

Evolution and plasticity of sleep

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Sleep is a highly conserved state across the animal kingdom. However, sleep duration, behavior and associated neural activity show great diversity across taxonomic groups, and sometimes even within the same species. Understanding sleep functions depends on understanding when sleep emerged, which of its characteristics have persisted throughout evolution, and what accounts for the similarities and differences in sleep behavior and neurophysiology across different species. Here, we provide an overview of the latest findings in comparative sleep neurophysiology and highlight remarkable examples of sleep flexibility. We discuss the implications that these findings have on the proposed functions of sleep.

Addresses

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Current Opinion in Physiology 2020, **15**:111–119

This review comes from a themed issue on **Physiology of sleep**

Edited by **Vladyslav Vyazovskiy** and **Jenny Morton**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 31st December 2019

<https://doi.org/10.1016/j.cophys.2019.12.013>

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Introduction

Sleep is a state that continues to challenge and intrigue researchers, even 100 years after the earliest contemporary observations of sleeping animals [1]. Many functions have been attributed to sleep, but no single hypothesis fully explains the diversity in which sleep manifests across different taxonomic groups. Understanding when sleep evolved, how it changed over evolutionary time, and which features of sleep are shared across taxonomic groups might shed light on the core functions of sleep. In this review, we will cover the latest advances in our understanding of sleep in animals — from mammals to jellyfish — and the implications these have for understanding the evolution and functions of sleep.

