, turtles, and geckos, use burrows as refuges during both active and 'inactive' (sleep) phases (Brown & Brooks, 1993; Bulova, 2002; Converse, Iverson & Savidge, 2002; Chapple, 2003; McMaster & Downs, 2006; Price-Rees & Shine, 2011; Das *et al*., 2013; Song *et al*., 2017). Most studies focus on the advantages of using burrows during the active phases (but see Wikramanayake & Dryden, 1993; Dorcas & Peterson, 1998), but burrows likely confer similar benefits for a reptile during sleep. Generally, burrows are more thermally stable compared to the surface, and thus, individuals might exploit burrows as a thermally optimal sleep site (Wikramanayake & Dryden, 1993; Whitaker & Shine, 2003; Table 1). It has been suggested that burrows confer other benefits, such as anti-predation and hydration, however, this remains to be systematically tested in the context of sleep (Henzell, 1972; Chapple, 2003).

In addition to using self-constructed burrows, several reptile species utilise both active and abandoned burrows of mammals, birds, and arthropods as sleep sites [e.g. *Heterodon platirhinos* (Plummer & Mills, 2000); *Tiliqua rugosa* (Kerr, Bull & Burzacott, 2003); *Laticauda saintgironsi* (Bonnet *et al*., 2009); *Tympanocryptis pinguicolla* (Stevens *et al*., 2010); *Lampropeltis getula* (Godley, Halstead & McDiarmid, 2017)]. Abandoned burrows seem to be exploited opportunistically by species that show no clear preference for these sites over others (Plummer & Mills, 2000; Bonnet *et al*., 2009; Stevens *et al*., 2010). Interestingly, the skink *Tiliqua adelaidensis* in Australia obligatorily uses spider burrows as both inactive (sleep) and active retreat sites (Hutchinson, Milne & Croft, 1994; Pettigrew & Bull, 2011). During the active phase of this species, burrows have been shown to provide thermoregulatory and anti-predator benefits (Milne, Bull & Hutchinson, 2003; Souter, Bull & Hutchinson, 2004). However, there are no studies to date that examine the mechanisms and ecological consequences of shared and obligatory interspecific burrow use for sleep.

Although seldom observed, a few studies have reported terrestrial and semi-aquatic reptiles sleeping in aquatic sites. Observations range from individuals semi-submerged in small pools of water [e.g. *Geochelone pardalis* (Rall, 1985); *Chelydra serpentina* (Brown & Brooks, 1993); *Urostrophus vautieri* (Henle & Knogge, 2009)] to full submergence in large water bodies [e.g. *Varanus salvator* (Wikramanayake & Green, 1989); *Tupinambis teguixin* (Ávila-Pires, 1995); *Intellagama lesueurii* (Doody *et al*., 2014)]. Opportunistic use of these aquatic sites for sleep could potentially confer hydration and/or thermoregulatory advantages, as well as provide safety from terrestrial predators (Rall, 1985; Wikramanayake & Green, 1989; Doody *et al*., 2014). Additionally, rapid escape from predators has been argued as a benefit of terrestrial sleep sites situated close to or overhanging large rivers or lakes (Ávila-Pires, 1995; Doody *et al*., 2014; Mora & Escobar-Anleu, 2017).

In aquatic habitats, fully aquatic reptiles select sleep sites that are apparently analogous to those found in terrestrial systems (e.g. rock crevices, burrows, vegetation cover); these sites, however, have vastly different functions when submerged. Marine turtles, for example, often select specific structural sleeping ('resting') sites, such as rock crevices and coral ledges, in order to remain neutrally buoyant and, thus, inactive for longer periods under water (Houghton, Callow & Hays, 2003; Blumenthal *et al*., 2009*a*; Stimmelmayr, Latchman & Sullivan, 2010; Proietti, Reisser & Secchi, 2012; Wood, Brunnick & Milton, 2017). Individuals utilising these structures as sleep sites demonstrate increased sleep quality (in terms of duration) compared to those at more exposed sleep sites, such as the seafloor (Houghton, Callow & Hays, 2003; Blumenthal *et al*., 2009*a*; Stimmelmayr, Latchman & Sullivan, 2010). Additionally, the cover of submerged structures can create low-light microhabitats and provides refuge from currents and predators (Houghton, Callow & Hays, 2003; Wood, Brunnick & Milton, 2017). Other aquatic reptiles likely use submerged structures for similar benefits during sleep (e.g. *Acrochordus granulatus*; Lillywhite, 1996). However, the functions of aquatic sleep sites in reptiles other than marine turtles, have rarely been investigated.

