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Author for correspondence:
Niels C. Rattenborg
e-mail: rattenborg@orn.mpg.de

Sleep research goes wild: new methods and approaches to investigate the ecology, evolution and functions of sleep

Niels C. Rattenborg[1], Horacio O. de la Iglesia[3], Bart Kempenaers[2], John A. Lesku[4], Peter Meerlo[5] and Madeleine F. Scriba[6]

[1]Avian Sleep Group, and [2]Department of Behavioral Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, 82319 Seewiesen, Germany
[3]Department of Biology, University of Washington, Seattle, WA 98195-1800, USA
[4]School of Life Sciences, La Trobe University, Melbourne 3086, Victoria, Australia
[5]Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700 Groningen, The Netherlands
[6]Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland

NCR, 0000-0002-1140-222X; MFS, 0000-0003-3046-5004

Despite being a prominent aspect of animal life, sleep and its functions remain poorly understood. As with any biological process, the functions of sleep can only be fully understood when examined in the ecological context in which they evolved. Owing to technological constraints, until recently, sleep has primarily been examined in the artificial laboratory environment. However, new tools are enabling researchers to study sleep behaviour and neurophysiology in the wild. Here, we summarize the various methods that have enabled sleep researchers to go wild, their strengths and weaknesses, and the discoveries resulting from these first steps outside the laboratory. The initial studies to 'go wild' have revealed a wealth of interindividual variation in sleep, and shown that sleep duration is not even fixed within an individual, but instead varies in response to an assortment of ecological demands. Determining the costs and benefits of this inter- and intraindividual variation in sleep may reveal clues to the functions of sleep. Perhaps the greatest surprise from these initial studies is that the reduction in neurobehavioural performance resulting from sleep loss demonstrated in the laboratory is not an obligatory outcome of reduced sleep in the wild.

This article is part of the themed issue 'Wild clocks: integrating chronobiology and ecology to understand timekeeping in free-living animals'.

1. Introduction

Sleep is a dangerous state of reduced environmental awareness [1] found in animals ranging from worms to humans [2,3]. Despite extensive efforts to reveal sleep's function(s), our understanding of sleep remains incomplete. The location for most sleep research is the laboratory or the bedside. Importantly, however, sleep evolved in the natural world, shaped by environmental factors and ecological forces resulting in species-specific sleep architecture (i.e. the amount, composition, continuity and intensity of sleep). Sleep is also a highly plastic trait that responds quickly to changes in local conditions, including the artificial laboratory environment. Here, we highlight the unique contribution that taking sleep research into the wild can make towards our broader understanding of the evolution and functions of sleep, and the ecological relevance that sleep plays in the lives of wild animals. We also discuss the strengths and weaknesses of the various techniques and technologies that allow sleep to be measured in captive and wild animals, including the recent ability to record sleep-related changes in brain activity in free-living animals. We then review the contributions towards our comprehensive understanding of sleep made by studies that have already 'gone wild' and emphasize the need for additional studies that link variation in sleep with

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evolutionary fitness. We end with an examination of sleep in humans living in pre-industrial and industrial environments.

2. What is sleep?

First and foremost sleep is a behavioural state [1,4]. A sleeping animal assumes a specific posture and remains immobile. In animals with eyelids, the lids usually close during sleep. Important exceptions to these ‘rules’ will be discussed in §5a(iii). In some species, sleep only occurs at a specific site (e.g. tree cavity) and only at certain times of the day. Sleep is distinguished from other ostensibly similar behaviours, like quiet wakefulness or energy-conserving states, such as torpor and hibernation in homeotherms, by the animal’s responsiveness to stimuli. The level of a stimulus required to elicit a response (i.e. the arousal threshold) is higher in a sleeping animal than one that is simply resting quietly awake. Sleeping animals also quickly resume adaptive waking behaviour once awakened, whereas animals aroused from torpor or hibernation take much longer to fully return to normal [5]. Finally, following a period of sleep loss, animals tend to sleep longer and/or more deeply, indicating that sleep is homeostatically regulated [4].

Mammals, birds [6], and possibly some reptiles [7,8] and cuttlefish (*Sepia officinalis*) [9] exhibit two different types of sleep—rapid eye movement (REM) sleep and non-REM (NREM) sleep. In mammals and birds, NREM and REM sleep are distinguished from one another and from wakefulness, in part, by changes in brain activity. During wakefulness, the electroencephalogram (EEG) shows low-amplitude, high-frequency activity. As mammals and birds fall asleep and transition into NREM sleep, EEG wave amplitude increases and frequency decreases. The amount of slow waves occurring during NREM sleep is typically quantified as slow wave activity (SWA, approx. 0.5–4.0 Hz power spectral density) [4,10]. Interestingly, SWA increases with time spent awake and decreases with time spent asleep in mammals [4,10] and birds [11,12], suggesting that it reflects homeostatically regulated sleep processes. Moreover, in mammals, and possibly birds, the level of SWA correlates positively with sleep intensity or depth, as measured with arousal thresholds [4,10,11].

In mammals and birds, episodes of NREM sleep alternate with episodes of REM sleep across a sleep phase. During REM sleep, the EEG reverts to an awake-like pattern [13]. By contrast to wakefulness, however, the animal has its eyes closed and arousal thresholds are elevated. Although muscle tone (as measured with the electromyogram, EMG) reaches the lowest levels during REM sleep, intermittent rapid movements of the eyes and twitches of the limbs occur. Owing in part to low muscle tone, thermoregulatory behaviours, such as shivering and panting, are suppressed [14]. The presence of these two dramatically different types of sleep suggests that sleep has multiple functions.

3. Why sleep?

The functions of sleep have been the subject of countless theories ranging from a behavioural function, such as sleep as an immobilizer that prevents animals from being active during unfavourable times of day [1,15], to physiological functions such as thermoregulation, energy management [16] and maintenance of the immune system [17]. However, the fact that sleep encompasses a seemingly dangerous reduction in environmental awareness suggests that it also performs functions for the brain that are incompatible with wakefulness [1]. Indeed, most current theories propose that sleep primarily serves a role in support of the central nervous system. In general, sleep is thought to play crucial roles in recovery, maintenance and plasticity of nerve cells and neuronal networks, which ultimately would support the workings of the brain in terms of alertness, information processing, information storage and behavioural control [18]. Finally, the prevalence of sleep, in particular REM sleep, early in life in mammals [19–21] and birds [22], also suggests that sleep serves a role in brain development [20,23,24].