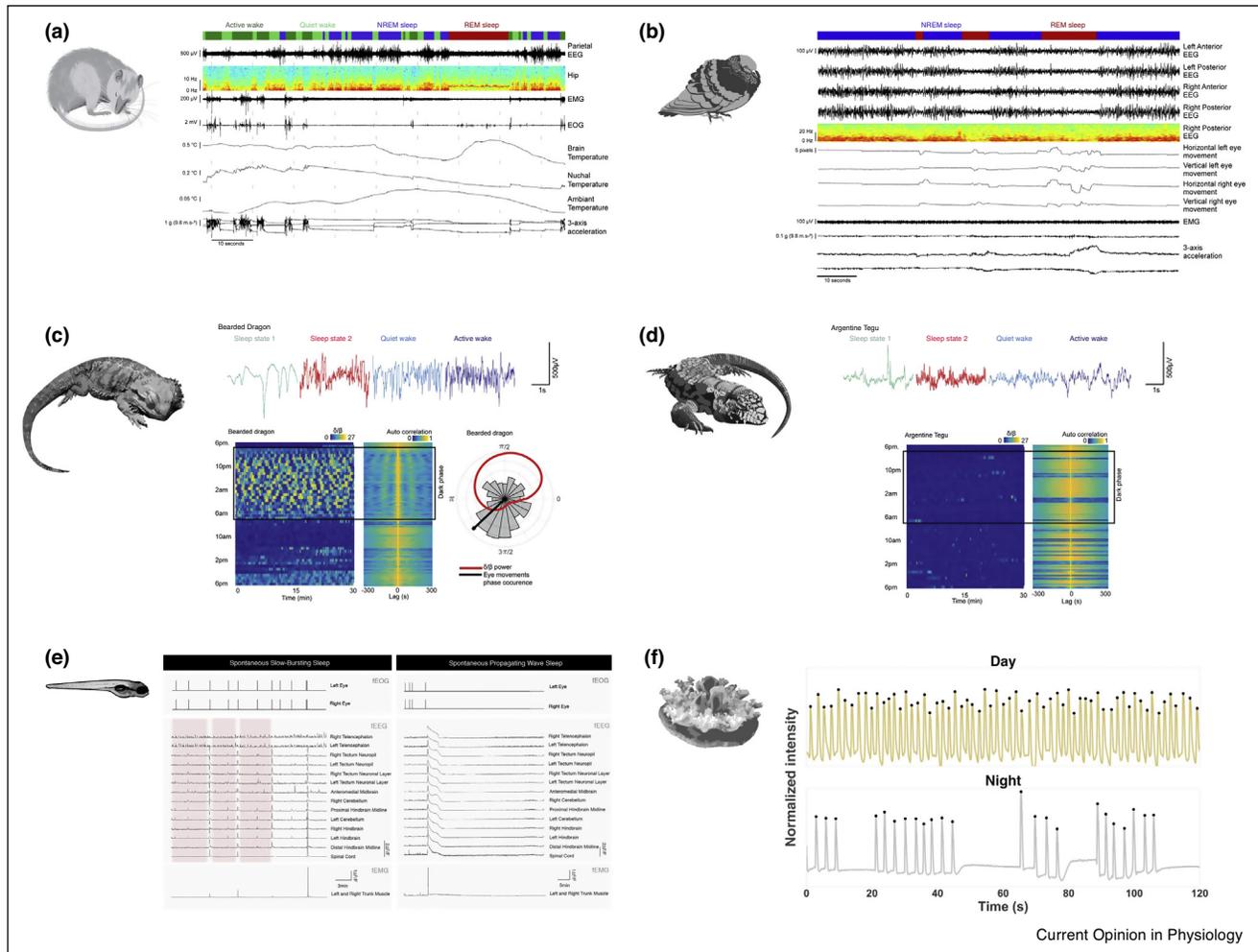
Mammalian sleep

Sleep is most intensively studied, and its mechanisms are best understood, in mammals. During sleep, most mammals cycle through two types of sleep, defined by changes in behavior and neural activity: non-rapid eye movement (NREM) sleep and rapid eye movement (REM) sleep. When compared to wakefulness, NREM sleep is characterized by slower and more regular respiratory and heart rates, reduced skeletal muscle tone and brain temperature, and a slow oscillation of membrane potentials in neocortical neurons (<1 Hz) between depolarized ‘up-states’ and hyperpolarized ‘down-states’, generating large, slow-waves on the electroencephalogram (EEG) [2,3] (Figure 1a). Thalamocortical spindles, consisting of short bursts of faster waves (6–15 Hz depending on the species), are also hallmarks of NREM sleep [4]. Hippocampal sharp-wave ripples (80–140 Hz) also occur during NREM sleep, as well as during pauses in waking activity, such as grooming and feeding [5]. Conversely, REM sleep is characterized by irregular respiratory and heart rates, skeletal muscle twitching occurring on a background of muscle atonia, increased brain temperature, greatly diminished thermoregulatory responses, rapid eye movements under closed eyelids, and wake-like EEG activity and a hippocampal theta rhythm (4–8 Hz) similar to that occurring in awake, ambulating animals [6]. The pattern of cycling between NREM and REM sleep changes throughout the sleep period, with larger amounts of NREM sleep and increased slow wave activity (SWA) early on and larger amounts of REM sleep later in the sleep bout [7]. Since SWA increases following extended wakefulness and decreases during sleep, it is thought to reflect homeostatically regulated processes [8]. SWA correlates with arousal thresholds and therefore reflects sleep intensity and depth [9]. Finally, the level of SWA increases (or decreases) locally in the mammalian cortex reflecting brain use (or disuse) during prior wakefulness [10,11].

Birds exhibit mammalian-like sleep states

Despite being distantly related, having last shared a common ancestor over 300 million years ago, birds exhibit two sleep states remarkably similar to mammalian NREM and REM sleep. As in mammals, NREM sleep is characterized by stable respiratory and heart rates, decreased brain temperature, and slow-waves on the EEG; and REM sleep is characterized by twitches, rapid eye movements, suppression of thermoregulatory behaviors, and awake-like EEG activity [12–14] (Figure 1b). Moreover, like mammals, SWA in birds is higher after

Figure 1



Comparative overview depicting the principal known neural and/or behavioral sleep characteristics in mammals, birds, two reptile species, zebrafish larvae and upside-down jellyfish.

