The ecology of resting behaviour in terrestrial vertebrates, and potential effects of anthropization

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Abstract: Inactive behaviours are a major component of animals' lives, generally representing important proportions of time budgets. The conditions in which they occur are thus likely to have key effects on individual fitness. Yet, relatively little research has focused on the determinants and ecological consequences of inactive behaviours, likely in part because of the inherent difficulties associated with observing inactive animals. In particular, the effects of anthropization as a disruptor of patterns of inactivity are largely unexplored. In this review, we propose to bring quiet wakefulness, sleep, and daily torpor together under the term of "resting", to facilitate the study of inactivity in terrestrial vertebrates, in wild settings. We detail the shared physiological and environmental drivers of resting behaviours, as well as their ecological outcomes. We suggest that the diversity of resting behaviours enables animals to respond flexibly to constraints linked with metabolism, resource availability, predation risk, and thermoregulation. We detail how the location, timing, duration, and social context in which resting occurs shape a resting strategy that may be adjusted in response to variable environmental conditions. Finally, we explore how anthropization may affect the resting strategies of terrestrial vertebrates through direct disturbances, alterations of landscapes and communities, and the effects of climate change.

Keywords: behavioural adjustments, daily torpor, disturbance, human activity, inactivity, perturbation, sleep

I. Introduction

An animal's life is a sequence of behavioural states, whose timing and duration are adjusted in response to physiological and environmental challenges, in a way that is assumed to be shaped by natural selection (Baum, 2013; Gunn *et al.*, 2022). A coarse, yet obvious and striking, classification of these behavioural states can be made between active (e.g., moving, foraging) and inactive ones, ranging from long-lasting dormant states (e.g., hibernation) to daily sleep, and quiet wakefulness. The costs and benefits of active states are usually well understood, and often quantified (Kacelnik & Houston, 1984; Pyke, 2019). By contrast, the costs and benefits associated with the full range of inactive states remain comparatively less well understood (Lesku & Rattenborg, 2022; Lesku & Schmidt, 2022). Yet, inactivity represents important proportions of daily time budgets, often spanning more than half of the 24-h period (Herbers, 1981; Campbell & Tobler, 1984). This prominence in time budgets suggests that the context under which inactive behaviours occur will likely affect individual fitness.

Inactivity may be imposed by both physiological and environmental constraints. For example, terrestrial vertebrates stay inactive to maintain their energetic balance (Walker & Berger, 1980; Korstjens, Lehmann & Dunbar, 2010; Ruf & Geiser, 2015), for thermoregulation (Kearney, Shine & Porter, 2009; Davimes *et al.*, 2018; Briscoe *et al.*, 2022), but also to avoid predators (Lima *et al.*, 2005; Bonnot *et al.*, 2020). More broadly, inactivity helps to avoid stressful conditions, both abiotic and biotic, often in response to multiple stressors. Animals also stay inactive when other behaviours are unprofitable (Korstjens *et al.*, 2010) and some remain inactive in groups to maintain social bonds (Anderson, 2000; Loftus *et al.*, 2024). In addition, all animals need sleep—a very remarkable inactive behaviour—on a regular basis to fulfil various metabolic, restorative, or developmental processes, at both cerebral and whole-body levels (Tononi & Cirelli, 2014). A number of metabolic and neurophysiological functions are specifically performed during sleep, which internally enforces a certain amount of daily sleeping time (Schmidt, 2014; Anafi, Kayser & Raizen, 2019). Yet, sleep patterns vary across species (Siegel, 2009; Ungurean *et al.*, 2020), and are largely influenced

by ecological factors (Roth, Rattenborg & Pravosudov, 2010; Aulsebrook *et al.*, 2016; Ungurean *et al.*, 2020; Mohanty *et al.*, 2022). By alternating over time, several inactive behaviours, such as quiet wakefulness, sleep, and daily torpor form consolidated inactive phases (Campbell & Tobler, 1984; Kräuchi & Deboer, 2011), which can show important variations, across individuals and environmental gradients (Gaynor *et al.*, 2018; Fradin *et al.*, 2025). Traits relative to daily inactive phases—such as their timing, duration, location, and the kinds of inactive behaviours involved—are highly adaptable (Daan, 1981; Reinhardt, 2020), and together define resting strategies, which animals may fine-tune to tackle ecological challenges (Nowack, Stawski & Geiser, 2017; Shukla, Kilpatrick & Beltran, 2021; Mohanty *et al.*, 2022). Disruption of inactivity and alterations of the context under which it occurs are thus likely to result in substantial negative ecological impacts.

As the anthropization of ecosystems increases, disruptions of animal behaviour are becoming common and widespread, with significant ecological consequences (Sih, Ferrari & Harris, 2011; Candolin, Fletcher & Stephens, 2023; Gilbert *et al.*, 2023). The impacts of landscape alterations, direct disturbances, climate change, and other anthropic disturbances on animal habitat use and foraging behaviour have been well described, but their effects on inactive behaviours remain poorly studied (Berger-Tal *et al.*, 2011; Tougeron & Abram, 2017; Candolin *et al.*, 2023). Yet, anthropization could affect animals' inactivity in a variety of ways, with potential impacts on individual fitness and species interactions. Animals disturbed while inactive might become exposed to unfavourable conditions or suffer from sleep disruption (deprivation, fragmentation or shift). Reactive behavioural adjustments such as flight (Price, 2008) or increased vigilance (McBlain, Jones & Shannon, 2020) can ultimately lead to long-lasting effects on animal behaviour, landscape use, and fitness (e.g., Ordiz *et al.*, 2013; Kolbe *et al.*, 2021). Indirect effects of anthropization, like climate change, landscape alterations (Bradsworth *et al.*, 2021), light pollution (Aulsebrook, Johnsson & Lesku, 2021), species introduction, and predator depletion are also likely to influence where, when, and how long animals remain inactive. Thus, a better understanding of animals' resting strategies is essential for a comprehensive assessment of anthropic impacts on animal behaviour and activity patterns (Shukla *et al.*, 2021).

In this review, we point out the importance of inactive behaviours from an ecological perspective and explore how human activities may interfere with them. Inactive behaviours, such as sleep, quiet wakefulness, and dormant states, correspond to very distinct physiological states (Blumberg & Rattenborg, 2017). Yet, under natural conditions, they are generally complicated to tell apart in practice (Rattenborg *et al.*, 2017). To overcome this issue, we propose to pool all inactive behaviours with a daily cyclicity under the term "resting", thus excluding seasonal dormancies. This concept offers a straightforward framework to study inactive behaviours in wild animals, thus facilitating the study of the ecological processes at play.

We first provide a detailed behavioural definition of resting, and point out how advances in biologging technologies facilitate the monitoring of this behaviour. We then review previous work on why animals rest, before describing how ecological constraints shape resting strategies. Finally, we explore the current knowledge on how anthropic disturbances might affect resting behaviour, and assess potential consequences. We tried, as much as possible, to broaden our thinking to any form of resting, although much of the available literature focuses specifically on sleep, generating an unavoidable bias. This review focuses on terrestrial vertebrates, and we intended to be as inclusive as possible in terms of taxa. Even though mammals are overrepresented in the literature on resting behaviours, we expect a wide taxonomic range of species to be concerned by the ecological mechanisms described in this review.

II. What is resting?

II.(1) A behavioural definition of resting

II.(1)(a) A behavioural continuum

The dichotomy between active and inactive behavioural states is useful, but behaviours can further be seen as fitting along a gradient ranging from low to high levels of activity (Siegel, 2009; Rial *et al.*, 2010; Lesku & Schmidt, 2022)(*Figure 1*). This continuum reflects energy consumption and awareness of the surrounding environment. It fits traditional behavioural states (e.g., sleep, daily

torpor) as well as their range in activity levels/energy consumption (e.g., deeper to shallower sleep and torpid states), and transition states (e.g., drowsiness). We propose to define 'resting' as any inactive behaviour occurring on a daily basis. This corresponds to a continuous interval on the continuum presented in *Figure 1*, excluding active behaviours and seasonal dormancies. Considering that, resting can be defined behaviourally by i) a low level of general activity, with little motion, ii) a specific relaxed posture, and iii) a duration and cyclicity comprised within the 24-h cycle. This definition fits three main resting states: quiet wakefulness, sleep, and daily torpor.