Sleep theories focused on the central nervous system can be divided into two general categories. One proposes that sleep is involved in maintenance and recovery processes such as replenishing essential molecules and fuel substrates that are being used by the central nervous system during the waking state [25,26] or removing potentially harmful waste products that accumulate during wakefulness [27]. The second category proposes that sleep is crucial for regulating the strength of neuronal connections or synapses between nerve cells. One version of this idea is that sleep allows global downscaling of synapses that have been strengthened as a consequence of waking neuronal activity [28–30]. Sensory input and brain activity during waking are assumed to gradually increase synaptic strength, and sleep would serve to weaken and reset synaptic connections, thereby conserving neuronal resources and enabling the processing of new information the next day. Another and equally popular plasticity theory suggests that sleep is important for strengthening synapses in specific circuits, thereby aiding memory formation and long-term storage of information in the brain [31,32]. The relative strengths and weaknesses of these opposing theories is hotly debated [30,31,33,34]. In the end, it may turn out that both types of plasticity occur during sleep, but determining exactly how remains a challenge.

A quick search of the literature might suggest that evidence in support of some theories is rather compelling but, in reality, unequivocal evidence does not exist for any of them (e.g. [15,34]). The fact that no single theory accounts for all aspects of sleep, especially when viewed across the animal kingdom, suggests that sleep serves many functions. Although sleep may have evolved once very early in evolution to perform an initial function shared by all subsequent animals, it is also possible that sleep evolved multiple times in response to different selective forces. In either case, once sleep evolved it likely took on additional functions, as certain processes may occur more efficiently in a sleeping animal. The nature of these functions may vary across species, reflecting their evolutionary history and ecological and physiological demands. While this potential mosaic of functions probably contributes to the debate over the functions of sleep, other factors undoubtedly play a role. In §4, we argue that the unnatural laboratory environment in which most sleep research is performed may hinder our ability to fully explore the functions of sleep.

4. Why go wild?

Natural habitats are characterized by a rich heterogenic tapestry of temperatures, light and sound levels, and structural complexities, overlaid with salient within- and between-species interactions. As a consequence, individuals in the wild are faced with multifarious demands, such as searching for sustenance and mates, and defending against competitors and predators, which limit the amount of time available for sleep. In stark contrast, the laboratory is a seemingly simple environment wherein many of the challenges faced by wild animals are removed and new challenges are introduced. For example, laboratory-housed animals do not need much time to forage, because food and water are typically provided *ad libitum*. Ambient conditions are usually fixed or vary across the day in an artificial manner. Moreover, the confines of laboratory enclosures often limit an animal's ability to move. Finally, regardless of whether a species is social or solitary in the wild, they are usually housed individually in the laboratory. Collectively, in addition to removing some natural challenges, these artificial conditions may create new challenges animals have not experienced over ecological or evolutionary time (e.g. chronic stress). For example, animals may perceive the novelty of the laboratory setting, combined with absent or artificial refuges and visits by caretakers and researchers as an environment of elevated and persistent danger. In such situations, animals may lack the means to reduce the threat with adaptive behavioural responses (e.g. hiding, flocking or fleeing). A wild animal brought into such a situation may never fully acclimate and instead develop changes in hormone and neurotransmitter levels brought on by recurring stress [35] that also can influence sleep [36]. Depending on the species, these factors can lead to captive animals sleeping more or less than their wild conspecifics.

If captive animals sleep differently than conspecifics in the wild, phylogenetic comparative analyses that attempt to explain the observed interspecific variation in the amount of time spent sleeping and in the different sleep states [37–39] face a big problem. Such between-species variation is assumed to reflect underlying variation in the need for sleep. The identification of factors that maintain this variation in sleep should then provide insights into the purpose of sleep and its substates. Indeed, this approach has provided comparative support for existing hypotheses for the functions of NREM and REM sleep [38,39] and also generated new ideas for the evolutionary determinants of sleep [37,40]. However, of the nearly 100 mammalian species for which electrophysiologically derived sleep data exist, the overwhelming majority is from wild animals brought into captivity or from domesticated laboratory animals, farm animals and pets [38]. Therefore, the relationships identified by these comparative studies may reflect plastic responses to a simplified, novel recording environment rather than fixed physiological requirements shaped by natural selection. As other physiological parameters differ between captive and wild individuals of the same species [41,42], there is good reason to think that sleep in captivity is unlike that of a wild animal sleeping in its natural habitat [43,44]. Thus, we need wild recordings from many more species.

Another advantage of studying sleep in the wild is that it can reveal informative intraspecific variation in sleep patterns. Such variation may arise from ongoing selection for specific sleep phenotypes. For example, under certain ecological circumstances, individuals with an ability to perform adaptively on little sleep may be favoured over individuals requiring more sleep to perform at comparable levels [45]. In this case, determining how some individuals are able to perform on little sleep could inform our understanding of sleep. Alternatively, interindividual variation in sleep may be maintained in a population via trade-offs. Although short sleeping individuals may have more time to fulfil waking ecological demands than longer sleeping individuals, short sleepers may suffer costs linked to sacrificing some of the benefits of sleep. In this case, identifying these costs can provide insights into the functions of sleep. In addition to selection for different sleep phenotypes, such costs may also manifest in an informative manner when individuals switch between different sleep tactics in response to changing ecological and physiological demands. An animal's optimal solution to trade-offs between sleep and other activities may depend on its age, sex, energetic state, immunological condition, cognitive demands and recent sleep/wake history. Collectively, we can use naturally occurring intraspecific variation in sleep to test existing hypotheses for the functions of sleep and to generate new hypotheses.

A final reason for 'going wild' is that certain animals living under challenging ecological circumstances exhibit dramatic behaviours, seemingly in competition with sleep, that cannot be replicated in captivity [45,46]. We expand on these ideas in §6 after discussing the various ways sleep is measured in the laboratory and more recently in the field.

5. Measuring sleep

(a) In captivity

(i) Sleep behaviour

Sleep is often measured using behavioural criteria in captivity. Initially, when examining a new species, it is important to assess arousal thresholds to establish that potential sleep behaviours (e.g. inactivity and eye closure) truly represent sleep, rather than quiet wakefulness [47,48]. Once the behavioural correlates of sleep have been defined for a given species, sleep can be quantified with video recordings of undisturbed animals. The videos are usually scored using labour intensive manual methods employed in the field of animal behaviour [49]. However, in some species, inactivity for a certain period of time is strongly predictive of sleep (i.e. increased arousal thresholds). This allows researchers to quickly measure sleep via automated activity monitoring devices. Activity/inactivity can be measured via actigraphy devices worn by the animal (e.g. humans) [50–52] or via motion sensors in the animal's home cage [47,48]. Recently, automated video analysis has also been used to quantify activity/inactivity in a variety of animals [53–56]. In captivity, these methods are commonly used to investigate sleep in small vertebrates [55,57] and invertebrates [2,3,47,48], given the technical challenges of measuring brain activity in these small animals [58–60].