(a) Raw signal traces over 90 s illustrating the correlates of different vigilance states in a rat. From top to bottom: hypnogram of the wake/sleep state scoring (active wake in dark green, quiet wake in light green, non-rapid eye movement (NREM) sleep in blue, and rapid eye movement (REM) sleep in red); parietal electroencephalogram (EEG); time frequency representation of the hippocampal local field potential; electromyogram (EMG) (high pass filter set at 10 Hz, order 2); electrooculogram; brain temperature; nuchal temperature; ambient temperature; 3-axial accelerometry (adapted from [79]).

(b) Raw signal traces over 90 s illustrating the correlates of NREM and REM sleep in a pigeon. From top to bottom: hypnogram of sleep state scoring (NREM sleep in blue and REM sleep in red); left anterior and posterior hyperpallial EEG; right anterior and posterior hyperpallial EEG; left and right eye movements along horizontal and vertical axes defined relative to the plan of eyelid closure. Positive increases in signal values represent rostral and dorsal movements respectively; EMG (high pass filter set at 10 Hz, order 2); 3-axial accelerometry.

(c) Correlates of different vigilance states in the bearded dragon. Top: example of raw signals from one local field potential (LFP) channel recorded in the dorsal ventricular ridge (DVR) of a bearded dragon during sleep state 1 (sharing similarities with mammalian NREM sleep) in turquoise, sleep state 2 (sharing similarities with mammalian REM sleep) in red, quiet wake in light blue, and active wake in dark blue. Bottom left: band power ratio (δ [0.5–4 Hz]/ β [11–30 Hz]). Each horizontal segment represents 30 min of the ratio computed with a 10-s window and a step of 0.1 s. The value of the ratio is color coded from 0 (blue) to 27 (yellow). Each line, from the top to bottom represents the changes in the ratio over 24 hour from 6 PM onwards. The dark rectangle indicates the dark period. Bottom center: normalized autocorrelation map of the δ/β ratio. The autocorrelation was computed within 600-s windows with a step of 1 s. Both figures reveal rhythmic cycling every 90 s between periods rich in δ frequencies (yellow) and periods rich in β frequencies (blue). This cycling takes place during the dark period, when the animal is lying on the floor with the eyes closed. Bottom right: The distribution of the eye movements within each δ - β cycle; the mean phase is represented with a black arrow. The red line represents the mean δ/β power ratio across the δ - β cycle.

(d) Neural correlates of different vigilance states in the argentine tegu. Top: example of raw signals recorded in the DVR of an argentine tegu using the same methodology and annotations as for the bearded dragon. Bottom: δ/β ratio (left) and autocorrelation (right) represented as for the bearded dragon. The two figures reveal the absence of a clear cycling pattern in the δ/β power ratio over the 24 hour. Panels C and D from [33*].

(e) Polysomnographic recordings of the two sleep states spontaneously exhibited by zebrafish larvae (left – 30 min recordings depicting slow bursting sleep (SBS) activity; right – 60 min recordings depicting propagating wave sleep (PWS) activity). From top to bottom: eye movements;

extended periods of wakefulness, and is higher in brain regions used more extensively during prior wakefulness [15,16]. During NREM sleep, slow-waves propagate through the avian hyperpallium as in the mammalian neocortex [17^{*}]. Additionally, REM sleep episodes are more frequent, and longer lasting, later in the sleep period in several species [18,19]. As in altricial mammals, REM sleep amounts are highest in young altricial owls and decline as the birds mature [20].

Despite these similarities, interesting differences exist between sleep in mammals and birds. While asleep, birds use their skeletal muscles for perching and maintaining an upright posture. Reductions in muscle tone, a characteristic of REM sleep, manifests only locally through head bobs or the modest sliding of wings off the sides of the body [21–23]. In terms of sleep architecture, REM sleep episodes are relatively short in both volant and flightless birds ([24], [25]), typically lasting <10 s, and the alternation between the two states is more frequent compared to mammals. For instance, pigeons (*Columba livia*) can have upwards of 1000 episodes of REM sleep during a single night [26].