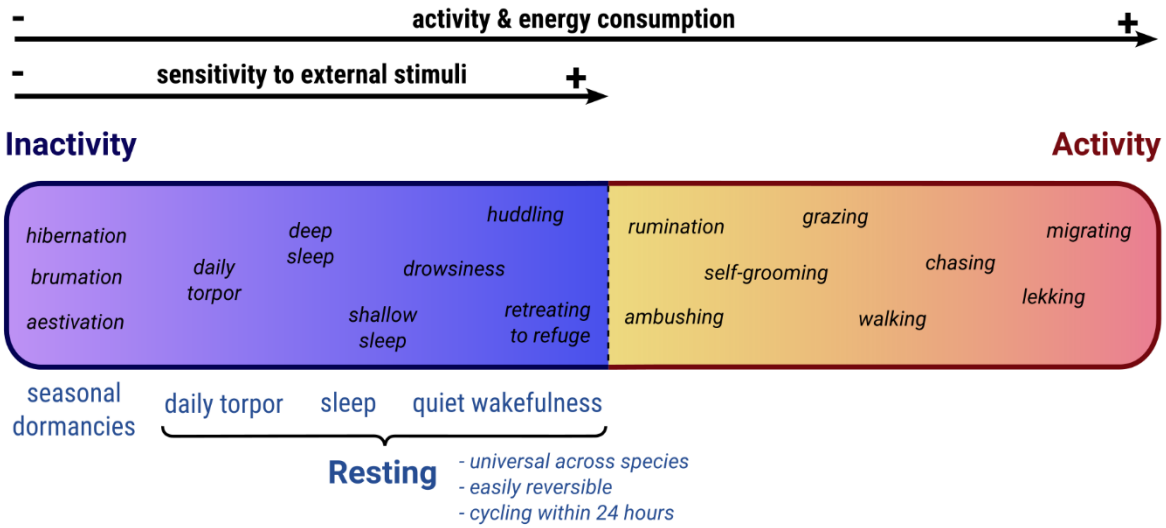

Figure 1. *Our definition of resting behaviour in terrestrial vertebrates, seen on a continuum ranging from energy-saving to energy-consuming behaviours.*

II.(1)(b) Quiet wakefulness

Quiet wakefulness is associated with a behavioural quiescence and a relaxed posture, but does not correspond to a standard neurological state, with a stereotypic electroencephalographic signature. It is easily distinguished from most active behaviours based on accelerometry. The distinction between active and inactive behaviours, however, is not always clear-cut, as some behaviours functionally related to activity involve motionlessness (e.g., ambushing, rumination). These ambiguous behaviours may sometimes be distinguished from resting as they are not

associated with a relaxed posture (e.g. ambushing), but ultimately whether they should be qualified as resting or not will likely depend on the focus of the study.

Telling quiet wakefulness apart from sleep is particularly difficult with behavioural criteria only (e.g., eyelids can be open or closed: Kortekaas & Kotrschal, 2019), and generally requires measuring brain activity with electroencephalography (EEG) (Bagur *et al.*, 2018). Among all resting states, quiet wakefulness has the lowest arousal threshold—the stimulus required to trigger a reaction—and allows for the most vigilance (Lima *et al.*, 2005; Rattenborg *et al.*, 2017). Animals are generally quietly awake before and after sleep, which leads to long-lasting contiguous resting phases. Despite reaching high proportions of daily time awake in many species (Herbers, 1981; Mohanty *et al.*, 2022), quiet wakefulness has received very little attention from ecologists.

II.(1)(c) Sleep

So far, sleep has received most attention from physiologists and neurologists, but interest from ecologists is growing. While humans and rodents had long been the sole focus (Rattenborg *et al.*, 2017), sleep has now been described in a wide range of vertebrate species (Libourel & Barrillot, 2020; Ungurean *et al.*, 2020). It is a reversible state of low responsiveness and awareness of the environment. Compared to quiet wakefulness, it shows an increased arousal threshold and usually a more specific relaxed posture. Compared to dormant states, it is quickly reversible to wakefulness after arousal (Campbell & Tobler, 1984). Another specificity is its homeostatic regulation: sleep cycles are interlaced with circadian rhythms (Borbély *et al.*, 2016) and sleep deprivation is generally followed by a compensatory increase in sleep behaviour called 'rebound' (Siegel, 2009). A reliable identification of sleep behaviour most often depend on EEG as behavioural criteria (e.g., increased arousal threshold) cannot be tested without disrupting the behaviour (Cirelli & Tononi, 2008).

Sleep comprises deeper and shallower states, associated with a variety of neurophysiological functions (Lima *et al.*, 2005; Mignot, 2008). In mammals, birds, and arguably other taxa (Libourel & Herrel, 2016; Libourel & Barrillot, 2020), EEG enables the distinction of two main sleep states that

alternate throughout sleep phases: slow-wave sleep (SWS) and rapid eye movement (REM) sleep. SWS is characterized by high amplitudes and slow frequencies of the EEG, and occurs in a variety of depths or intensity (Rodriguez *et al.*, 2016). Among terrestrial vertebrates, some birds (Rattenborg, Amlaner & Lima, 2000) and possibly crocodiles (Kelly *et al.*, 2015) are also able to perform unihemispheric SWS, in which one cerebral hemisphere is awake while the other sleeps. REM sleep is associated with a wake-like EEG profile, the inhibition of the thermoregulation mechanisms, and—excepting muscular twitches and eye movements—the loss of muscle tone (Blumberg *et al.*, 2020). This last criterion sometimes implies a postural change compared to SWS, possibly making REM sleep recognizable behaviourally (e.g., in giraffes: Burger *et al.*, 2020). In most cases however, EEG is required to differentiate REM sleep and SWS with certainty (Rattenborg *et al.*, 2017). In reptiles, two cerebral sleep states can also generally be identified, showing some similarities with mammalian SWS and REM (Libourel & Barrillot, 2020). In endotherms, sleep is accompanied by a slight decrease in body temperature (Walker & Berger, 1980; Harding, Franks & Wisden, 2019). Sleep patterns differ greatly between species—with daily duration ranging from a few hours to more than half of the 24-h period (Campbell & Tobler, 1984)—and could also be highly flexible within species, although empirical evidence from the wild is limited (Capellini *et al.*, 2010; Ungurean *et al.*, 2020).

II.(1)(d) Daily torpor

Daily torpor is a deep behavioural quiescence similar to hibernation, but with a 24-h cyclicity. It is displayed by many small mammals and in some birds, called daily heterotherms, when exposed to acute energetic stress (Walker & Berger, 1980; Geiser, 2013). Under such conditions, daily heterotherms are able to alternate daily between normothermic phases—with high body temperature—and heterothermic torpid phases—with drastically reduced body temperature and metabolic rate (Ruf & Geiser, 2015). Reduction of body temperature and metabolic rate is less substantial during daily torpor than during seasonal hibernation, but is largely greater than that during sleep (Walker & Berger, 1980). Although it is entered through sleep, daily torpor does not

fulfil the neurophysiological functions of sleep, and thus may not replace sleep altogether (Kräuchi & Deboer, 2011; Blumberg & Rattenborg, 2017).

II.(2) Currently available tools and methods for the study of resting

Most animal species are difficult to observe in the wild, and ecologists increasingly rely on biologgers (animal-borne sensors) to collect behavioural data, a trend facilitated by progress in electronics and embedded systems (Whitford & Klimley, 2019). The use of biologgers is particularly adapted to the study of resting, which lasts long periods, and often happens in hidden places. Various sensors can be relevant for this purpose, each with pros and cons, as summarized in *Table 1*. We briefly highlight below some key points.

For years, only location data—often collected using GPS loggers—were available to ecologists, but these data alone are not sufficient to study resting properly. When acquired at a reasonably high frequency, location data can be segmented across 'behavioural modes' (Edelhoff, Signer & Balkenhol, 2016) and classified using hidden Markov models (McClintock & Michelot, 2018), for instance. Even so, they are affected by GPS errors and most importantly, they are insufficient to discriminate inactive versus active behaviours occurring within a limited space (R. Dejeante, S. Chamaillé-Jammes, A. Mosser, A.R. Rodgers & J.M. Fryxell, in preparation). As a result, any 'resting' behavioural mode detected is generally a mixture of active and inactive behaviours. Although this approach can be useful to quickly gain a coarse view of when and where resting occurs, a proper study of resting requires different sensors.