(ii) Sleep electrophysiology

Researchers studying relatively large vertebrates (mouse-sized and larger) in captivity usually focus on the electrophysiology (i.e. EEG and EMG) of sleep for several reasons. First, NREM and REM sleep usually cannot be reliably distinguished from one another based on behaviour alone (see §5a(iii)). Second, EEG SWA serves as a proxy for NREM sleep intensity, obfuscating the need to disturb sleep to assess its depth. Third, many researchers are interested in exploring the functions of sleep through examining the link between sleep-related brain rhythms and waking behaviour (e.g. [6,11,61]). Finally, in some species and/or conditions, the association between traditional sleep behaviour and electrophysiologically defined sleep is weak.

(iii) Dissociations between behaviour and electrophysiology

Several studies of captive animals have revealed that traditional behavioural signs of sleep and wakefulness (e.g. activity/inactivity, eyes open/closed) do not always match the electrophysiologically defined brain state. As the possibility for such dissociations needs to be taken into consideration when studying sleep in the wild, we first outline the types of dissociations described in captivity, before discussing how sleep can be measured in the wild.

Most of the described dissociations involve NREM sleep-related EEG slow waves occurring in conjunction with behavioural signs of wakefulness, including open eyes, a standing position and/or body movements. Ruminants [62], rabbits [63] and several birds [64–68] can exhibit NREM sleep-related EEG activity with both eyes partially and fully open. The absence of eye closure in these species questions whether they are even asleep. From a strictly behavioural perspective, they look awake, whereas from an EEG perspective they appear asleep. The notion that SWA occurring with open eyes reflects NREM sleep is supported by its temporal relationship with REM sleep. In mammals and birds that typically keep both eyes closed during NREM sleep, REM sleep occurs after a period of NREM sleep. Similarly, in the species listed above, REM sleep (with closed eyes) occurs after periods of inactivity with open eyes and high EEG SWA, suggestive of NREM sleep, rather than wakefulness. An unlikely alternative interpretation, based strictly on behaviour, is that these animals sleep very little and only engage in REM sleep which would be unprecedented. Sleeping with eyes open might reflect an ecological compromise between sleep and visual vigilance that allows animals to monitor the environment for predators while obtaining some of the benefits of sleep [1,69]; however, the characteristics of visual processing and associated behavioural responses have not been systematically examined.

In addition to sleeping with both eyes open, several animals sleep with only one eye closed. This behaviour is common among birds [66,69–71] and has also been observed in reptiles [69,72,73]. In mammals, unilateral eye closure has only been reported in aquatic species, including several cetaceans, manatees and pinnipeds (Otariidae and Odobenidae, but not Phocidae) [74,75]. In mammals and birds, unilateral eye closure is associated with an interhemispheric asymmetry in NREM sleep-related SWA with the hemisphere opposite to the open eye showing lower SWA than the hemisphere opposite to the closed eye. The asymmetry in SWA is the most pronounced in cetaceans, wherein one cerebral hemisphere typically shows high SWA, while the other shows low SWA characteristic of wakefulness [75]. In the cetaceans examined with EEG, such unihemispheric sleep is the primary form of sleep. In Otarid seals and walruses (*Odobenus rosmarus*), the interhemispheric asymmetry ranges from high, as in cetaceans, to low as in terrestrial mammals, with intermediate levels often referred to as asymmetric sleep [75]. In birds, the asymmetry in SWA is typically lower than in cetaceans, but varies across species and ecological conditions [46,66,69–71]. In pigeons (*Columba livia*), the asymmetry in SWA is quite small [66]. By contrast, unihemispheric sleep (as defined using EEG criteria applied in marine mammals) was recently observed in free-living great frigate-birds (*Fregata minor*) while on land and in flight [46]. Finally, unilateral eye closure has been observed in several reptiles, but the electrophysiological correlates of this behaviour remain unclear [69,72].

Although sleep is usually defined, in part, by inactivity, several animals present exceptions to this ‘rule’. Ruminants can chew while in NREM sleep, even while standing [62]. Cetaceans can swim as a cohesive group while sleeping unihemispherically [75–78]. Fur seals can also swim during unihemispheric or asymmetric NREM sleep. While sleeping in the water, fur seals float on one side while the flipper in the water, which is connected to the more awake hemisphere, paddles to maintain this posture [74]. Finally, several types of fish swim continuously [79]. However, due to the absence of electrophysiological recordings and the fact that most fish cannot close their eyes, it is unknown whether they sleep while swimming.

Collectively, the EEG-based studies on captive animals reveal that traditional behavioural signs of sleep (eye closure and inactivity) are not always associated with EEG signs of sleep. The potential for such dissociations should be taken into consideration when measuring sleep using only behaviour in the wild.

(b) In the wild

Owing to technological constraints, sleep has traditionally been studied in the wild via direct observation (e.g. [80,81]). However, recent technological advances have expanded the toolkit available to researchers interested in examining sleep in the wild. Miniature, inexpensive cameras allowed researchers to monitor sleep behaviour in many individuals (see below), animal-borne motion detectors revealed previously unknown sleep behaviours [82,83] and EEG-data loggers [84] enabled researchers to investigate electrophysiologically defined sleep in the wild [22,43–46]. Given the growing interest in using these methods, we review the strengths and weaknesses of old and new approaches to measuring sleep in the wild. Some of the challenges of measuring sleep discussed in this section also apply to studies of captive animals, but are exaggerated under field conditions.

(i) Direct observation

Of all the behaviours exhibited by animals, sleep may be particularly difficult to study via direct observation in the wild. Obviously, it is difficult, if not impossible, to observe sleep in animals that retreat to burrows, cavities or dense foliage. Sleep can also be difficult to observe and quantify in animals that sleep in the open, as some animals seemingly habituated to an observer may be reluctant to sleep when watched. Moreover, even if an animal is not influenced directly, the presence of an observer can influence the animal’s sleep through altering the behaviour of other animals, such as their predators or prey [85]. Even when blinds provide effective concealment of the observer, the mobility of an animal and the effort needed to observe it throughout the 24-h day can limit the utility of this approach. In animals that change states rapidly, such as some birds [81], keeping track of these changes in real time can also be challenging. For these reasons, most recent studies of sleep behaviour rely on video recordings.