(*b*) *Spatio-temporal distribution of sleep sites*

Recurrent use of a site, known as site fidelity, is widespread in the animal kingdom. Fidelity to one or more sleep sites has been observed in several reptilian taxa, including lizards (Clark & Gillingham, 1990; Stevens *et al*., 2010), snakes (Webb & Shine, 1997*a*), and marine turtles (Wood, Brunnick & Milton, 2017). Measures of sleep site fidelity, however, are variable and dependent on the duration of observation (Koenig, Shine & Shea, 2001; Beck & Jennings, 2003). The spatial cognitive ability of a species (Zuri & Bull, 2000) is also likely to influence site fidelity. Ultimately, spatio-temporal variations in resources (e.g. optimal sleep sites in terms of predator presence, and thermal and structural suitability) determine levels of site fidelity, with high site fidelity expected under low temporal variations in these resources (Gerber *et al*., 2019; Table 1). Sleep site fidelity could ensure repeated access to optimal sites (e.g. 'safe' sites; Mohanty, Harikrishnan & Vasudevan, 2016) and reduce the cost of locomotion, establishment, and familiarity (Switzer, 1993). The location of sleep sites within the home range could be influenced by locations used for active behaviours, such as feeding, basking, and mate seeking (Singhal, Johnson & Ladner, 2007). For example, sleeping at the edge of the actively defended territory could help in early morning displays ('dawn chorus'; Ord, 2008). Sleep sites could also form the core of the animal's home range (Kerr & Bull, 2006*a*) and can shift based on resource availability for active behaviours (e.g. foraging; Whitaker & Shine, 2003). Finally, when optimal sleep sites are limited in availability, evidence suggests that high sleep-site fidelity is actively maintained with defence against conspecifics (Kondo & Downes, 2007).

(2) Behaviour, morphology, and physiology

(*a*) *Sleep posture and position*

Apart from the selection of sleep sites that provide the numerous benefits described above, animals can modulate how they use these sites. Head direction, body orientation (with respect to the ground), and distance to branch tip of a sleeping arboreal animal may influence the effectiveness of predator detection and escape (Shew *et al.*, 2002; Ikeuchi, Hasegawa & Mori, 2012; Mohanty, Harikrishnan & Vasudevan, 2016). Only a few studies on arboreal lizards have explicitly quantified this aspect. Sleeping with the head facing 'inward' to the point of origin of the perch (e.g. the trunk for individuals sleeping on a branch) is prevalent in many *Anolis* spp. (Kattan, 1984; Clark & Gillingham, 1990; Cabrera-Guzmán & Reynoso, 2010), *Coryphophylax* spp. (Mohanty, Harikrishnan & Vasudevan, 2016), and *Monilesaurus rouxii* (Bors, Mohanty & Shankar, 2020). Rand (1967) documented an *A. lineatopus* turning around in order to face the petiole of the leaf before sleeping. Conversely, *A. fuscoauratus*, *A. punctatus*, *A. transversalis*, *A. gingivinus* and *Lygodactylus tolympae* were found to sleep with their head directed 'outward', facing the end of the branch (Shew *et al.*, 2002; Vitt *et al.*, 2003*a*,*b*; Ikeuchi, Hasegawa & Mori, 2012).

Clark & Gillingham (1990) posit that facing inward likely provides a benefit as this would be towards the path of an approaching arboreal predator (Table 1). The intentional positional adjustment of 'turning around' to face inward indicates the importance of visual cues to detect approaching predators, once a sleeping lizard is awakened by tactile cues (Mohanty, Harikrishnan & Vasudevan, 2016). This role of visual cues is further supported by the relative exposure of sleep sites on vegetation (Burrage, 1972; Kattan, 1984; Lardner *et al.*, 2019). Although some authors consider exposure of the sleep site to increase predation risk (Lesku *et al.*, 2006), it could also be beneficial by providing visual cues of potential risk (but see Kattan, 1984; Yorks *et al.*, 2003). The combined use of multiple cues, both tactile and visual, likely provides a better 'threat-sensitive' assessment of risk (Helfman, 1989; Kats & Dill, 1998) and for diurnal species reduces the potential energetic and predatory cost of moving at night. Conversely, facing outward could aid in faster escape from the perch plant to an adjoining substrate. How predator assemblage (e.g. relative risk of arboreal predators *versus* avian predators) across habitats and environments influences sleep posture and position remains to be examined in reptiles.