Most GPS loggers used for tracking animals now include an activity logger or an accelerometer. These can reveal whether an animal has been mostly immobile during an interval of a few minutes (activity loggers) or less than a second (accelerometers) (Brown *et al.*, 2013; Whitford & Klimley, 2019). The accelerometric signature of resting usually differs greatly from that of active behaviours, and it is therefore generally easy to segment time budgets between active and inactive behaviours based on the data obtained from activity loggers or accelerometers (e.g., Fradin & Chamaillé-Jammes, 2023; Mortlock *et al.*, 2024). Because these sensors require little energy,

they can record high-resolution data for months or even years, allowing the study of temporal patterns of resting from daily to seasonal timescales.

Table 1. *Brief description of various animal-borne loggers that can be relevant when studying resting in wild animals.*

Logger	Data	Pros	Cons	Example of case study
Location loggers (e.g., GPS)	- Geographic coordinates - 2D spatial data - Custom acquisition frequency	- Commercial products available for many species - Easy deployment - Can sometimes transmit data remotely - Efficient to detect resting sites when resting times are known and last long	- Subject to noise due to location errors - Insufficient to discriminate immobility and spatially restricted activity	(Markham, Alberts & Altmann, 2016)
Activity loggers	- Either continuous 'activity level' or binary 'active or inactive' data - 1D signal - Collected every few minutes	- Often sufficient to detect immobility - Easy deployment - Very long monitoring (months to years) - Can sometimes transmit data remotely	- Not usable for fine-scale behavioural classification - Cannot be used to infer posture	(Fradin & Chamaillé-Jammes, 2023)
Accelerometers	- Acceleration data - Usually 3D signal - Temporal resolution higher than 1 Hz	- Easy deployment - Very long monitoring (months, years) - Sometimes provides information on posture - Allow precise timing of inactivity vs activity	- Huge data files - Only short bursts can usually be transmitted remotely - Complex data analysis compared to activity data	(Mortlock *et al.*, 2024)
Brain activity loggers	- Electrical activity measured from an electrode - 1D signal, although several electrodes are generally used, at several locations in or above the brain - Temporal resolution higher than 100 Hz	- Allow the detection of sleep - Allow the identification of sleep states	- Trade-off between invasiveness and performance (stability and constraints on deployment). - Usually short monitoring imposed by power consumption - Huge data files that cannot be transmitted remotely	(Libourel *et al.*, 2025)
Heart rate loggers	- Heart beats per minute - 1D signal	- Long monitoring (months) - Effective to monitor torpor	- Invasive (internal logger)-Insufficient to detect immobility - Noisy during activity	(O'Mara *et al.*, 2017)
Body temperature loggers	- Body temperature (cutaneous, subcutaneous, or internal) - 1D signal	- Long monitoring (months) - Effective to monitor torpor	- Trade-off between invasiveness (internal logger) and precision (cutaneous logger) - Insufficient to detect immobility - Subject to temporal inertia	(McGuire *et al.*, 2014)
Video loggers	- Video files - Often collected in	- Allow detecting immobility (during bursts	- Short monitoring imposed by great power consumption	(Dejeante *et al.*, 2025)

	bursts of a few seconds following a custom schedule	of recording only) - May sometimes provide information on posture - May allow the study of social aspects of resting	- Huge data files that cannot be transmitted remotely - Video analysis is complex and cumbersome	

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209 Specifying the neurophysiological state of a resting animal is challenging. In particular, for a
210 robust assessment of whether an animal is quietly awake or asleep, it is necessary to record its
211 brain activity with a neurologger (Rattenborg *et al.*, 2017). Indeed, sleep cannot be directly
212 observed: even in an apparently obvious sleep posture, an animal might be awake. Conversely,
213 many animals can sleep standing with open eyes, which makes them look awake (Rattenborg *et al.*,
214 2017). Recording brain waves clarifies these situations, and allows distinguishing SWS and REM
215 sleep, which likely serve different functions (Libourel *et al.*, 2025). However, it requires surgery,
216 with varying degrees of invasiveness depending on the device. Some require drilling through the
217 skull to reach the brain (Malungo *et al.*, 2021), while others only involve a subcutaneous electrode
218 right above the skull (Libourel *et al.*, 2025). Besides, the duration of data collection is limited to a
219 few days or weeks for most species, as the position of the logger—directly on the head—strongly
220 constrains battery size. Therefore, the study of sleep in the wild, although highly needed, still
221 remains limited to specific settings and short durations (Rattenborg *et al.*, 2017). Some recent
222 papers argue that sleep in wild animals can be derived from posture and accelerometry (e.g.,
223 Burger *et al.*, 2020; Mortlock *et al.*, 2024), but validations with neurologgers are rare, and when
224 conducted, suggest a low to moderate correlation between accelerometry and sleep (Libourel *et*
225 *al.*, 2018; Malungo *et al.*, 2021; van Hasselt, Piersma & Meerlo, 2022).

226 A few other loggers may be useful to study resting animals. Heart rate and body temperature
227 loggers are effective to detect torpor (McGuire, Jonasson & Guglielmo, 2014; Ruf & Geiser, 2015), and
228 may help identifying sleep (Kreeger *et al.*, 1989), although they are never self-sufficient for that
229 purpose. While these loggers have improved greatly in quality in recent years, there still remains
230 a trade-off between performance and invasiveness (Williams *et al.*, 2021). Finally, video loggers
231 may be used to detect resting through direct observation of behaviour and posture (Dejeante,

Valeix & Chamaillé-Jammes, 2025). Although this approach is highly battery-consuming, it can provide rare information on the social context in which resting happens.

To sum-up, although studying the various resting states independently would bring much insight to ecologists (Rattenborg *et al.*, 2017), this is still complex in the wild, and only possible over short periods. In the current context of tools and methods available to ecologists, studying resting viewed as a concatenation of quiet wakefulness, sleep, and daily torpor is therefore relevant, if interpreted based on commonalities between resting states (e.g., energy savings, space use restrictions, predation risk management, thermoregulation benefits).

III. Why rest?

As proposed by Dunbar et al. (2009), the time allocated to resting can be seen as a mixture of two functionally distinct categories. Rest can be "enforced", when it is a functional response to intrinsic or extrinsic constraints, or "uncommitted" when it can be seen as a 'by default' behaviour, when other behaviours are not required or would not bring a net benefit. When more time is required every day for any given activity (e.g., when distance between foraging and resting sites increases, thus imposing additional travel time), animals adjust their time budget by drawing on uncommitted resting time. As such, uncommitted rest corresponds to spare time, which may be allocated to any other activity as required. On the contrary, enforced rest cannot be forgone as easily. It is displayed not because no other activity is required, but as a functional response to a variety of constraints. When all uncommitted resting time has been reallocated to activity, animals in need of additional time (for more travelling in the example above) must reduce other activities (e.g., social time), because enforced resting time is incompressible (Dunbar *et al.*, 2009; Korstjens *et al.*, 2010).

Obviously, rest—just as any behaviour—is highly plastic. A behavioural response to intrinsic or extrinsic constraints results more often of a compromise than of a life-or-death necessity. Consequently, animals will sometimes be able to forgo even enforced rest in case of emergency

(just as they will generally be able to skip feeding for one day). However, to reduce or bypass enforced rest is not sustainable in the long term, which contrasts with uncommitted rest. It is therefore essential to distinguish between these functional categories of resting to understand how animals manage their time budgets. Here, we list the major drivers of enforced and uncommitted rest to describe i) what compels animals to spend time at rest, and ii) what drives animals to remain at rest when no other activity is required (*Figure 2*).