(ii) Video recording

Under certain circumstances, video can be used effectively to quantify sleep behaviour. By contrast to direct observation, videos can be analysed off-line, in greater detail, by multiple investigators and via automated methods [53–56]. Despite the benefits of assessing sleep behaviour non-invasively via video, there are also limitations to this approach, many of which also apply to direct observation. One challenge is obtaining camera coverage of all the sleep sites used by an animal in a day [86]. For birds that sleep in nest-boxes at night, a single camera may be sufficient [87–90], as long as the birds do not nap outside the box during the daytime. Another challenge with video is that the animal's eyes can be oriented away from the camera, making sleep-related eye closure difficult to detect with a single camera. A similar problem arises when an animal hides its head and eyes under feathers, fur or appendages (e.g. [91]). Although it is likely that this behaviour is usually associated with sleep, some wakefulness may be occurring covertly. In large, mobile animals that use multiple sleep sites, sleep behaviour can be monitored with cameras mounted on the animal [92]; however, this method may not provide much information beyond that provided from activity monitoring (see §5b(iii)) if the animal's eyes are not in the field of view of the camera.

In animals that sleep with one eye open, the eyes are typically positioned laterally on the head making it difficult to see both from a single vantage point. Birds, in particular, use this form of sleep to visually monitor their environment for threats. If the orientation of the open eye relative to the surrounding environment is not random, a single camera cannot accurately measure sleep. For example, mallards (*Anas platyrhynchos*) sleeping at the edge of a group spend more time sleeping with one eye open and direct that eye away from the other ducks, as if watching for approaching threats [71]. Consequently, a camera placed on the side from which the bird perceives the greatest threat will underestimate the time spent sleeping (based on eye closure), whereas the opposite would be true for a camera (or observer) positioned on the safe side of the bird [81,93]. In swimming dolphins, an added complication is that they tend to open both eyes when they surface to breathe [94] and to close one eye when below the surface, confounding estimates of sleep based on above surface recordings [95]. Even with the use of subsurface cameras, determining the state of both eyes in captive dolphins is difficult, especially when they swim as a group [76–78].

Another limitation of measuring sleep via video is that it is usually not possible to reliably distinguish between NREM and REM sleep. Although twitching of the eyes and limbs can be observed during REM sleep, REM sleep also includes periods without twitching that are behaviourally indistinguishable from NREM sleep. Twitching is typically only used to quantify REM sleep in neonatal mammals, wherein twitching is prevalent and EEG signs of NREM and REM sleep have not yet developed [23]. Nonetheless, a more refined assessment of the timing of twitching, in combination with sleep state-related changes in posture, may allow for REM sleep to be quantified in adult animals using behaviour. For example, McShane *et al.* [96] obtained reasonable agreement between electrophysiological measures of NREM and REM sleep and subtle changes in the shape of mice resulting from the reduction in muscle tone that occurs during REM sleep. Other species may exhibit even more pronounced sleep state-related changes in posture. For example, behavioural observations of giraffes (*Giraffa camelopardalis*) suggest that their posture changes dramatically when they transition from NREM to REM sleep. Although sleep has not been studied electrophysiologically in giraffes, like other ungulates in which the EEG has been measured [62], they appear to engage in NREM sleep while standing or lying down with their eyes open and their head held off the ground [97]. During apparent REM sleep, they lie down with eyelids closed, eyes and ears twitching, and the head falling until it rests on the animal's side, presumably reflecting the loss of muscle tone observed during REM sleep in other mammals [97]. Asian elephants (*Elaphus maximus*) also appear to engage in NREM sleep while standing, but lie down for REM sleep [98]. Similarly, sea otters (*Enhydra lutris*) can float on their back with their head held up and out of the water during apparent NREM sleep, but during REM sleep they roll on their side and the head falls below the surface [99]. If verified with electrophysiological recordings, these behavioural changes could be used to quantify the time spent in NREM and REM sleep via video or other measures of behaviour.

(iii) Actigraphy

Several actigraphy methods have been used to measure movement in free-living animals. Radio tags used to determine an animal's location also provide information about their movements [100,101], even on a fine scale. Depending on an animal's orientation, the strength of the radio signal emanating from the tag varies relative to a fixed receiving location, thereby providing an estimate of movement [102]. Owing to the small size and mass of radio tags, small animals can be studied using this method in the wild [103,104]. Also, unlike video which requires that all sleep sites have camera coverage, with radio telemetry all activity can be quantified as long as the animal remains within the reception range of a receiver station.

Accelerometry is another method for measuring animal activity. Accelerometers measure acceleration due to gravity and the animal's movement along the three cardinal axes, and hence provide measures of movement and orientation [85]. Accelerometry studies are capturing periods of inactivity that might provide novel insights into sleep [82,83,105–108]. For example, this method has revealed that sperm whales (*Physeter microcephalus*) occasionally float motionless and vertically in the water, a posture attained passively due to the buoyancy of spermaceti (oil) in their head [82]. Anecdotal observations of whales exhibiting this posture suggest that they have increased arousal thresholds [82] and therefore might be sleeping. In addition to large changes in body movement and position, accelerometry can also detect finer movements, such as REM sleep-related relaxation of muscle tone and twitching [22,46,65].

Activity monitors can also be used to detect potential physiological correlates of sleep. For example, while actively hunting, hawksbill turtles (*Eretmochelys coriacea*) perform buccal pumping consisting of opening and closing the beak to gain olfactory information. This was measured in the wild with a device that detects the opening and closing of the beak [109]. Interestingly, when the turtles rested on the seafloor, buccal pumping ceased, suggesting that they might be sleeping at this time. Obviously, under certain circumstances, such physiological correlates of sleep can also be monitored via direct or video monitoring, as shown in honeybees (*Apis mellifera*) [49].