Notably, the effect of sleep state on sleep posture remains completely unexplored in reptiles. Since muscle tone reduces during REM sleep (Libourel *et al.*, 2018) this may influence the ability to retain a stable position on narrow or unstable perches, which may explain why many lizards have been documented to sleep in a horizontal orientation that confers the greatest stability on perches (Clark & Gillingham, 1990; Shew *et al.*, 2002; Singhal, Johnson & Ladner, 2007; Razafimahatratra, Mori & Hasegawa, 2008; Mohanty, Harikrishnan & Vasudevan, 2016; Bors, Mohanty & Shankar, 2020). Distance to the tip of a branch is considered important for tree-dwelling chameleons, which demonstrate an affinity to sleep closer to a branch's distal tip than to the trunk (Carpenter, 2003; Measey, Raselimanana & Herrel, 2014). Although this is, in part, due to perch width, this positioning could also enable escape by providing proximity to a nearby tree. Escape in reptiles during active hours has been extensively researched (Samia *et al.*, 2016) and is known to be determined by perceived predation risk and the cost of escape, moderated by the thermal environment and refuge availability (Cooper, 2011). How sleeping reptiles decide to escape when awakened by a threat remains unknown, even though knowledge of the types of stimuli that elicit escape and the escape strategy are critical to where and how animals sleep. Most species that use narrow perches consistently employ the strategy of dropping to the ground (Raxworthy, 1991; Vitt *et al.*, 2003*b*; Mohanty, Harikrishnan & Vasudevan, 2016; Bors, Mohanty & Shankar, 2020), indicating that predator avoidance is probably directed at arboreal predators.

(*b*) *Colour patterns while sleeping*

Depending on their conspicuousness and function, body colour and pattern can have considerable costs and benefits. This raises the question of whether sleeping reptiles use this phenotypic trait in a way that maximises their benefit (e.g. thermoregulation during the day) or minimises their risk (e.g. from visually oriented predators). At the evolutionary scale, body pattern and activity period seem to be closely linked in some reptiles. In geckos, Allen *et al.* (2020) described an interesting association between nocturnal activity and the evolution of horizontal bands, suggesting that this body pattern may provide better camouflage than stripes or spots when geckos are motionless and sleeping during the day. The effectiveness of blotches and banded patterns to enhance camouflage in heterogeneous substrates, such as rocky crevices or leaf litter (Egan *et al.*, 2016) is further supported by similar colour patterns seen in sit-and-wait ambush hunting snakes, which need to be camouflaged while motionless during hunting as well as resting (Allen *et al.*, 2013). A clear exception to the evolutionary adaptation to minimise detection while motionless is in aposematically patterned snakes (Allen *et al.*, 2013). Thus, for species with static colours and patterns that do not change once developed (e.g. most tortoises, turtles, snakes, and crocodilians), sleep site selection that either hides their conspicuous colour patches or that enables effective camouflage is likely to be critical.

For many other reptiles, body colour can change dynamically to varying degrees (Cooper, Greenberg & Gans, 1992), from lightening and darkening seen in most lizards and even crocodilians (e.g. Boyer & Swierk, 2017; Merchant *et al.*, 2018) to the rapid multi-hue changes seen in chameleons and some agamids (Stuart-Fox & Moussalli, 2009). Thus, physiological colours can play an interesting and possibly adaptive role in the ecology of sleep. Evidence that colours and patterns change in a circadian pattern has been documented in several reptiles (Caswell, 1950; Das *et al.*, 2014; Fan, Stuart-Fox & Cadena, 2014). Interestingly, circadian patterns of pigmentation do not seem to depend on whether the species is sleeping at night or during the day. For example, when *Hemidactylus* spp. are sleeping during the light phase, their body colours are paler and less patterned than when they are active during the dark phase (Das *et al.*, 2014). By contrast, in the diurnally active bearded dragons, skin colour shifts from darker during the day to lighter at night (Fan, Stuart-Fox & Cadena, 2014). In these examples and others (e.g. chameleons), body colour during the sleep state is lighter than the darker or variable colours seen when lizards are active. This circadian pattern suggests that the adaptive functions of colours, such as background matching, thermoregulation, and social signalling (Stuart-Fox & Moussalli, 2009), are mainly relevant during the active phase [but see Vroonen, Vervust & Fulgione (2012) for background matching during the day by a nocturnal gecko].

We currently lack enough data across reptilian species to understand whether lighter colours during sleep are a result of a high cost to induce darker or chromatic skin, or whether the benefits of darkening while sleeping are low. For example, diurnal chameleons revert to a lighter colour while sleeping at night, which makes them more conspicuous to nocturnal visually hunting predators, but their exposed perch choice may allow them to respond quickly and effectively when attacked. Thus, the combined expression of various sleep traits can result in a net benefit to the sleeping individual. Many questions about body colours remain unexplored in the context of sleep; importantly, we currently have no systematic data on whether body colour varies during sleep and whether these changes are a by-product of cognitive processes (e.g. REM sleep) or relaxation of muscles associated with REM. In the common European cuttlefish *Sepia officinalis*, Iglesias *et al.* (2019) showed rapid changes to chromatophores (patterning and brightness) during distinct sleep states, resulting in a camouflaged quiet sleep-like state and conspicuous REM-like state. Although such sleep state-dependent colour change has not yet been demonstrated in reptiles, the occurrence of such a phenomenon and its effect on predation risk would be worth exploring.