Moreover, unlike mammals, previous studies of birds did not detect hippocampal sharp-wave ripples during NREM sleep or wakefulness, or a hippocampal theta rhythm during REM sleep [27]. In addition, recent intracerebral recordings failed to detect thalamocortical spindles in pigeons [17^{*}]. In mammals, thalamocortical spindles, hippocampal sharp-wave ripples and neocortical slow-waves are thought to function as an interacting network of rhythms involved in transferring memories from short-term storage in the hippocampus to the neocortex for long-term storage and integration with preexisting memories [28,29]. The apparent absence of thalamocortical spindles and sharp-wave ripples suggests that hippocampal memories might be processed differently at the systems level in birds, as also suggested by differences in neuroanatomy and the absence of evidence of memories transferring from the hippocampus to other parts of the avian brain [27]. Nonetheless, avian slow-waves might be involved in processing memories either at a local level, as suggested by their local use-dependent regulation [16], or at a systems level, perhaps via their propagation across regions [17^{*}].

Studies on reptiles reveal large intrataxonomic diversity in the neural signatures of sleep

The presence of similar states in mammals and birds suggests that either these states were already present in

their most recent common ancestor, or that they evolved independently in each lineage via convergent evolution. Since birds are a derived type of reptile, one would expect their closest living relatives (the non-avian reptiles) to show similar states if they were present in the common ancestor to mammals and birds. Unlike most studies on these endothermic animals which revealed largely consistent findings across a diverse array of species [30], early studies on reptiles reported highly variable results across species, and even contradictory results within the same species [31,32]. As the source of this variability remains uncertain, it has been difficult to reach a firm conclusion on how NREM and REM sleep evolved in mammals and birds. Recent work suggests some of this diversity may in fact reflect real, unexpected differences in the way sleep manifests across non-avian reptiles [33^{*}].

Shein-Idelson *et al.* recently recorded the intracerebral activity of bearded dragons (*Pogona vitticeps*) during the dark period while the animals assumed a sleep posture with closed eyes [34]. They reported two distinct patterns of activity that alternated with an unprecedented regularity every 80 s (Figure 1c). The first state was characterized by frequent local field potential (LFP) depolarizations, which they named sharp-waves, based on their morphology. Most sharp-waves were accompanied by a burst of high (>70 Hz) frequency activity. The second state was characterized by LFP activity similar to wakefulness and was correlated with eye movements under closed eyelids.

The authors noted the similarities between the sharp-waves in dragons and the sharp-wave ripples recorded from the hippocampus in mammals during NREM sleep, as did earlier researchers who also found sharp-waves during sleep in a variety of reptiles [35]. However, the sharp-waves in dragons, and those described in earlier studies, were recorded from non-hippocampal brain regions that generate slow-waves in birds [36,16,17^{*},37]. Moreover, high-frequency activity is not unique to sharp-wave ripples, as it also occurs during the depolarized upstate of the slow oscillation in neuronal membrane potential that gives rise to EEG and LFP slow-waves in mammals [38]. Consequently, sharp-waves in dragons may reflect a phenomenon less comparable to mammalian hippocampal sharp-wave ripples, and instead be simply a variant (or evolutionary precursor) of slow-waves, with upstates shorter than those found in mammals and birds [39]. Interestingly, the latter suggests that mammals and birds independently evolved increased investment into upstates, and decreased investment into downstates, and the purported benefits of each:

(Figure 1 Legend Continued) neural activity; muscular activity. Red boxes in the middle right panel show transient synchrony in the dorsal pallium, indicative of SBS, occurring between muscle twitches. The large amplitude signals in the middle left panel reflect the transient activation of the entire neural axis, followed by a period of neural silence. A large, prolonged contraction of the tail muscles occurs at the onset of neural axis activation. Figure adapted from Ref. [45^{*}].