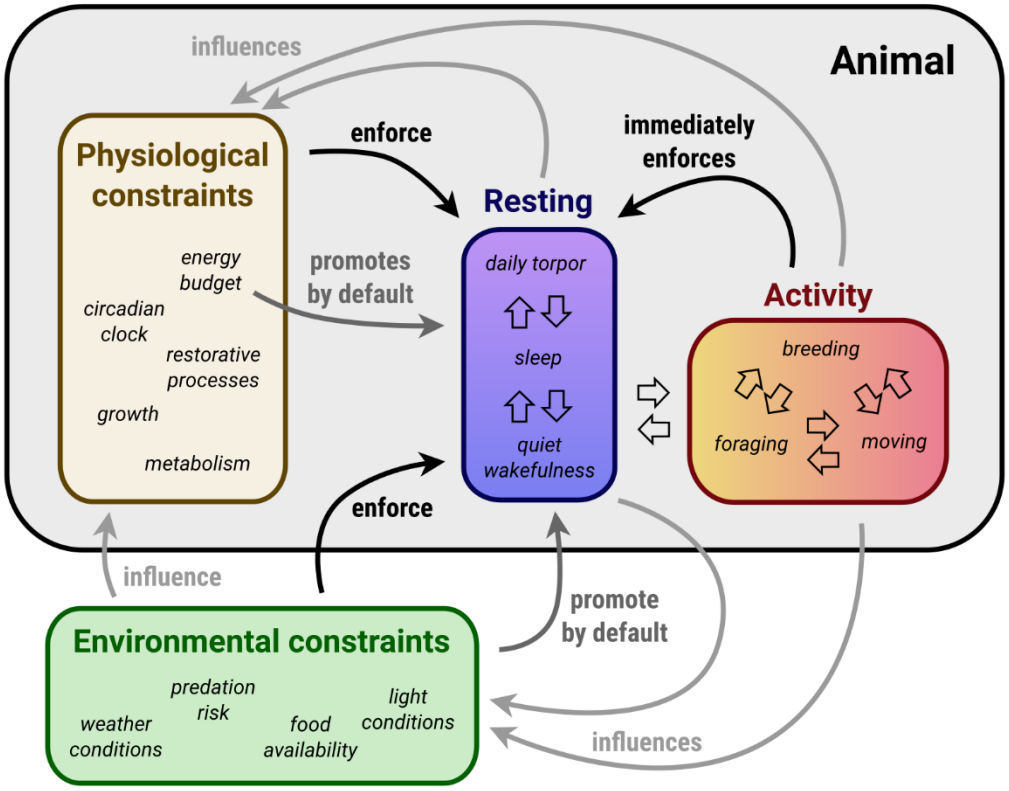

Figure 2. *Physiological and environmental drivers of resting. Empty arrows indicate shifts between behavioural states.*

III.(1) Enforced rest

III.(1)(a) Immediate recovery resting

Resting may be displayed as a homeostatic reaction closely following specific active behaviours. Muscle fatigue, for instance, may call for immediate compensatory resting (Rozier-Delgado *et al.*, 2025). Such need for post-effort recovery is particularly important for ectotherms,

due to their low aerobic capacity (Wagner & Gleeson, 1997). Similarly, both ectotherms and endotherms may need resting for thermal recovery after being active significantly outside their thermoneutral zone (St Juliana & Mitchell, 2016; Parlin, Schaeffer & Jezkova, 2020; Taylor *et al.*, 2021). Because it immediately follows activity, this kind of state-dependent resting is highly constrained in time and space. However, it is usually short-term and generally accounts for small proportions of total resting time.

III.(1)(b) Physiological constraints

Because it allows energy savings, resting may be enforced by energetic constraints (Dunbar *et al.*, 2009). For example, animals with low-digestibility diets generally need to rest for extended periods of time every day, to both aid digestion, and to comply with their tight energy budgets (Korstjens *et al.*, 2010; Ryan *et al.*, 2013). Likewise, adjustments of resting behaviour to compensate for temporarily increased energetic needs have been described in many contexts including reproduction (Willisch & Ingold, 2007; Geiser, 2013), migration (McGuire *et al.*, 2014; Ferretti *et al.*, 2019), and illness (Hart, 1988; Imeri & Opp, 2009; Duriez *et al.*, 2023). Such adjustments include both the augmentation of resting time and the specific use of energy-saving resting states. For instance, daily torpor is extremely effective at saving energy and may be used preferentially under energetic stress (Ruf & Geiser, 2015).

In addition to the above, all animals need to sleep regularly to maintain the homeostatic balance of their physiological processes (Ungurean *et al.*, 2020; but see Lesku & Rattenborg, 2022). Although it is observed universally across vertebrate taxa, suggesting an ancestral and vital shared function (Schmidt, 2014), whether sleep has one fundamental underlying function remains unclear (Freiberg, 2020; Libourel & Barrillot, 2020). Sleep has been linked to a diversity of essential restorative processes, ranging from energy homeostasis to synaptic plasticity, memory consolidation, and maintenance of the immune function (Mignot, 2008; Imeri & Opp, 2009; Roth *et al.*, 2010; Tononi & Cirelli, 2014; Schmidt *et al.*, 2017). Schmidt's energy allocation theory (2014) states that some necessary physiological functions (involved in repair, maintenance, cognitive, and

297 growth processes) are downregulated during wake and upregulated during sleep, to optimize
298 overall daily energy consumption across the sleep-wake cycle. This suggests that sleep enables
299 animals to perform energy-consuming physiological processes linked with body maintenance at
300 a specific time of the day (sleeping time), so that performance in other activities is enhanced at
301 other times of the day (when awake). As a result, all terrestrial vertebrates must sleep on a regular
302 basis, with their sleep-wake cycle being most often interlaced with circadian rhythms (Borbély *et*
303 *al.*, 2016). In fact, sleep deprivation is usually followed by adverse effects on cognition and
304 behavioural performance (Lesku *et al.*, 2012; Lesku & Rattenborg, 2022), and by a sleep rebound—
305 although examples from the wild are scarce (Raap, Pinxten & Eens, 2016; Reinhardt, 2020).

306 The amount of sleep that is needed for the homeostatic balance of physiological processes
307 depends on individual characteristics, with potentially important, yet rarely investigated, inter-
308 individual and intra-individual variability (Ungurean *et al.*, 2020; Mortlock *et al.*, 2024). In particular,
309 it strongly depends on life stage, as sleep is involved in developmental processes (Jouvet-Mounier,
310 Astic & Lacote, 1969; Frank, 2020). REM sleep is especially predominant during development
311 compared to adult life (Blumberg *et al.*, 2020). How much time is needed for an animal to fulfil its
312 physiological need for sleep is also influenced by ecological factors (e.g., trophic position,
313 reproductive status: Schmidt, 2014; Blumberg & Rattenborg, 2017; Siegel, 2022) in ways that are not yet
314 fully understood (Lesku *et al.*, 2009; Lesku & Rattenborg, 2022).

315 *III.(1)(c) Environmental constraints*

316 For many terrestrial vertebrate species, the daily fluctuations of abiotic (e.g., temperature) and
317 biotic factors (e.g., activity patterns of predators) impose resting for a significant proportion of
318 the 24-h cycle (Dunbar *et al.*, 2009).

319 Resting is an efficient strategy for thermal stress mitigation (Kearney *et al.*, 2009; Terrien, Perret
320 & Aujard, 2011), as well as to maintain hydric balance (Moore, Stow & Kearney, 2018), as it allows to
321 retreat to buffered sites (e.g., burrows, crevices, shelters). In addition, many postures associated
322 with proactive thermoregulation (e.g., basking, huddling solitarily or in groups) are only

compatible with resting (Dasilva, 1993; Gilbert *et al.*, 2010; Terrien *et al.*, 2011). Therefore, rest is frequently displayed as an adaptive behavioural response to periods of the 24-h with ambient temperature and hygrometry significantly away from animals' neutral zone (Dunbar *et al.*, 2009; Moore *et al.*, 2018). For many small endotherms, daily torpor is required to survive repeated and intense thermal stresses, as it keeps energy expenditure at the lowest when extreme environmental conditions make the maintenance of body temperature too costly (Geiser, 2013; Hetem *et al.*, 2016). The other resting states (sleep, quiet wakefulness) vary in terms of thermoregulatory performance, and animals use them alternatively to maintain their thermal equilibrium under adverse weather conditions, while dealing with other constraints at the same time (e.g., Davimes *et al.*, 2018; Mortlock *et al.*, 2024). While most resting states improve thermoregulation capacity compared to active states, REM sleep is a notable exception, as it suspends temperature regulation in mammals and birds (Schmidt, 2014; Blumberg *et al.*, 2020), and seems to be maximized at thermoneutral temperature (Davimes *et al.*, 2018; Komagata *et al.*, 2019; but see van Hasselt *et al.*, 2024). In many ectotherms, the fluctuations of ambient temperatures enforce long bouts of resting every day, either because too cold conditions reduces metabolic activity, or too hot conditions forces them to retreat to a refuge to avoid overheating (Taylor *et al.*, 2021).