(*c*) *Sleep architecture*

The time, duration, and composition of sleep (i.e. sleep architecture) are likely to be under selection by ecological factors such as predation (Lima *et al.*, 2005; Table 1). Of these three aspects, the time of sleep onset and awakening are relatively easier to measure and have therefore been recorded more frequently in reptiles (e.g. Bull, McNally & Dubas, 1991). Time of awakening, in particular, is known to be governed by predator avoidance (Ikeuchi, Hasegawa & Mori, 2012) and the thermal environment (Judd, 1975). For diurnal species, emerging early from sleep may help avoid exposure to diurnal predators (Ikeuchi, Hasegawa & Mori, 2012), but could have thermal costs, hindering escape (Cooper, 2000), whereas emerging late could result in lost opportunities for thermoregulation. Duration of sleep has rarely been quantified in relation to ecological factors in reptiles [see Libourel & Herrel (2016) for a detailed discussion on sleep architecture in reptiles]. Nevertheless, sleep duration is governed by temperature and day/night length in *Dipsosaurus dorsalis* (Huntley, 1987). In the same species, Revell & Hayes (2009) report increased vigilance and a reduction in sleep duration when exposed to a predator. Reducing sleep for other activities (e.g. increased courtship) can have fitness benefits, a phenomenon termed as 'adaptive sleeplessness' (Lesku *et al.*, 2019). In reptiles, such bouts of reduced sleep could potentially occur during dispersal (e.g. swimming frenzy in turtles; Scott *et al.*, 2014), mating (Shine *et al.*, 2000; Keogh *et al.*, 2012), and hyperphagia (i.e. increased foraging) before entering a state of torpor or hibernation (Price, 2017), although this remains to be tested.

Knowledge on the ecological regulation of sleep composition (e.g. proportions of NREM and REM sleep) is hindered by variable evidence on sleep states in reptiles (Libourel & Herrel, 2016) and a likely complex evolution leading to distinct sleep patterns, even between closely related species (Libourel *et al.*, 2018). Unihemispheric sleep, a distinct form of slow-wave sleep that is manifested in one hemisphere of the brain while the other hemisphere remains active, is hypothesised to occur in a few reptilian taxa based on behavioural evidence (for a detailed review see Rattenborg, Amlaner & Lima, 2000). Behaviourally, unihemispheric sleep is correlated with unilateral (asynchronous) eye closure in birds and cetaceans, where the eye linked to the sleeping hemisphere is shut (Rattenborg, Lima & Amlaner, 1999; Lyamin *et al.*, 2008). Although there is no electrophysiological evidence for this sleep state in reptiles, unilateral eye closure has been observed in testudines, squamates, and crocodilians (Rattenborg, Amlaner & Lima, 2000; Kelly *et al.*, 2015) and could potentially have a 'sentinel' role (Tauber, Roffwarg & Weitzman, 1966). For example, such unilateral eye closures have been documented to increase after exposure to predators, with the open eye directed at the last known location of predator (Mathews *et al.*, 2006; Kelly *et al.*, 2015). Other sleep attributes likely to have anti-predatory functions, such as micro-arousals (Lima *et al.*, 2005), also remain unexamined in reptiles.

Over a 24 h cycle, the time allocated for sleep is traded off with time to acquire resources such as a conducive thermal environment or food (Eban-Rothschild, Giardino & de Lecea, 2017). Apart from the strong influence of predation and thermoregulation on sleep discussed in this review, aspects of foraging, including metabolic rate (associated with diet type) as well as individual-level satiation state can also affect sleep architecture (Lesku *et al.*, 2006; Eban-Rothschild, Giardino & de Lecea, 2017; Ferretti *et al.*, 2020*b*). Species with a higher basal metabolic rate are expected to forage more frequently or for longer durations, thereby reducing the time available for sleep (Lesku *et al.*, 2006; Capellini *et al.*, 2008*b*). The influence of foraging on sleep architecture has not been explicitly explored in reptiles, perhaps owing to the paucity of data (Libourel & Herrel, 2016). In marine iguanas, Wikelski & Hau (1995) argued for the presence of endogenous rhythmicity in foraging time based on tides and its relationship with sleep. The authors proposed the presence of a circa-semilunar rhythm that informs the iguanas of neap tides that make intertidal zones available for both foraging and sleeping, likely reducing the energetic expenditure of movement between sleep sites and foraging grounds. Given the diversity of diet and metabolic rates in reptiles, a phylogenetically informed analysis on the influence of these factors on sleep duration would be timely.