(f) Bell pulsing traces for an individual jellyfish during day and night over 120 s. Note the reduced pulsing frequency and occasional pauses in pulsing during sleep. Figure adapted from Ref. [58^{*}].

memory reactivation and neuronal rest, respectively [39]. In this respect, even if reptilian sharp-waves do not reflect the same phenomenon as mammalian sharp-wave ripples, they nevertheless may still be involved in memory consolidation.

Viewed in isolation, the findings from bearded dragons suggest that two sleep states with features suggestive of NREM and REM sleep were present in the common ancestor to mammals and birds. However, several earlier studies failed to detect two distinct states in reptiles, including crocodylians, the closest living relatives to birds [40–42]. Although methodological differences might explain some of the differences between the earlier studies and the findings in the dragon, a recent study suggests that there may be real and unexpected diversity in the way sleep manifests across reptiles. Libourel and colleagues examined sleep in the bearded dragon and another lizard, the argentine tegu (*Salvator merianae*), using the same methods [33*]. Importantly, they replicated the findings previously reported in the bearded dragon and found that the argentine tegu also exhibited two sleep states. However, the brain activity during these states differed markedly from that described in the dragon (Figure 1d). During the first sleep state, no particular LFP frequency was dominant; sharp-waves occurred, but they were infrequent and had shorter durations when compared to the sharp-waves found in dragons. Conversely, the second sleep state was dominated by a 15 Hz oscillation not found during wakefulness that correlated with the occurrence of eye movements and a slight decrease in muscle tone compared to the first state. Unlike the regular cycling between sleep states observed across the night in dragons, switching between states in tegus was irregular, and the second state was more likely to occur at the beginning and end of the night.

Collectively, these studies suggest that some lizards exhibit two sleep states, which share some similarities to NREM and REM sleep in mammals and birds. However, the large differences in terms of sleep neural signature and architecture in the two lizard species, suggests that some of the diverse findings in the older reptile literature may in fact be correct. As this earlier research failed to detect REM sleep in crocodylians, the closest living relatives to birds, and in the cortex and brainstem of sleeping turtles [43], their sister group, it remains unclear whether REM-like sleep was present in the stem amniote or evolved independently several times. Further research on crocodylians and turtles is needed to determine if REM sleep was somehow missed in the earlier studies.

Two sleep states might also be present in other taxonomic groups, including invertebrates

Studies of amphibians and fishes can likewise shed light on the evolution of sleep states in vertebrates [31,44].

Amphibians remain understudied; however, a new study using state-of-the-art imaging on young zebrafish (*Danio rerio*) reveals two sleep states in these aquatic animals [45*]. As larva, zebrafish are transparent, allowing for whole brain and body imaging. Researchers trained larvae to sleep while embedded in an agarose gel that allowed brain and muscle activity, and eye movements of transgenic fish to be recorded using light-sheet microscopy. Interestingly, the authors described two spontaneous states. The first state, named slow bursting sleep (SBS), was characterized by synchronized activation of the neurons in the dorsal pallium (a homologue of the mammalian neocortex) alternating with periods of neural silence (Figure 1e). Sleep deprived fish that were more likely to enter this state, showed stronger activations with a higher degree of synchrony, but longer intervals between successive activations, when compared to spontaneous sleep. In non-sleep deprived individuals, this state was associated with decreased muscle tone, isolated eye movements, and was interrupted by brief trunk muscle activity. The onset of the second sleep state, named propagating wave sleep (PWS), was characterized by eruptions of activity across the entire neuroaxis that lasted around five minutes, during which a wave of muscular activity propagated through the trunk for 10–15 s. This activation was followed by around 20 min of reduced brain activity. During PWS, eye movements were absent. The administration of hypnotics known to induce NREM and REM sleep in mammals induced two states with similar brain activity to those expressed spontaneously, albeit with different temporal dynamics.