Resting is also an efficient and widespread anti-predator strategy, as it allows to retreat to safe areas, and promotes motionlessness and camouflage (Lima *et al.*, 2005). Some animals rely on this strategy to survive periods of high predation risk, suggesting that predators' patterns of activity can impose a portion of daily resting time (Halle, 2000). Animals resting under the risk of predation must balance their energy consumption with their ability to assess predation risk and react to imminent danger. Resting states range from energy-saving, low-vigilance states to less energy-saving vigilant states. Torpid animals are most vulnerable, as they are unable to react to external stimuli. However, they may remain inactive for longer periods. Daily heterotherms may even trade foraging efficiency for more safety, by reducing overall energetic needs using more daily torpor (Turbill & Stojanovski, 2018). Quiet wakefulness allows for efficient responses to predator

encounters but is more energy consuming. Although sleep is often viewed as a vulnerable state, it is a compromise between those two extremes (Lesku & Schmidt, 2022). It permits some energy savings but remains quickly reversible and allows some processing of sensory information (Lima *et al.*, 2005; Siegel, 2009), particularly with unihemispheric SWS (Rattenborg *et al.*, 2000). Therefore, animals often alternate between quiet wakefulness and sleep when predation risk is high (Lesku *et al.*, 2008; Burger *et al.*, 2020).

In conclusion, a significant proportion of daily resting time may be enforced by environmental factors such as adverse weather conditions and predation risk. When facing such constraints, animals may display different resting states to adjust their level of awareness of the environment, their thermoregulation capacity, and thus enhance survival and energy conservation. The physiologically enforced resting time (e.g., the time needed for sleep) is generally allocated specifically at times when environmental conditions also enforce (or at least promote) rest. As a result, many animals undergo a daily rest-activity cycle, that encompasses the homeostatically regulated sleep-wake cycle (Riede, van der Vinne & Hut, 2017).

III.(2) Uncommitted rest

Resting is not always a functional response to intrinsic or extrinsic constraints. A portion of daily resting time displayed by animals is uncommitted, which means that it can be reallocated to other activities if necessary.

Environmental conditions sometimes make activity unprofitable and promote rest by default. For instance, species that rely on vision for foraging most often rest throughout the night (Daan, 1981), and coastal foragers rest during high tide when feeding grounds are inaccessible (Dominguez, 2003). In these examples, not being able to forage does not compel these animals to rest. Part of the time they spend resting (the uncommitted part) could be reallocated to travel or social activities if required. Physiologically enforced rest (e.g., through the need for sleep) may be specifically allocated to times when activity is least beneficial, but such unprofitable conditions may last longer than needed to fulfil these physiological requirements, which makes room for

uncommitted resting time. In these conditions, resting may be preferred over other behaviours, for safety and energetic benefits. For example, insectivorous bats such as *Molossus molossus* tune their activity with the daily peaks of insect catchability (which may last less than an hour), and spend much of the remaining time at roosting sites, to reduce energy consumption and predation risk (O'Mara *et al.*, 2017).

Even when environmental conditions could be compatible with activity, animals tend to keep resting when they have met their daily energetic requirements, in accordance with the satisficing theory of foraging (Ward, 1992). Such uncommitted rest, sometimes referred to as 'laziness' (Herbers, 1981) has been evidenced in primates (Korstjens *et al.*, 2010) and is commonly observed in animals kept captive with consistent food supply (Fureix & Meagher, 2015). The allocation to resting of any spare time left after the achievement of obligate daily tasks may allow energetic savings. However, as time is a precious and limited resource, uncommitted rest most importantly constitutes a time capital, available to be allocated to other behaviours whenever needed (Dunbar *et al.*, 2009). Because an important part of daily rest is enforced by physiological and environmental constraints, it is generally complicated to assess how much resting time is uncommitted, in a given individual. Yet, this would provide an interesting insight into how tight an individual's time budget is, and thus how much time it could reallocate to activity, in the case of a change in environmental conditions (Dunbar *et al.*, 2009).

IV. How to rest?

Given the variety of drivers of resting behaviour, it is not surprising that resting strategies are extremely diversified. The range of available resting states provides a way to adjust several potentially conflicting parameters, such as energy conservation, awareness of the environment, and ability to answer external stimuli (Ferretti *et al.*, 2019). The integration of those distinct inactive states in a global resting strategy offers flexibility in animals' behavioural responses to environmental conditions. The temporal organization of resting and the spatial and social

contexts in which it occurs are key to understanding how animals respond to physiological and environmental pressures to rest (Shukla *et al.*, 2021).

IV.(1) How long to rest?

Resting accounts for important proportions of all animals' time budgets. Even species that are famous for sleeping little, like large ungulates and elephants, spend at least 20% of their time resting (Owen-Smith & Goodall, 2014; Gravett *et al.*, 2017). Total resting time depends on how much of the 24-h cycle is available and profitable for activity, and how much rest is needed to fulfil physiological demands (through sleep and energy savings). This is influenced by numerous interacting ecological traits, such as habitat or trophic level, physiological traits, such as diet or basal metabolic rate (Dunbar *et al.*, 2009; Capellini *et al.*, 2010), and individual characteristics, such as age (Frank, 2020) or health condition (Imeri & Opp, 2009). This great diversity of interacting drivers means that establishing correlations between daily resting time and ecological traits is rarely simple (Lesku *et al.*, 2009). This has almost exclusively been attempted for sleep duration (rather than rest), and in mammals, with limited results (Lesku *et al.*, 2009; Siegel, 2022). A few rare studies focused on resting rather than sleep, showing for instance that frugivorous primates, which need time to travel between fruiting trees, rest less than folivorous ones, which need more time for digestion (Dunbar *et al.*, 2009; Masi, Cipolletta & Robbins, 2009). Reports on the drivers of rest duration in non-mammals are even rarer (e.g., in reptiles Mohanty *et al.*, 2022).

Individuals may further adjust resting time in response to environmental changes. When increased foraging time is required (e.g., when increased predation risk reduces foraging efficiency), animals may adjust by reducing uncommitted rest (McFarland *et al.*, 2014). They may also compensate a reduction of resting time with more energy-saving resting states (Turbill & Stojanovski, 2018). Studies of animals facing demanding situations in which sustained activity is strongly selected for (e.g., migration: Rattenborg *et al.*, 2004; sexual competition: Lesku *et al.*, 2012; see Lesku & Rattenborg, 2022 for a review) have shown that in some species, sleep can also be drastically reduced, or even suppressed altogether without subsequent rebound. In conclusion, although

ecological and physiological traits are expected to shape resting durations across species, modelling these effects could be particularly challenging, given the lack of available data, the diversity of resting drivers, and the potential intra-individual variability of resting duration.

IV.(2) When to rest?

When immediately enforced for post-activity recovery (for example after a high-speed chase), resting is temporally very constrained. This kind of resting typically consists of quiet wakefulness and produces short bouts of resting embedded within longer bouts of activity. However, most of the resting displayed by animals occurs within consolidated bouts, usually several hours long, alternating cyclically with similarly long phases of activity. This is because physiologically enforced rest (through the need for sleep and energetic balance) is less constrained in time and can be tuned to occur at the time of day when environmental conditions also promote resting. This tuning is achieved by following endogenous rhythms (e.g., the circadian clock) and is regulated by exogenous rhythms called zeitgebers (e.g., solar cycle, tides)(Hazlerigg & Tyler, 2019; Aulsebrook *et al.*, 2021).