One of the biggest issues with documenting sleep architecture in reptiles is the extended periods of inactivity in a day which, based on behavioural features, are extremely difficult to distinguish from sleep. The resultant paucity of data on sleep architecture in reptiles must be remedied to enable comparative assessments of potential predictors (e.g. diet, phylogeny). A better understanding of sleep and the associated behavioural features in reptiles is thus critical in order to quantify the ecological contexts driving variation in sleep architecture.

(3) Inter-individual interactions

(*a*) *Aggregations*

Sleeping with conspecifics or in aggregations is common in several reptilian taxa, including geckos (Kearney *et al.*, 2001; Lancaster, Wilson & Espinoza, 2006; Barry, Shanas & Brunton, 2014), beaded lizards (Beck & Jennings, 2003), skinks (Chapple, 2003; Leu, Kappeler & Bull, 2010), iguanas (Boersma, 1982), varanids (Guarino, 2002), agamids (Das *et al.*, 2013; Mohanty, Harikrishnan & Vasudevan, 2016) and snakes (Aubret & Shine, 2009). These associations can be broadly explained by ecological (e.g. limited availability of sleep sites; Table 1) or social factors (e.g. conspecific attraction). Benefits of associating with conspecifics while sleeping include predator avoidance through increased vigilance and/or dilution of individual risk (Boersma, 1982; Lanham & Bull, 2004), preventing heat loss (Boersma, 1982; Lanham, 2001; Shah *et al.*, 2003; Aubret & Shine, 2009), reducing evaporative water loss (Lancaster, Wilson & Espinoza, 2006), and mate guarding (How & Bull, 2002). Conversely, aggregations could increase parasite load (but see Wikelski, 1999; Leu, Kappeler & Bull, 2010; Sih *et al.*, 2018). Little is known about the composition of such sleep aggregations, although the presence of male–female pairs or single adult males in a group of females appears common (Downes & Shine, 1998*a*; Kearney *et al.*, 2001; Leu, Kappeler & Bull, 2011; Barry, Shanas & Brunton, 2014; Vasconcelos, Rocha & Santos, 2017). In some species, (e.g. *Underwoodisaurus milii*), juveniles are excluded from certain sleep associations (e.g. with females; Kearney *et al.*, 2001), but when included, juveniles gain increased protection as they are more vulnerable to predation (Boersma, 1982). Increased associations during sleep in otherwise solitary species has led to the hypothesis that such associations could be a precursor to more complex sociality (e.g. stable social aggregations; Gardner *et al.*, 2016), however, supporting evidence is lacking (Leu, Kappeler & Bull, 2011; Table 1).

(*b*) *Ontogenetic and sex differences*

Sleep traits are likely to change with ontogeny; juveniles experience changes in predation pressure, thermal requirements, and intraspecific competition as they develop, and are even morphologically constrained with respect to some locomotory tasks (Keren-Rotem, Bouskila & Geffen, 2006). In semi-arboreal squamates, perch height tends to increase with body size, a good proxy for age (Keren-Rotem, Bouskila & Geffen, 2006; Singhal, Johnson & Ladner, 2007; Montgomery, Lips & Ray, 2011; Mohanty, Harikrishnan & Vasudevan, 2016), but this pattern has several exceptions (e.g. Ikeuchi, Hasegawa & Mori, 2012; Bors, Mohanty & Shankar, 2020). Increased perch height might confer better thermal and anti-predatory benefits (Chandler & Tolson, 1990; Mohanty, Harikrishnan & Vasudevan, 2016), but higher perches could be difficult to attain for small-sized individuals due to reduced arboreal performance (e.g. 'gap-bridging' ability in *Oxybelis*; Montgomery, Lips & Ray, 2011). Sleep sites of juveniles can diverge to the extent of being completely different from those used by adults (Christian, Tracy & Porter, 1984; Keren-Rotem, Bouskila & Geffen, 2006). Apart from structural differences, thermal properties of sleep sites may differ between juveniles and adults, with juveniles using sub-optimal sites prone to overheating (Vasconcelos, Santos & Carretero, 2012; de Fuentes-Fernández, Suárez-Rancel & Molina-Borja, 2019). Finally, sleep architecture is known to change with age in mammals and birds, with juveniles displaying increased sleep duration and an increased proportion of REM sleep, yet this remains to quantified in reptiles (Roffwarg, Muzio & Dement, 1966; Scriba *et al.*, 2013; Libourel & Herrel, 2016).