The authors relate the two states to NREM and REM sleep, suggesting that they emerged at least 450 million years ago. However, in contrast to the slow oscillations between neuronal activity and neuronal quiescence occurring during NREM sleep in the mammalian neocortex, telencephalic neurons in the zebrafish oscillate at much lower frequencies. Moreover, an increase in neural activity spanning the entire brain network, followed by long-lasting neural suppression of activity has never been described in animals exhibiting REM sleep. The prolonged wave of muscular activity that propagates through the trunk during the onset of PWS is also unlike the brief twitches observed during REM sleep in mammals and birds. Consequently, whereas there are some general similarities between SBS and mammalian and avian NREM sleep, as well as NREM sleep-like state in reptiles, the link between PWS and REM sleep is less clear. Nonetheless, the brain-wide bursts of activity are certainly fascinating and warrant further study to determine their relationship with REM sleep or other processes.

Interestingly, two electrophysiological states have also been described in the fruit fly (*Drosophila melanogaster*) [46]. LFP recordings revealed decreased activity during

sleep compared to wakefulness, as in earlier recordings of the medial brain of *Drosophila* [47,48]. However, unlike these other studies, which employed different methodologies, intermittent oscillations in the range of 7–10 Hz were observed during spontaneous sleep. These oscillations were most likely to occur during the first and last minutes of a sleep bout suggesting that they reflect a transitional sleep stage. In general terms, the presence of a change in brain activity is in line with another arthropod, the crayfish (*Procambarus clarkii*), which also shows a sleep-related change in brain activity, albeit at different frequencies [49]. However, the study by Yap and colleagues is the first to electrophysiologically describe two sleep states in an invertebrate. Whether these two states are in any way homologous, or analogous, to NREM and REM sleep is unknown.

Other lines of evidence support the existence of two sleep states in invertebrates, with behavioral features suggestive of NREM and REM sleep. For instance, some insects twitch their antennae during rest, and fruit flies exhibit more leg and proboscis twitches when they are young [50], similar to the frequent twitches observed in mammals during early development [51]. Perhaps an even more convincing example is the case of cuttlefish (*Sepia officinalis*). During wakefulness, cuttlefish exhibit complex changes in skin color and pattern, mediated by chromatophores that are used to communicate with conspecifics and camouflage themselves from predators or prey. During rest, they cycle through periods when they are quiescent with constricted pupils and mimic the substrate, and periods when their tentacles twitch, the eyes move and their color and patterning changes, resembling only fragments of the patterns commonly displayed during wakefulness [52]. Interestingly, chromatophores are controlled by striated muscles, the very same type of muscle that twitches during mammalian REM sleep. Although these periods of activity are tantalizingly reminiscent of the twitching that occurs during REM sleep, brief arousals have not been ruled out as the cause of this REM sleep-like behavior. Further research on cuttlefish and other mollusks [53], is certainly warranted, as it might reveal whether NREM and REM sleep evolved very early in the evolution of animals, or independently multiple times.

Studying early phylogenetic branches is important for tracking back the origins of sleep

Until recently, all animals tested for sleep behavior had a centralized nervous system. That is, behavioral sleep had been demonstrated in members of all vertebrate groups, arthropods (insects, arachnids, and crustaceans) [49,54,55], mollusks [52,53], roundworms [56] and flatworms [57], but is the brain a requisite for sleep? Jellyfish, members of the phylum Cnidaria, lack any form of cephalization and instead have their neurons distributed