Since most terrestrial habitats undergo strong daily fluctuations of temperature, relative humidity, and luminosity across the day-night cycle, many animals, called monophasic, rest in one single consolidated bout, either diurnally or nocturnally (Riede *et al.*, 2017). Diel activity patterns are often governed by the need to rest when thermal conditions are least favourable. Nocturnal resting allows to buffer colder temperatures at night, a strategy widespread among lizards (Vidan *et al.*, 2017), and cold-adapted endotherms (Levy *et al.*, 2019). Conversely, most desert dwellers and many ectotherms in tropical regions rest diurnally to evade the heat (Vidan *et al.*, 2017; Moore *et al.*, 2018; Davimes *et al.*, 2018). Similarly, diurnal resting as a strategy to minimize water loss is observed in arid habitats, during dry seasons (Riede *et al.*, 2017), and in most amphibians (Anderson & Wiens, 2017). Diel activity patterns may also be driven by activity. For instance, many species that rely heavily on vision, like the vast majority of birds, have to be active under daylight, and thus rest at night (Daan, 1981; Anderson & Wiens, 2017). Finally, some monophasic species tune

their activity pattern to that of other species (Vallejo-Vargas *et al.*, 2022). Many small mammals rest diurnally to avoid generalist predators (Riede *et al.*, 2017; Shukla *et al.*, 2021), while insectivorous bats tune their activity to match their prey's peak of activity (O'Mara *et al.*, 2017).

Resting in one consolidated bout per day, however, is not the only strategy (Halle, 2006). Many species are rather crepuscular (Vallejo-Vargas *et al.*, 2022), and thus spend most of both day and night at rest. Others, called polyphasic, switch between shorter bouts of resting and activity throughout day and night (Bloch *et al.*, 2013; Hazlerigg & Tyler, 2019). Polyphasic rhythms are observed in polar environments, where abiotic diel rhythms disappear altogether for most of the year, and in species constrained by metabolism (Bloch *et al.*, 2013). Small herbivores using microbial fermentation (voles and some ruminants) and tiny endotherms (like shrews) have metabolic requirements that would not allow them to interrupt foraging for more than a few hours. Thus, they spread short bouts of resting throughout the day and night (Hazlerigg & Tyler, 2019).

IV.(3) Where to rest?

Short moments of immediate compensatory resting following active behaviours sometimes happen directly at the sites used for activity. For longer bouts of rest, however, animals usually select specific resting sites. Animals choose their resting sites according to their location in space and physical properties. For example, a few often-favoured resting sites qualities include: difficulty of access (e.g., in marmosets: Duarte & Young, 2011; in pigeons: Tisdale *et al.*, 2018), dense structural cover (e.g., in otters: Weinberger *et al.*, 2019; in lynx: Hočevar, Oliveira & Krofel, 2021), possibility to sense approaching predators (e.g., in uakaris: Barnett *et al.*, 2012; in anoles: Mohanty *et al.*, 2022), thermal insulation (e.g., in martens: Larroque *et al.*, 2015; in squamates: Mohanty *et al.*, 2022), and a low density of predators (e.g., in zebras: Courbin *et al.*, 2019) or parasites (e.g., in baboons: Hausfater & Meade, 1982). Trade-offs may emerge from the diversity of qualities expected from resting sites. For example, wolverines (*Gulo gulo*) are willing to rest in riskier sites, to gain

thermal benefits (Glass *et al.*, 2021), contrarily to velvet geckos (*Oedura lesueurii*), which rather trade thermal efficiency for safety at resting sites (Downes & Shine, 1998).

Species differ in how selective they are about resting sites. Large-bodied species, with no option to retreat underground or up trees, are unavoidably less specific in their choices. Yet, even for them, parameters like vegetation cover, visibility or predator and parasite density drive resting site selection (e.g., in bison: Schneider, Kowalczyk & Köhler, 2013; in zebras: Courbin *et al.*, 2019; in giraffes: Burger *et al.*, 2020), and resting sites are sometimes used repeatedly (e.g., in elephants: Wittemyer *et al.*, 2017). Many smaller species depend on specific structures for resting (e.g., tall trees, burrows, fissures, cavities). For them—and especially those unable to craft the required structures themselves, or only able to craft one or a few—resting sites may easily be a limiting resource (e.g., in feral cats: Briscoe *et al.*, 2022), and repeated use of the same resting sites over time is common (e.g., in mouse lemurs: Lutermann, Verburgt & Rendigs, 2010; in geckos: Taylor, Daniels & Johnston, 2016; in gibbons: Fei *et al.*, 2022). Such resting site fidelity is expected when resting sites are rare, scattered, and when their quality is stable over time (Gerber *et al.*, 2019; Kaiser & Kaiser, 2021). Fidelity to resting sites may enhance predation risk through increased predictability (Smith *et al.*, 2007; Markham *et al.*, 2016; Fei *et al.*, 2022). Resting site availability and quality may also vary seasonally (Lutermann *et al.*, 2010). When availability is low, competition may arise over high quality sites (e.g., in geckos: Kondo & Downes, 2007; in baboons: Markham *et al.*, 2016), potentially increasing parasite transmission (e.g., in sleepy lizards: Payne *et al.*, 2025).

Selectivity over resting sites is also affected by the rhythmicity of resting. Monophasic species must choose a single resting site each day and remain at this location for several hours. For them, resting site selection has implications that last many hours, which implies an anticipation of how environmental conditions (e.g., weather conditions, predation risk) might change. Polyphasic species select resting sites several times a day. Each of these choices should be less critical than in monophasic species, because less time is spent at each resting site. However, resting site

503 selection should be spatially more constrained for them, as travel time between resting sites is
504 reduced (Halle, 2006).

505 Resting site selection is always constrained by connectivity with sites where activity is
506 profitable, like foraging sites. Animals with a strong dependency on specific foraging sites must
507 select resting sites close-by (Chapman, Chapman & McLaughlin, 1989; Hočevar *et al.*, 2021) or commute
508 between distant resting and foraging sites (Janmaat *et al.*, 2014; Courbin *et al.*, 2019). Their selection
509 of resting sites is thus influenced by landscape patchiness and resource distribution. Conversely,
510 when resting sites are a limited resource, they may determine the range of animal movements
511 (Barnett *et al.*, 2012; Fradin *et al.*, 2025) and species distribution (Anderson, 2000; Larroque *et al.*, 2015;
512 Briscoe *et al.*, 2022). Considering resting and foraging in a framework of landscape
513 complementation could help to understand how resting strategies affect landscape utilization and
514 species distribution (Dunning, Danielson & Pulliam, 1992). Finally, territoriality influences where
515 animals rest within their home ranges. Resting on the edge of the defended area can improve
516 territorial defence and early access to contested sites (Day & Elwood, 1999; Singhal, Johnson &
517 Ladner, 2007; Génin, 2010), while resting near its core helps securing the exclusive use of
518 aggregated resources (Smith *et al.*, 2007).

519 ## IV.(4) With whom to rest?

520 Coordinating when and where they rest allows gregarious animals to benefit from resting
521 together. Social resting has thermoregulatory benefits, as huddling reduces heat loss (Gilbert *et al.*,
522 2010; Mohanty *et al.*, 2022). Resting in groups also helps to reduce predation risk through the
523 dilution effect (e.g., in baboons: Bidner, Matsumoto-Oda & Isbell, 2018) and increased vigilance (e.g., in
524 teals: Gauthier-Clerc, Tamisier & Cezilly, 1998). When resting animals are numerous, asynchronous
525 vigilance enables less individual vigilance (e.g., in skinks: Lanham & Bull, 2004; in giraffes: Burger *et*
526 *al.*, 2020; in oystercatchers: McBlain *et al.*, 2020), which could benefit mixed-species groups too. As a
527 result, resting in groups can increase both the quantity of resting time, and its quality, through
528 enhanced thermoregulation, and reduced need for vigilance. The outcome of resting in groups,

however, might yield unequal benefits to individuals, depending on their position within the resting aggregation. For example, in ducks and shorebirds resting in dense groups, peripheral individuals often show more vigilance behaviours (like peaking and unihemisherical SWS) than central individuals (Rattenborg *et al.*, 2000; Dominguez, 2003; Lima *et al.*, 2005). Finally, although resting in groups generally increases the risk of parasite transmission (Smeltzer *et al.*, 2022; Respicio *et al.*, 2024), it can also help to dilute the exposure to others, such as blood-sucking insects (e.g., in chimpanzees: Samson *et al.*, 2019).