Males are hypothesised to select sleep sites that aid in territoriality during the active phase (Chandler & Tolson, 1990). Temperature requirements during sleep may differ between males and females, with females using warmer sleep sites (Sabo, 2003). Females, especially gravid individuals, have higher energetic requirements and may thermoregulate by selecting warmer sleep sites (Huey *et al.*, 1989). However, there are few data on sex differences in the context of sleep ecology in reptiles.

V. EVOLUTIONARY CONSEQUENCES

Although the evolutionary consequences of sleep have been poorly investigated in reptiles, sleep is likely to have shaped some of their phenotypic, behavioural, and ecological diversity. For example, it has been suggested that sleeping on smooth substrates may have been an evolutionary precursor for the evolution of adhesive pads in geckos and *Anolis* lizards (e.g. Russell *et al.*, 2015). In the same vein, the evolution of limb dimensions could be impacted by sleep site selection to some degree. The need to reach narrow substrates that are often selected as sleep sites (see Section IV.1*a*) may impose an important selective pressure that could drive the evolution of shorter limbs. Indeed, in *Anolis* lizards, short limbs have been demonstrated to improve stability on narrow substrates (Losos & Sinervo, 1989). Moreover, one of the Greater Antillean *Anolis* ecomorphs is characterised by having short limbs and specialises in the use of narrow substrates (Losos, 1990; Irschick & Losos, 1996; Huyghe *et al.*, 2007). One could imagine that the use of narrow sleep perches might have been a precursor for the evolution of short limbs in *Anolis*, ultimately leading to the use of this narrow branch habitat throughout the day, and potentially driving the evolution of this ecomorph. Similarly, sleeping in actively constructed burrows would impose selective pressures on the efficiency of creating burrows and ultimately shape the evolution of forelimb morphology (e.g. Lowie *et al.*, 2018).

Beyond generating selection pressure on limb morphology or other phenotypic traits, use of specific sleep sites could have been a precursor for the evolution of habitat partitioning in some species. In *Anolis* lizards, multiple species often occur syntopically, yet specialise in different microhabitats (Losos *et al.*, 2003). If different sleep sites are selected by these different species (e.g. Singhal, Johnson & Ladner, 2007), then this may drive subsequent habitat-use patterns and could ultimately result in habitat partitioning. Similarly, if suitable sleep sites are scarce in the environment, then communal sleep sites may be preferred. This ecological constraint has been suggested to have facilitated the evolution of sociality (Leu, Kappeler & Bull, 2011). High predation or competition could also impact sleep architecture (Lima *et al.*, 2005; Lesku *et al.*, 2012), which may in turn, impact energy budgets (Ferretti *et al.*, 2019) and immune function (Besedovsky, Lange & Born, 2012) and as such drive the evolution of associated life-history traits.

VI. APPLIED SLEEP ECOLOGY IN AN ALTERED WORLD

Global change (e.g. urbanisation and artificial light at night) alters how ecological factors influence sleep (Raap, Pinxten & Eens, 2015; Ouyang *et al.*, 2017; Aulsebrook *et al.*, 2018). The dependence of many reptiles on specialised sleep sites may make them vulnerable to alterations of macro- and microhabitat features of these sites. For example, species that typically sleep in rock crevices are threatened by commercial rock collection (Schlesinger & Shine, 1994*a*) and minor displacement of rocks by tourists or reptile enthusiasts (Pike *et al.*, 2010*b*). Human modification of habitats (e.g. plantations) may limit optimal sleep sites (Bors, Mohanty & Shankar, 2020) and potentially affect the morphology (Miller, 2017) and demography (Taylor, Daniels & Johnston, 2016) of species that are now forced to sleep in unsuitable sites. Anthropogenic alterations to habitats have not gone unnoticed and several restoration programs have aimed to augment optimal sleep sites artificially by providing microhabitat features (Souter, Bull & Hutchinson, 2004; Goldingay & Newell, 2017) or altering the macrohabitat (e.g. canopy cover; Webb, Shine & Pringle, 2005). Artificial retreats mimicking the thermal and structural properties of sleep sites are also a popular method for restoration (Croak *et al.*, 2008*b*; Thierry *et al.*, 2009).