The accuracy of all activity monitoring devices needs to be validated against behavioural observations of sleep, at a minimum, and preferably against electrophysiological measures of sleep [45]. The sensitivity of the device will depend on the nature of species-specific wake-related movements, and thus where it is placed on the animal. For example, many animals raise their head during brief awakenings, but do not change their overall body position. Video recordings from blue tits (*Cyanistes caeruleus*) in nest-boxes showed up to 230 of these awakenings per night [89]. Activity monitors placed on the bird's back may fail to detect these awakenings. In larger mammals, collar-mounted devices may be more likely to detect head movements than back-mounted devices, but in some animals, such as sloths, slow head movements may not cause sufficient displacement of the collar. When feasible, head-mounted devices provide the best measure of wakefulness-related movements under such conditions. In elephants, movement of the trunk appears to provide an even more accurate measure of wakefulness than movement of the head [98,106]. Finally, activity monitoring devices can detect 'false' wake-like movements in a sleeping animal resulting from the environment (e.g. wind and water) or conspecifics (e.g. allopreening). Twitching occurring during REM sleep can also be misinterpreted as a sign of wakefulness. Conversely, cryptic animals may remain motionless during wakefulness [44].

Once validated, activity monitors can provide insights into when animals are sleeping. For example, when sleeping in the water fur seals lay on their left or right sides and sleep primarily with one hemisphere [74]. Given this association between posture and sleep established in the laboratory, accelerometry has yielded data on the timing and amount of sleep in the wild. Interestingly, in northern fur seals (*Callorhinus ursinus*) caring for land-based young, accelerometry suggests that they sleep very little during commutes between foraging sites and land that last up to 3 days [110].

Although GPS, satellite and geolocator tags are typically used to track large-scale movements of animals across the globe, they can provide insights into sleep [111]. For example, these tags have uncovered long-lasting movements that seemingly leave little time for sleep (reviewed in [112]). Tracking studies have shown that bar-tailed godwits (*Limosa lapponica baueri*) fly non-stop from Alaska to New Zealand, a flight spanning 11 680 km and lasting 9 days [113], and GPS has shown that great frigate-birds fly non-stop for up to two months [114]. Geolocators, small devices that detect large-scale movements based on changes in the length and timing of the day suggest that some songbirds also engage in multiday flights while crossing parts of the Atlantic Ocean [115]. Finally, geolocators combined with accelerometry suggest that Alpine swifts (*Tachymarptis melba*) fly non-stop for up to 200 days [116] and common swifts (*Apus apus*) fly non-stop for up to 300 days [117]. Although these findings raise questions about whether and how birds sleep during long flights, sleep in flight has only been confirmed with EEG recordings in great frigate-birds [46].

GPS has also revealed that other animals engage in prolonged movements that are seemingly in conflict with the need for sleep. Notably, due to the loss of sea ice, polar bears (*Ursus maritimus*) occasionally swim for over 9 days [118]. Although it is conceivable that they sleep while floating, as sea otters do [99], or even while swimming, as in dolphins [75], it is also possible that they are unable to sleep in the water. Therefore, the loss of sea ice might be exposing polar bears to unprecedented periods of sleep deprivation.

(iv) Sleep electrophysiology

The non-invasive methods for measuring sleep can provide meaningful insights into how animals sleep in the wild. However, in some cases, these methods may fail to accurately quantify sleep duration. In addition, with perhaps some notable exceptions, non-invasive measures of sleep do not provide information on the proportion of time spent in NREM and REM sleep. Finally, sleep intensity cannot be measured via these methods without assessing arousal thresholds and thereby disturbing the animal. Consequently, there has been a long-standing call for electrophysiological studies of sleep in the wild [43,119–121].

Obtaining high-quality EEG recordings from free-moving animals under field conditions is challenging. In humans, neuronal activity in the neocortex generates electrical fields strong enough to be detected by metal electrodes glued to the scalp. As a result, ecologists interested in studying EEG-defined sleep often question whether similar methods can be used in other animals [122]. Unfortunately, this non-invasive method is not suitable for most animals. First, many animals will simply remove the sensors. Second, scalp electrodes are vulnerable to artefacts arising from muscle activity, eye movements and movements of the animal. Finally, scalp electrodes require frequent replenishment of conductive gels to maintain signal quality [122], which may disturb an animal's normal sleep pattern. For these reasons, surface electrodes are rarely used to record sleep-related changes in brain activity in animals.

In some cases, minimally invasive methods can be used to record the EEG under field conditions. Subcutaneous electrode wires inserted under the skin overlying the cranium have been used in the wild to record EEGs in three-toed sloths (*Bradypus variegatus* and *B. pygmaeus*) [43,44], hibernating lemurs (*Cheirogaleus crossleyi* and *C. sibreei*) [123] and barn owl chicks (*Tyto alba*) in nest-boxes [22]. An obvious advantage of this approach is that the electrodes can be inserted with hypodermic needles under local, rather than general, anaesthesia. A drawback of this minimally invasive method is that the electrodes are sensitive to artefacts resulting from movements of the electrodes and the overlying skin.

More stable EEG recordings can be obtained from electrodes placed on the dura overlying the brain [45,46], as typically done under laboratory conditions. Briefly, under full anaesthesia, the dura is accessed by making an incision in the scalp and drilling holes through the cranium. The electrodes are secured to the skull with dental acrylic and attached to a connector mounted on the head. The incision is then closed, leaving only the connector exposed, much like the external connectors used with cochlear implants in humans with impaired hearing. Alternatively, under field conditions, the incision can be closed around the electrode cables running directly to a recording device mounted on the animal's head [46] or back [45]. As recording the EEG from the dura requires surgery, this method likely has a larger impact on animals than the non-invasive methods for measuring sleep. After a post-surgical recovery period, comparisons of the behaviour of instrumented and uninstrumented animals are therefore important to assess the impact of this EEG recording method [45].

Although the EEG provides a direct measure of sleep-related changes in brain activity, by itself it provides an incomplete view of sleep. As EEG activity during wakefulness and REM sleep is remarkably similar, the reduction in muscle tone that distinguishes REM sleep from wakefulness also needs to be measured. Typically, muscle activity is measured directly via EMG wire electrodes placed on or in the neck muscles [65].

Until recently, the greatest obstacle to studying sleep electrophysiology in the wild was the absence of devices suitable for recording the signals detected by the EEG/EMG electrodes. In captivity, the electrodes can be connected to a transmitter, either mounted externally or surgically implanted in the animal, which broadcasts the signals to a receiver near the animal's cage. Although telemetry allows animals to be housed in large structurally complex environments [124–126], the transmission range of commercially available transmitters is limited to several metres at most. Consequently, in the wild, telemetry is likely to only be effective in animals that reliably sleep in one place. By contrast, a recently developed data logger that records and stores the signal to a memory chip mounted on the animal [65,84] allows sleep to be recorded over distances spanning thousands of kilometres [46]. In addition, these data loggers incorporate a tri-axial accelerometer, which, when mounted on the head of birds, has revealed head dropping resulting from the reduction in muscle tone occurring during REM sleep [22,46,65].