The dynamics of social relationships also continue during resting, and influence how animals rest (Smeltzer *et al.*, 2022). The time spent resting with different partners often reflects social relationships and hierarchical situation (Anderson, 2000). In mammals, sociality also influences the time animals spend in quiet wakefulness, SWS, and REM sleep, suggesting that social species face a trade-off between socializing and sleeping (Capellini *et al.*, 2010). The position within a resting aggregation, influenced by social relationships, can affect safety, thermal conditions, and the risk of being disturbed while at rest, which in turn affect the quantity and quality of resting (Anderson, 1998; Loftus *et al.*, 2022). The social dynamics during resting times are recently getting more attention from ecologists, as it is now possible to track several individuals from a social group at the same time (Loftus *et al.*, 2022). However, their great complexity would require a specific focus to be treated properly, which is why they are not discussed further in this review (see Smeltzer *et al.*, 2022; Chakravarty *et al.*, 2024).

V. Potential effects of anthropization on resting

The globally increasing pressure humans put on ecosystems affects animal behaviour through a variety of pathways (Sih *et al.*, 2011; Gunn *et al.*, 2022). Animals respond to habitat destruction, landscape fragmentation, direct disturbances, alteration of communities' compositions, light and noise pollution, and increased temperature by modifying their behaviour (Candolin *et al.*, 2023). Obviously, resting is also affected. In general, however, very little is known about how anthropic pressures affect resting, and what consequences this may have on individual fitness, species

abundance and distribution. The effects of anthropization on resting behaviour are likely to interact both with one another and with its effects on other behaviours (Lopez *et al.*, 2023). As a result, making predictions on the consequences of the anthropic disruptions of resting is certainly challenging. Nevertheless, here, we explore some of the possible pathways through which human activity, at local or global scales, may interfere with resting behaviour.

V.(1) Landscape alterations

The landscape alterations caused by anthropization, including habitat destruction and fragmentation, affect animal resting behaviour by redefining the availability, quality and distribution of resting sites.

In many landscapes, anthropization has resulted in the replacement of many natural structures that animals use for resting with anthropogenic structures. For example, while deforestation, forest management, and urbanization have led to a global decline in hollow trees (Le Roux *et al.*, 2014; Terry & Goldingay, 2025), urbanized environments provide countless artificial shelters that can be used for resting (Lowry, Lill & Wong, 2013; Sarkar & Bhadra, 2022). For any given species, this can mean either an increased or a decreased overall availability of resting sites. If they can make use of anthropogenic structures, even animals with specialized needs in terms of resting sites may thrive in these altered landscapes (e.g., in blue-tongued lizards: Koenig, Shine & Shea, 2001; in small carnivores: Bateman & Fleming, 2012), sometimes reaching higher densities than in natural landscapes (e.g., in lava lizards: de Andrade, 2020). However, if anthropogenic structures are too few to compensate the loss of natural shelters (e.g., in semi-anthropized landscapes such as managed forests), or do not match their specific requirements, other species may suffer from resting site shortage (e.g., in marbled geckos: Taylor *et al.*, 2016; in otters: Weinberger *et al.*, 2019; in hollow-dependent species: Terry & Goldingay, 2025). In such cases, the scarcity of resting sites may contribute to reshape landscape utilization (e.g., in possums: Martin & Martin, 2007) and species distribution (Anderson, 2000; Terry & Goldingay, 2025).

When resting site availability is reduced in altered landscapes, the overall quality of the few remaining sites may also be reduced. Scarce resting sites may be over-utilized by several individuals, enhancing aggression, and parasite and disease transmission (Respicio *et al.*, 2024). In addition, intense utilization of the same resting sites can increase predictability, and thus predation risk (Markham *et al.*, 2016). Finally, competition can arise from a limited availability of resting sites (Markham *et al.*, 2016), thus increasing the risk of being evicted while at rest. Animals may also use alternative sites of lower quality, with additional costs in terms of predation risk (e.g., in an agamid lizard: Bors, Mohanty & Gowri Shankar, 2020) and thermoregulation (e.g., in hollow dependent species: Griffiths *et al.*, 2018).

In addition to the availability and quality of resting sites, anthropic alterations of the landscape may modify their spatial distribution, in relation to each other, and to the sites used during activity (e.g., foraging grounds). In fragmented anthropized landscapes, the patches used for resting and for activity may be separated, and animals may be forced to travel greater distances, possibly through more hostile environment, to commute between these sites (e.g., in wild boars: Podgórski *et al.*, 2013; in wolves: Torretta *et al.*, 2023). Such landscape complementation (Dunning *et al.*, 1992) involves energetic costs and risks linked with transit (e.g., predation, vehicle collisions), and should also imply a reduction of resting time (Dunbar *et al.*, 2009), with potential drawbacks that remain poorly understood. In fragmented landscapes with scarce resting sites, landscape utilization patterns should strongly depend on the location of available resting sites (Torretta *et al.*, 2023; Fradin *et al.*, 2025). Conversely, human-altered habitats can also offer opportunities to rest and be active in the same patches, for example through food provisioning, thus relaxing time budgets by reducing the time needed for transit (e.g., in macaques: Koirala *et al.*, 2017). This should be particularly important for animals that tolerate human presence, and are released from predation pressure by the 'human shield' effect (Berger, 2007; Gaynor *et al.*, 2025).

V.(2) Risk of direct disturbances

As human presence increases in all landscapes, animals are ever more likely to encounter and be disturbed by people, in particular during daytime. The risk of direct disturbances leads to both proactive and reactive adjustments related to resting behaviour.

In response to human presence in their habitat, many diurnal or crepuscular species shift to nocturnality, a proactive adjustment frequently documented in mammals, in particular in apex predators (Shukla *et al.*, 2021) and large species (Gaynor *et al.*, 2018). For this shift to be beneficial, the risk mitigation allowed by resting diurnally must compensate the additional costs of being active at night, for species that are normally diurnal or crepuscular (Riede *et al.*, 2017; Hazlerigg & Tyler, 2019). Besides, it also has important consequences on the context in which resting occurs. Shifting to daytime resting may have important physiological consequences—that remain largely unexplored—related to the alteration of the circadian regulation of sleep, and to the increased temperatures experienced during resting (e.g., in wild boars: Mortlock *et al.*, 2024). Animals that shift to rest during daytime could become more dependent on cool resting sites, which could be scarce for large species that rest out in the open. These effects, however, remain largely unexplored.

Whether or not they shift to nocturnality to reduce the risk of anthropic disturbances, animals can also proactively adjust to the risk of being disturbed while resting by modifying where they rest. The fear of humans as an apex predator leads to spatial avoidance in general (Corradini *et al.*, 2021; Doherty, Hays & Driscoll, 2021), which commonly impacts resting site selection, even in species that fear no other predator (e.g., in elephants: Wittemyer *et al.*, 2017; in lynx: Belotti *et al.*, 2018; in wolves: Rio-Maior *et al.*, 2025). The reshaping of the landscape of fear by human presence in animals' habitats may affect resting sites availability, quality, and distribution, just like any alteration of the landscape, with the same consequences as discussed above. As a result, the pressure on resting site selection is augmented for animals that shift to nocturnality to avoid human encounters, and large species that rest out in the open are particularly affected. If areas free of disturbances become rare, the lack of quiet and safe resting sites could drive population

decline, even in landscapes where food is available, and movements are unrestricted (Anderson, 2000; Beale, 2007).

In spite of any proactive adjustment, some animals get exposed to actual disturbances while they rest, which compels them to increase vigilance. High-awareness resting behaviours—such as quiet wakefulness—are then favoured at the expense of sleep, thus potentially initiating sleep deprivation, fragmentation, or shift (e.g., in oystercatchers: McBlain *et al.*, 2020; in wild boars: Olejarz *et al.*, 2023). If disturbances are repeated, this might have important drawbacks on performance during subsequent activity (e.g., in anoles: Kolbe *et al.*, 2021), as animals may not be able to compensate with delayed resting (e.g., in macaques: Kaburu *et al.*, 2019). Anthropic disturbances during resting can also have lasting effects on the subsequent temporal pattern of activity (e.g., in bears: Ordiz *et al.*, 2013), use of resting sites (e.g., in wolves: Wam, Eldegard & Hjeljord, 2012), and more generally on landscape utilization. Finally, some animals decide to leave their resting site upon getting disturbed, either because of the perceived threat, or because prolonged high vigilance would be too costly (Gauthier-Clerc *et al.*, 1998; Price, 2008; Ferretti *et al.*, 2019). The costs of such an immediate reaction include increased energy expenditure, exposure to predators, thermal stress, and increased need for subsequent travel time during subsequent activity (Price, 2008).