Apart from localised alterations to the environment, global change processes such as urbanisation, climate change, and biological invasions could influence the sleep ecology of reptiles. Urbanisation is associated with exposure to artificial light at night, known to alter sleep patterns in birds and mammals (Aulsebrook *et al.*, 2018). The reptilian pineal complex, consisting of the pineal gland and the parietal eye, is highly photosensitive (Tosini, 1997). This likely renders diurnal reptiles (sleeping at night) vulnerable to disturbance by artificial light (e.g. Kolbe *et al.*, 2021). However, behavioural adjustments such as selection of sheltered sites at night could reduce impacts (Aulsebrook *et al.*, 2018). On the other hand, nocturnal species could be affected by environmental change depending on their choice of sleep sites. For example, climate warming may be detrimental to geckos sleeping under rocks (Dayananda, Murray & Webb, 2017), but could be buffered by burrows used by skinks (Moore, Stow & Kearney, 2018). Flesch, Rosen & Holm (2017) posit that an increase in minimum temperatures due to climate warming may incur metabolic costs during nocturnal inactivity of diurnal lizards and in turn reduce energy allocation to other life-history traits, such as reproduction. A complete shift of activity phase for ratsnakes (*Pantherophis* spp.) from diurnal to nocturnal has been predicted with climate warming, which could potentially alter predator–prey dynamics (DeGregorio, Westervelt & Weatherhead, 2015).

The negative impacts of invasive species on environments can also include the displacement of native species from limited sleep sites (Cole, Jones & Harris, 2005; but see Yang *et al.*, 2012). Conversely, targeted capture–removal of sleeping individuals may aid in management of invasive species (Savidge *et al.*, 2011) and sleep ecology could form the basis of reintroduction plans for imperilled or protected taxa (Rehm *et al.*, 2018). We speculate that in rapidly expanding invasive populations, sleep itself may be reduced (e.g. Pérez-Santigosa, Hidalgo-Vila & Díaz-Paniagua, 2013) to facilitate exploration of novel environments. As an extreme case, in invasive populations undergoing 'spatial sorting', where selection pressure on dispersal differs between the core and periphery of the population, peripheral individuals may encounter novel environments at a much faster rate (Phillips & Perkins, 2019) and could potentially sleep less.

VII. PROSPECTUS

Although we found a sizeable number of studies that describe various characteristics of sleep in reptiles, most were not designed with a focus on sleep ecology, but were instead indirect observations of sleeping reptiles. Going forward, the field of sleep ecology in reptiles requires directed studies that ideally address outstanding questions (Fig. 4) and test hypotheses (Table 1). There are promising research directions in sleep ecology at the individual, ecological, and evolutionary scales (Fig. 4). At the individual level, research focussing on trade-offs among sleep traits, and repeatability within sleep traits can lead to a comprehensive, mechanistic understanding of sleep trait expression. The role of cognitive learning in reptilian biology is a promising field (Szabo, Noble & Whiting, 2021) and holds immense potential with respect to questions on sleep ecology, especially for quality discrimination (e.g. sleep site selection), spatial memory (e.g. spatio-temporal distribution of sleep sites), social learning (e.g. intra-specific sleep aggregations) and responses to change (e.g. sleep under global change processes).

At the ecological level (populations and communities), the benefits and costs of sleep traits can be understood better by quantifying differential success rates of each sleep trait type with respect to fitness (Fig. 4). Even in the few systematic studies on sleep ecology in reptiles, a comparative approach over space (e.g. Bors, Mohanty & Shankar, 2020) and time (Kolbe *et al.*, 2021) is seldom used and should be encouraged. Finally, at the evolutionary scale, patterns of repeated expression of sleep traits across lineages need to be quantified (e.g. Lesku *et al.*, 2006; Roth *et al.*, 2006; Libourel & Herrel, 2016). The severe trade-off often posed by the requirements of the active and sleep phases sets up potential conflicts in phenotypic traits, such as morphology, which could have fitness consequences over evolutionary timescales (Fig. 4).

Finally, with the advent of miniaturised technology (i.e. loggers), it has become increasingly possible for studies to collect ecophysiological data on sleep in the wild (Aulsebrook *et al.*, 2016). Notably, miniature loggers that are capable of recording key variables, such as accelerometry, EEG, EMG, and EOG, have been deployed to quantify sleep in the wild in sloths (Voirin *et al.*, 2014), sandpipers (Lesku *et al.*, 2012), frigate birds (Rattenborg *et al.*, 2016) among others (for details see Rattenborg *et al.*, 2017). Recent advances in logger miniaturisation (e.g. Massot *et al.*, 2019) have opened up the possibility for their use in small-sized reptiles (>50 g) to evaluate quantitatively the response of sleep traits to ecological factors. Reptilian sleep ecophysiology in the wild is likely to be a promising future direction to understand the evolution of sleep.

VIII. CONCLUSIONS

(1) Our review synthesises the previously disparate knowledge on the ecological context of sleep in reptiles and provides a comprehensive set of aspects to consider when studying sleep ecology. We find evidence for strong effects of predation, thermoregulation, and competition on sleep traits in reptiles, shaping their choice of sleep sites, their behaviour, morphology, and physiology during sleep, as well as their inter-individual interactions. We speculate on the evolutionary consequences of ecological constraints on sleep, especially in shaping morphology and sociality. Further, we identify gaps in each of these research themes and systematically quantify existing taxonomic bias.