In addition to detecting REM sleep, combined EEG/accelerometry recordings can also provide valuable information on the behaviour of an animal when video recording is not possible. During soaring, but not flapping flight, great frigate-birds engage in unihemispheric and bihemispheric NREM sleep [46]. Although bihemispheric NREM sleep can occur in flight, NREM sleep is more asymmetric in flight than on land. Interestingly, accelerometry recordings that detected centripetal forces revealed that the asymmetry in SWA is associated with the direction of flight: when the frigate-birds circle to the left or right, SWA in the hemisphere connected to the eye facing the direction of the turn is usually lower than in the other hemisphere, suggesting that they use this form of sleep to watch where they are going. Finally, as accelerometry is being widely used to characterize waking behaviours, such as walking, flying and feeding [85], when combined with EEG recordings, it provides a means to assess the impact that these ecological demands have on subsequent sleep duration and intensity.

As with other methods for recording sleep in the wild, there are limitations to EEG data logging. Notably, the recordings cannot be monitored in real time and the animal has to be recaptured to remove the logger. Also, although the logger used in the field-based EEG sleep studies to date is relatively light (less than 2 g without a power supply), an obvious trade-off between recording duration and logger mass exists when the size of the battery is taken into consideration. In some cases, the combined mass of the logger and battery may be within the acceptable range for an animal to carry only when placed on the animal's back. In this case, the accelerometer will detect movements of the body, but not those of the head. In addition, when the logger is placed on the back, a cable is needed to run the electrode wires from the head to the logger [45]. Collectively, these limitations need to be evaluated when considering using this method to study sleep in the wild.

6. Ecological flexibility and sources of variation in sleep and its timing

Studies in the wild have revealed extensive variation in the timing and amount of sleep between populations and individuals of the same species (e.g. [22,45,89,127]). The systematic study of intraspecific variation in sleep phenotypes in the wild offers largely untapped opportunities to gain insights into the function of sleep and in the evolution of different sleep strategies. Here, we advocate a behavioural ecology approach that involves studying the sleep of individuals in an ecological context and with an evolutionary perspective, considering the—past and present—fitness costs and benefits of different sleep phenotypes.

Field studies can be used to describe variation in the timing and duration of sleep both within and between individuals of a particular species, and to formulate and test hypotheses about the ecological and individual-specific factors that underlie this variation. For example, the relationship between the frequency of peeking (brief eye opening) during sleep and various ecological factors has been examined in a variety of duck species in the wild (e.g. [80,81]). In the blue tit and great tit (*Parus major*)—small passerine birds that use nest-boxes for breeding and roosting—the sleep behaviour of many individuals has been measured repeatedly based on video-recordings during the winter and early breeding season [89,90]. These studies showed that sleep duration not only varied seasonally, following changes in night length (e.g. blue tits slept 14.8–15.5 h in December, but only 9.7–10.9 h in April), but also depended on the individual's age and sex (adult birds slept less than juveniles and males slept less than females). Other environmental factors that can affect sleep duration are local light conditions [89,90], temperature [127], the presence of predators [1,53,71,128] and ectoparasites [129]. Even after controlling for season and other variables, sleep duration in tits still varied considerably and consistently between individuals [89,90], suggesting that sleep behaviour is an individual-specific trait that reflects an individual's experience, condition and/or genes [130,131].

Interestingly, phenotypic variation in other traits can be linked to sleep in unexpected ways via pleiotropic effects of the underlying genes. For example, barn owls show marked interindividual variation in the extent of melanin (eumelanin) in their feathers resulting in individuals with few or many dark spots, even in the same brood. Surprisingly, this variation in plumage predicts variation in a variety of physiological and behavioural traits [132]. The link between such seemingly unrelated traits apparently results from pleiotropy in the melanocortin system. An EEG/accelerometry study of barn owl chicks in the wild showed that this pleiotropy extends to sleep during development [22]. Although the time spent sleeping did not vary with age, the amount of REM sleep decreased with age in owlets, an ontogenetic pattern implicated in brain development in mammals [19–21]. Interestingly, variation in this pattern was associated with variation in the expression of *PCSK2* in the feather follicles, a gene encoding an enzyme involved in melanin synthesis. Owlets with higher levels of *PCSK2* expression had less REM sleep than expected for their age, suggesting that they developed faster than owlets with lower levels of *PCSK2* expression. The genetic basis and the pathways involved in this link between sleep and the melanocortin system remain unresolved. Moreover, it is unknown whether these differences in sleep, or their potential impact on brain development, persist into adulthood, and what the consequences are—if any—earlier or later in life. Nonetheless, this study illustrates how naturally occurring variation can serve as a resource for probing the mechanisms and functions of sleep.

Hypotheses derived from descriptive, field-based studies about environmental factors or individual-specific traits that affect sleep can then be tested more rigorously through experimentation either in captivity or in the wild. For example, in great tits, the influence of local light conditions has been tested by illuminating the interior of nest-boxes at night [87,88] or the surrounding forest [133], and the effect of ectoparasites has been studied by manipulating their abundance in the nest [129]. In free-living gulls, the effects of manipulating thermal stress [134] and foraging demands [135] on sleep behaviour have also been examined. Interestingly, when compared to naturally foraging gulls, those provisioned with food at their nest foraged less, slept less and experienced fewer territorial incursions from other gulls, suggesting that foraging increases sleep need at the expense of other behaviours, such as territorial defence.

A next step in the behavioural ecology approach is to link the observed between-individual variation in sleep phenotypes to measures of reproductive success (e.g. [136]). Variation in the amount of sleep has been studied in a population of pectoral sandpipers (*Calidris melanotos*), a polygynous shorebird that breeds in the high Arctic [45]. First, activity patterns of males and females, recorded using a radiotelemetry-based system, revealed that males were much more active than females during a three-week period of intense male–male competition for access to fertile females. There was substantial between-male variation in the amount of activity, with the most extreme one being active for more than 95% of the entire time over a period lasting 19 days. Combined EEG and EMG recordings from free-living, competing males on the tundra confirmed that these activity measures were valid proxies for the amount of sleep. Time spent sleeping indeed varied substantially among males (2.4–7.7 h per 24 h). Then, the parentage of all eggs laid in nests on the study site was determined using molecular markers. This revealed that variation in levels of activity among the territorial males was linked to their siring success: short-sleeping males sired more offspring. If variation in male activity is heritable, and if there are no detrimental effects of reduced sleep (e.g. mortality costs), this would lead to strong ongoing sexual selection for reduced sleep. Although pectoral sandpipers are polygynous and breed in an extreme environment with continuous daylight and a short, intense breeding season, sexual selection might play an important role in the evolution of sleep duration in many animals. For example, it is interesting to note that male blue tits and great tits slept less than females during the early breeding season [89,90], when defending the territory, guarding the fertile female mate and pursuing extra-pair copulations determine reproductive success.