V.(3) Alterations of communities

Altered communities in anthropic landscapes may imply increased or decreased predation pressure to resting animals. Exotic predators (wild and domestic) have been introduced in many areas, sometimes in high densities, thus affecting anti-predator resting strategies. When exposed to an exotic predator, some species effectively adjust resting site selection, thus successfully mitigating the risk of predation while at rest (e.g., in marmosets: Duarte & Young, 2011). Conversely, others may fail to select appropriate anti-predator resting sites, with potentially severe consequences for survival (e.g., in Australian native fauna: Short, Kinnear & Robley, 2002). This may happen either because such sites are not available, or because of inaccurate risk assessment, reflecting an evolutionary mismatch—or ecological trap—where prey make decisions based on

cues that previously put them in high-quality resting sites but now exposes them to exotic predators (Pollack *et al.*, 2022). On the other hand, human-dominated landscapes are often characterized by the lack of large predators, producing a 'human shield' effect for some prey species (Berger, 2007; Gaynor *et al.*, 2025). The release from predation pressure could allow these to select resting sites that would otherwise be riskier, potentially compensating for the lack of available resting sites in some anthropized landscapes. It could also allow them to shift when they rest to other times, if resting was previously timed to avoid predation (e.g., in mesopredators: Shores *et al.*, 2019).

Besides predator-prey dynamics, the alterations of animal communities linked with anthropization may affect competition and cooperation at resting sites. Exotic species may generate intense competition over resting sites (e.g., in geckos: Cole, Jones & Harris, 2005; in parakeets: Giuntini *et al.*, 2022), which contributes to reducing resting site availability for the native species. In socially resting species, population declines can reduce the benefits of resting in groups, such as social thermoregulation, potentially forcing some species to compensate through increased resting site selectivity, or by using more energy-saving resting states (e.g., in little brown bats: Dzal & Brigham, 2013).

V.(4) Light and noise pollution

Artificial lights at night (ALAN) are an important characteristic of anthropization in populated areas and along roads, and their effects may extend well away from light sources, through skyglow (Gaston & Sánchez de Miguel, 2022). ALAN may decrease the anti-predator quality of resting sites, thus pushing animals to avoid resting in artificially lit areas. Although empirical evidence is scarce (Kolbe *et al.*, 2021), this could affect the spatial distribution of suitable resting sites, especially if anthropogenic structures have replaced natural resting sites. Avoiding ALAN exposure during resting might simply be impossible for some animals, due to the wide spread of anthropic lighting. Besides, some animals might prefer artificially lit roosts—for example for increased foraging opportunities at night—despite physiological costs and exposure to predators

(e.g., in great tits: Ulgezen *et al.*, 2019). Exposure to ALAN has been linked with sleep disruption in diurnal birds (Aulsebrook *et al.*, 2021) and reptiles (Mohanty *et al.*, 2022), sometimes leading to altered activity patterns (e.g., in blackbirds: Dominoni *et al.*, 2014), impaired performances during activity (e.g., in crows: Taufique & Kumar, 2016; in anoles: Kolbe *et al.*, 2021), and even to sleep rebounds (e.g., in great tits: Raap *et al.*, 2016).

Anthropized landscapes are also characterized by noise pollution, which has been shown to alter activity patterns in some urban animals (e.g., in robins: Fuller, Warren & Gaston, 2007; in great tits: Dominoni *et al.*, 2020), and are thus expected to influence resting behaviour. Exposure to artificial noise impairs sleep quality, with potential physiological drawbacks (Kight & Swaddle, 2011; Grunst *et al.*, 2023). Animals are expected to exhibit increased vigilance when exposed to anthropogenic noise, especially if it is threatening (e.g., dog barks), sudden, and unexpected (Beale, 2007). Animals may habituate to constant noise pollution (e.g., in wild boar: Fradin & Chamaillé-Jammes, 2023), but even background noise may decrease their chances to hear an approaching predator (e.g., in nuthatches: Chou *et al.*, 2023). As a consequence, animals could account for the anthropogenic soundscape to select quiet resting sites (e.g., in wolves: Bojarska *et al.*, 2021).

In general, light and noise pollution are likely to interact with each other, and with the risk of direct disturbances by people, to reduce resting sites availability and quality, and to disrupt resting animals (Dominoni *et al.*, 2020; Grunst *et al.*, 2023). The impact of these effects on individual behaviour and fitness, however, are largely unknown. Species that manage to find alternative resting sites or habituate to these anthropogenic constraints are likely to be favoured in highly anthropized landscapes (Lowry *et al.*, 2013).

V.(5) Increased temperature

Air temperature affects how long, when, and where animals rest (Korstjens *et al.*, 2010; Rattenborg *et al.*, 2017; Mohanty *et al.*, 2022), as well as the form of resting that is displayed (Harding *et al.*, 2019; Mortlock *et al.*, 2024). Consequently, global warming is expected to strongly affect

animals' resting strategies. Because resting is often an efficient response to adverse thermal conditions, some diurnal animals might adjust to climate warming by shifting to nocturnality to avoid extreme daytime temperatures (Levy *et al.*, 2019). Whether or not they do so, most species will have to be resting under warmer conditions, as nighttime temperatures also increase. Increased temperatures experienced during resting should lead to various metabolic costs, including sleep deprivation, with important drawbacks on subsequent activity (e.g., in fruit bats: Downs *et al.*, 2015; in squamates: Rutschmann *et al.*, 2024). Increased dependency on cool resting sites should be observed in a number of species (e.g., in desert lizards: Flesch, Rosen & Holm, 2017; in reindeers: Williamsen *et al.*, 2019), potentially causing competition over resting sites, especially where they are already rare. This could be particularly true in urban environments because of the urban heat island effect (Battles & Kolbe, 2019).

As temperatures keep increasing, animals' ability to cope with change through behavioural adjustments will decrease. Extreme weather events should become the most important pathways through which temperatures could affect resting behaviour (Downs *et al.*, 2015). During heatwaves, animals should increase resting time at the expense of other activities, thus tightening time budgets (Korstjens *et al.*, 2010). Animals capable of using daily torpor flexibly in response to unpredictable and severe weather events are predicted to stand better chances of survival during extreme events (Geiser & Turbill, 2009; Nowack *et al.*, 2017). In general, however, the effects of climate change on animal resting behaviour remain largely unknown.

VI. Conclusions

(1) Resting often represents substantial proportions of animals' time budgets and yet has received little attention from ecologists.

(2) Resting strategies are shaped by a diversity of constraints, are highly variable between species, and often show great plasticity within species and individuals. A future direction for

research could be the relationship between individual differences in sleep patterns and consistent individual differences in personality.

(3) Decision making related to resting behaviour has crucial implications for energy balance, thermoregulation, predator avoidance, and landscape utilization. As such, a future direction for research can involve the use of state-dependent or dynamic energy budget models to provide a theoretical basis for understanding how sleep patterns reflect the balance of multiple conflicting demands.

(4) Although the states that compose resting (quiet wakefulness, sleep and daily torpor) do not have the exact same drivers and functions, studying them together has the potential to facilitate large-scale monitoring, while allowing interpretations on their shared consequences (e.g., energy savings, space use restrictions, predation risk reduction, thermoregulatory benefits).

(5) Anthropization may greatly influence where, when, and how animals rest, with potentially important consequences for individual fitness, and species abundance and distribution. A future direction for research can involve the study of how resting patterns are influenced by multiple interacting stressors associated with human-induced environmental change, with effects mediated by multi-species interactions.

(6) To date, the effects of anthropization on resting behaviour seem to have been overlooked by ecologists.

(7) We call ecologists to recognize resting as more than just the flip-side of active behaviours and treat it as a valuable research topic of its own, with both empirical studies (given the wide availability of relevant biologging tools) and theoretical approaches (for example through dynamic state-dependent modelling).

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