(2) Currently, a range of non-specific terminology is used to describe probable sleep behaviour or sleep sites (e.g. 'rest', 'roost', 'retreat', 'inactivity', 'refuge'), which are also used to describe other behaviours such as hibernation and escape from predators. To distinguish sleep from other behaviours, we recommend studies use the behavioural criteria of sleep characterised by behavioural quiescence, typical sleep posture, an increased

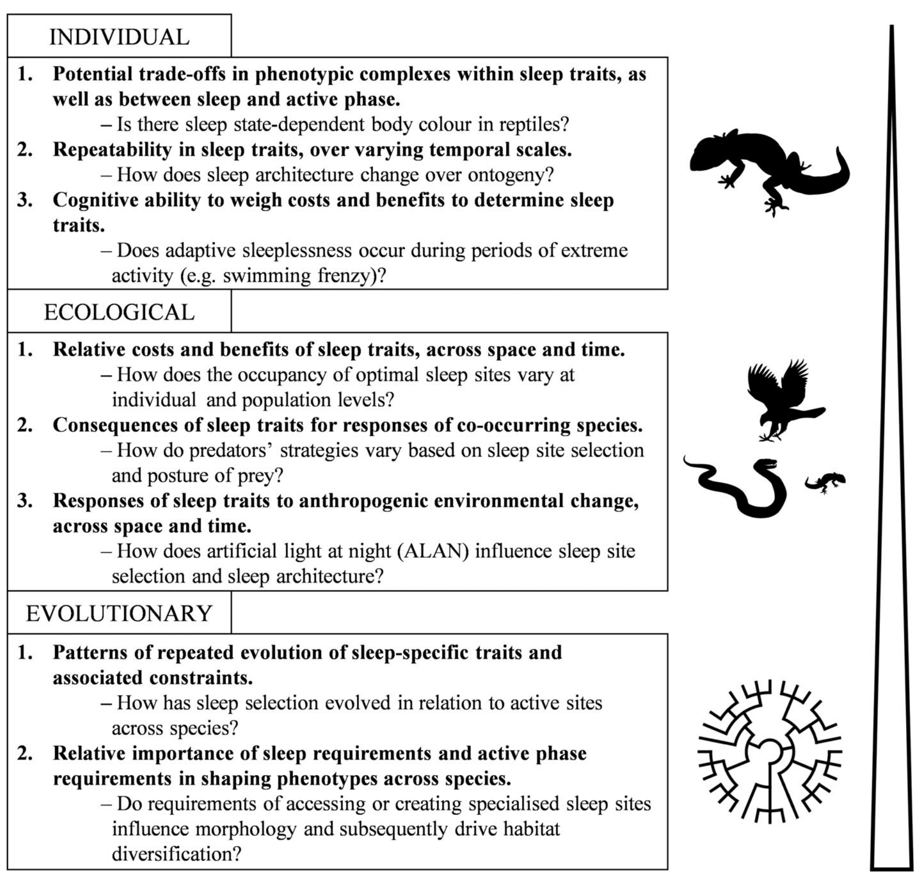

Fig. 4. Prospectus on key research directions, and corresponding examples of questions that examine the sleep ecology of reptiles at individual, ecological, and evolutionary levels.

stimulus threshold for arousal, rapid reversibility to wakefulness, and homeostatic regulation (Piéron, 1912; Flanigan, 1973; Tobler, 1995). This would enable consistency in the classification of sleep and serve as a stop-gap measure awaiting electrophysiological evidence to validate actual sleeping.

(3) Squamates, in particular, can serve as a model system to test the potential ecological, climatic, and energetic drivers of various aspects of sleep. This specious vertebrate order (*ca.* 11000 species) displays substantial ecological variability, under differing climatic environments, and therefore is ideal to study variation in sleep traits in a comparative context.

(4) Finally, our review lays the foundation for studies targeted at sleep ecology in reptiles (Fig. 4) and moreover provides direction for cross-taxa comparisons to find generalities in the drivers of ecological sleep traits across vertebrates.

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X. REFERENCES

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XI. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. PRISMA flow diagram describing stepwise literature assessment for the systematic review of sleep in reptiles, from the *Web of Science* on 23rd December 2019.

Fig. S2. Taxonomic patterns at the level of reptilian family observed in the literature on sleep.

Table S1. Compiled literature on sleep in reptiles, scored for the various ecological aspects of sleep studied.

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