Selection on the timing and duration of sleep is also expected during migration [70,137], other long periods of movement and during other phases of reproduction, in particular during the period of parental care. For example, in seabirds, one parent typically goes out to sea to forage, while the other parent stays at the nest, relying only on energy stores. Such foraging trips can last multiple days to weeks (e.g. greater than 40 days in the king penguin, *Aptenodytes patagonicus*) [138]. The ecological demands for wakefulness are likely to be greater when foraging at sea than when confined to the nest. For example, a recent EEG/accelerometry study in great frigate-birds showed that females slept for only 42 min d^{-1} while at sea for up to 10 days, but for over 12 h d^{-1} once back on land [46]. The difference between sleep duration at sea and on land may be particularly extreme in this species as frigate-birds never rest on the water and all sleep occurred in flight. Indeed, tracking studies have shown that other seabirds, such as albatrosses, typically float on the surface of the ocean at night for several hours [139], although it is unknown whether they sleep at this time. Consequently, additional EEG-based studies are needed to determine whether seabirds in general cycle between periods of low and high amounts of sleep while switching between sea and land, respectively, and to understand the selection forces acting on these sleep strategies.

Comparing populations living in different environments is another useful approach to investigate how ecology and life-history influence sleep. Albeit performed under artificial photoperiods in captivity, a recent study of cavefish illustrates this comparative approach that could be applied in the wild. Comparing surface and three cave-dwelling populations of the characin fish *Astyanax mexicanus* showed that individuals from cave-dwelling populations converged not only on traits such as loss of eyes and pigmentation, but also on a strong reduction in the duration of sleep behaviour (surface-living fish slept on average 800 min, while fish from three independent cave populations slept on average 110–250 min per 24 h period under a 12 L : 12 D photoperiod) [140]. The distribution of sleep duration in individuals from hybrid crosses and from backcrosses between surface and cave populations suggested that variation in the amount of sleep is based on only few loci with dominant effects. Although this is a clear example of convergent evolution, the exact genetic mechanism probably differs between the three cave populations, given that there were more subtle differences in their behavioural rhythms. For example, individuals in only one of the three cave populations still showed a pronounced diurnal rhythmicity in activity similar to that observed in surface-dwelling fish [140]. Assuming that sleep in the cavefish was not suppressed by light (i.e. [141]), *A. mexicanus* may inform our understanding of the function of sleep. Why might cave-dwelling fish (need to) sleep dramatically less than their surface-living conspecifics? We do not know, but the blind fish that live in a constant cave environment might receive less sensory input than surface-living individuals, and this may reduce their need for sleep if sleep plays a role in processing information in the brain [142] or in getting rid of waste products related to such information processing [27].

Ultimately, as with studying sleep in captivity, studies in the wild also come with some caveats. Many ecological and individual-specific factors can affect sleep variables, and it may not be easy to disentangle them or even to take important variables into account. For example, an EEG-based study of two sister species of free-living three-toed sloths (only one of which was naturally exposed to predation risk from nocturnal cats) revealed differences in the timing of sleep consistent with the idea that sloths prefer to be active when their predators are sleeping, and sleep when their predators are active [44]. However, this is only a comparison of two species, and many other unidentified factors could have accounted for this difference. Comparisons between individuals of a species can also be difficult to interpret, because the individual's recent history in terms of sensory experiences [11] and exposure to parasites [129] or predators [128] is usually unknown, but can have a strong influence on sleep phenotypes. Similarly, it may be difficult to relate current sleep patterns to current ecological conditions in a meaningful manner if the ecological conditions have changed relatively recently. Such a situation could arise during natural cycles in predation pressure wherein periods of high pressure can have effects on an animal's stress physiology (and thereby sleep) that extend into periods of low pressure [143]. Also, as noted in §5b(iii), due to global warming, polar bears forced to swim for several days [118] may be exposed to periods of sleep deprivation for which they have no evolutionary 'solution'. In effect, this anthropogenically altered 'wild' condition suffers from some of the same concerns (e.g. novelty and stress) expressed regarding the unnatural laboratory environment.

The studies mentioned in this section have shown that extensive variation in sleep phenotypes exists and that some of this variation can be explained by local environmental conditions. However, these studies also highlight that sleep seems to be an evolutionarily pliable trait on which natural and sexual selection can act quickly. There is much to be learned about the evolution of sleep strategies from field studies, by highlighting the selective forces on sleep phenotypes and by measuring the strength of selection. In addition, identifying trade-offs related to variation in sleep duration may provide clues to the functions of sleep.

7. An ecological approach to understanding human sleep

Humans spend about a third of their life sleeping. As in other animals, understanding the function(s) of sleep calls for its study in the natural environment. However, the extensive body of work on human sleep has primarily been conducted in artificial laboratory environments. One of the challenges (and opportunities) in studies of human sleep is that we quickly and dramatically change our 'natural' environment, thereby removing ourselves from some of the selective pressures that shaped our sleep, while exposing ourselves to new ones. To provide insights into ancestral sleep patterns, it may be most informative to examine sleep in societies that have changed little over recent time. In addition, comparisons between individuals living in those societies and individuals from those societies now living in an industrialized environment may reveal plasticity in human sleep, as well as new selective forces and associated responses that are shaping our sleep.

Recently, actigraphy has been used to measure sleep and light levels in humans living in pre-industrial environments in Africa and South America. One study including two communities in Africa and one in South America, all of them near the equator, found relatively short daily sleep durations, which seem to be accounted for by low ambient temperatures in the morning [52]. The authors suggest that these sleep patterns are central to the physiology of humans living in tropical latitudes near the locations of the studied populations. By contrast to this study, three other studies in communities living in tropical or subtropical latitudes without access to electricity found longer sleep durations [51,144,145]. These studies also included urban communities of similar ethnic and sociocultural background with free access to electricity and showed that the urban environment was always associated with later sleep onset; however, in only two of these studies, was this later sleep onset associated with shorter sleep duration. In people working as rubber tappers in the Amazon rainforest, subjective sleep duration (recorded through sleep questionnaires) was shorter in those with access to electric lights than those without access, although this difference was not significant when sleep was assessed with wrist activity monitors [144]. Interestingly, the same study found that rubber tappers with access to electricity had a delayed melatonin release onset, a reliable marker of the phase of the circadian clock [146]. A study that compared sleep based on wrist actigraphy in two ethnically and socioculturally uniform communities of Toba/Qom in the Argentinean Gran Chaco that differ in access to electricity revealed that the community with electricity slept up to 1 h less per day (depending on the season) than that without access to electricity, and this difference was entirely accounted for by later bedtimes and sleep onsets in the former [51]. This study also revealed that both communities slept significantly longer during the winter than during the summer, a phenomenon previously described in more modern settings [147,148]. The lengthening of sleep during the winter in the Toba/Qom was due to a later sleep offset. Accordingly, a recent report showed that people exposed to natural daylight while camping have a longer 'biological night' (length of nocturnal melatonin release) during the winter than during the summer [149]. This lengthening of the circadian night was also accounted for by a delayed melatonin offset [149]. Finally, the interindividual timing of sleep was more variable in the community with access to electricity. This finding is consistent with the fact that sleep timing in individuals in the community under natural daylight was tightly linked to sunrise and sunset and suggests that natural daylight serves as a common *Zeitgeber* in this community, as it does in other animals (see the examples of blue and great tits in §6). Interestingly, the earlier sleep onsets and longer sleep times in the Toba/Qom community without electricity were evident, despite the fact that participants from this community included proportionately more adolescents than the community with electricity. Adolescents in industrialized societies are known to have a later 'chronotype', the preferred sleep time [150]. This suggests that extremely late chronotypes only manifest when people can control their own exposure to artificial light, and is consistent with the disappearance of late chronotypes in a group of participants after transitioning from modern living conditions to a natural light : dark photoperiod while camping [151]. Other field (questionnaire-based) and laboratory studies revealed that light [152] and social demands [153] have a large, even detrimental effect, on sleep in people living in industrialized societies [154].

Although the spectrum of chronotypes narrows in rural environments under natural daylight, some interindividual variability remains. A recent study found that in hunter–gatherer Hadza groups, the natural spectrum of chronotypes in combination with nocturnal awakenings resulted in constant environmental awareness, i.e. at least one person was awake at nearly every time of the night [155]. These results provide support for the sentinel hypothesis [1,156], which postulates that interindividual variability in sleep timing and the presence of nocturnal awakenings increase the likelihood of detecting predators. This hypothesis is also supported by the observation that communities living under more rural conditions, which potentially experience increased predation pressure or risk, experience more restless sleep than those in urban environments [51,145].

Although these kinds of studies can teach us how sleep differs between different environmental conditions, the sleep patterns encountered in less industrialized human communities might not necessarily reflect optimal (ancestral) values for humans in general. Our modern lifestyle in highly industrialized regions not only allows sleep to take place in highly protected environments, but also might demand different amounts of sleep. For instance, living in cities poses different cognitive demands related to spatial orientation, face recognition and sensory stimulation, which could, in turn, require different amounts of sleep. Moreover, how sleep responds to these demands may vary depending on an individual's genetic background. Genes selected under certain environmental conditions in less industrialized populations (e.g. humans in the Arctic versus in the tropics) may lead to different sleep-related responses to industrialization. Another possibility that needs to be considered is that individuals living in pre-industrial environments may actually be sleep deprived or display suboptimal sleep patterns. In other words, not all sleep traits we see in 'natural' environments are necessarily 'optimal'. For example, individuals in small homogeneous communities could display sleep phenotypes that reflect a prior genetic bottleneck [44], rather than adaptation to the local environment. Overall, the issues related to interpreting data from 'wild' human populations are complex and, not surprisingly, subject to debate [157,158]. Resolving this debate through further study is an important endeavour, especially given that such findings could lead to medical recommendations for how much time people should spend sleeping that either underestimate or overestimate sleep need.

The study of human sleep in more natural and ecologically meaningful environments is still in its infancy and limited to the measurement of sleep duration via actigraphy or questionnaires. Research on sleep states (NREM and REM sleep) selected for in different environments is limited by the need to use electrophysiological recordings to accurately measure sleep state. Nevertheless, the use of new algorithms that could determine sleep states from simple activity records and/or the development of new portable EEG technology for recording human sleep in an unobtrusive way may shed light on this topic. Perhaps the most important conclusion from the human studies so far is that, as in other animals, there is extensive interpopulation and interindividual variation in the amount of daily sleep. This is clear from studies done in similar latitudes and environmental conditions, which yield differences in daily sleep of up to 3 h [51,52,144,145]. Future studies should determine the extent of phenotypic sleep plasticity under different environments and whether specific sleep genotypes have been favoured under certain conditions.

8. Summary

Despite the prominence of sleep in the lives of animals, we lack a comprehensive understanding of sleep and its functions. The study of sleeping animals in the wild is an emerging avenue for delivering new insights into the ecological relevance of sleep. The first studies along this unbeaten path have shown that sleep is an extremely pliable trait that should respond quickly to natural and sexual selection. By exploiting existing intraspecific variation in the amount of sleep, studies have revealed the evolution of different sleep strategies with consequences for fitness [45,102]. Monitoring sleep in a species over weeks and months has shown that sleep quotas can vary seasonally [90], with ambient temperature [127] and the prevalence of ectoparasites [129]. Animals can also substantially reduce their sleep when faced with demands that favour extended periods of wakefulness [45,46]. Interestingly, the persistence of small amounts of sleep in these animals intimates an apparently inescapable need for at least some sleep-dependent processes.

The continued success of this behavioural ecology approach to the study of sleep detailed above depends on the further development of methods for quantifying sleep, determining its intensity and, in animals with more than one type of sleep, the time allocated to each type. For example, the power of studying sleep in established blue and great tit systems would be enhanced by the further miniaturization of EEG technology. In the interim, sleep intensity can be readily assessed in nest-boxes by video-taping behavioural responses to sounds or other titratable stimuli. In addition to elaborating on existing systems for studying sleep in the wild, the accuracy of using non-invasive methods (e.g. head-mounted accelerometry) to quantify NREM and REM sleep should be assessed in animals such as sea otters, wherein it might be possible to distinguish between these states based on behaviour alone. Undoubtedly, such developments will be realized in the coming years, and sleep research having 'gone wild' will continue to yield new insights into the plasticity, evolution and functions of sleep.

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