in a radially symmetric neural net. In a recent study, upside-down jellyfish (*Cassiopea* spp.) were shown to meet all the behavioral criteria for sleep; that is, quiescence, specific sleep posture, reduced responsiveness, rapid reversibility, and a homeostatic rebound following deprivation [58]. This state occurred at night, when the bell pulses were less frequent compared to wakefulness, and showed occasional long pauses between pulses (Figure 1f). Furthermore, compounds that promote sleep in diurnal mammals — melatonin and pyrilamine — increased sleep in jellyfish in a dose-dependent manner. Interestingly, sleep-like behaviors have been observed in other jellyfish and their coral relatives, suggesting that sleep may be widespread across cnidarians [59]. These results suggest that sleep evolved before the emergence of a centralized nervous system. They also raise the interesting question as to whether jellyfish sleep because their neurons need to sleep, or if sleep also occurs in organisms lacking neurons. The fact that plants exhibit circadian rhythms [60], seemingly raises the likelihood that some of the cellular processes occurring during sleep predate the evolution of neurons. Further studies on simpler organisms lacking a nervous system, such as sponges, might provide some of the answers.

Many animals show surprising sleep flexibility

When we think about sleep diversity across taxa, we generally think about it as a largely fixed need for sleep, on a daily basis, and specific to each species. For instance, on average, humans sleep 8 hours per day. Across mammals, the daily amount of sleep varies greatly: horses (*Equus caballus*) sleep just 3 hours per day, whereas the northern night monkey (*Aotus trivirgatus*) sleeps upwards of 17 hours [30]. The amount of each sleep state is also highly variable across species: 25% of sleep in humans is REM sleep, but ranges between 3% and 45% across mammals. Similar variation has been observed in birds [61]. However, there are other ways in which sleep variability and flexibility manifest across species. First, within the same species there can be variation in how long different individuals sleep. Second, individuals can modulate sleep according to ecological demands, by reducing their time spent sleeping, changing the timing of sleep, and/or changing the composition of sleep. The composition of sleep can be modulated by switching between bihemispheric and unihemispheric NREM sleep in some animals, sleeping more or less deeply, and/or suppressing REM sleep. These types of flexibility in sleep can (and usually do) manifest in virtually any combination possible. In this section, we will cover examples of studies on mammals, birds, fishes, and invertebrates depicting the variability and flexibility in sleep behavior.

Some marine mammals change their sleep composition when sleeping in water. Northern fur seals (*Callorhinus ursinus*) spend most of the time in water, but breed on land. Like other seals of the family Otariidae, they exhibit REM sleep,

and bihemispheric and unihemispheric NREM sleep. In a recent study, researchers showed that when forced to sleep in water, fur seals suppress most of the REM sleep and replace large amounts of bihemispheric NREM sleep with unihemispheric NREM sleep. Interestingly, when they were allowed to return to land, they recovered some of the NREM sleep while sleeping bihemispherically, but not REM sleep [62].

Flexibility in sleep in response to ecological demands has been shown in both wild-based and lab-based EEG studies of birds. Male pectoral sandpipers (*Calidris melanotos*), for instance, intensively compete for territories and access to fertile females during the three weeks-long breeding season. The time spent sleeping varies considerably between males, with the shortest sleepers obtaining only around one hour of sleep per day. Interestingly, the males that slept the least sired the most offspring, suggesting that sleep loss and adaptive waking performance are not necessarily incompatible [63]. Another EEG-based study in the wild showed adaptive sleeplessness in great frigatebirds (*Fregata minor*) [64]. Nesting female frigatebirds go on foraging trips over the ocean that last up to 10 days. Since they quickly become waterlogged if they alight on the water, they must fly continuously while over the ocean. Frigatebirds reduce the time spent sleeping from over 12 hours/day on land to just 42 min per day in flight on average. The little sleep that they do obtain on the wing occurs primarily (albeit not exclusively) with one hemisphere in NREM sleep and the other awake, or with one hemisphere engaged in deeper NREM sleep than the other. On land, NREM sleep is deeper (based on SWA) and more symmetrical than in flight. Although sleep in flight has only been established with EEG recordings in great frigatebirds, other birds that fly non-stop for long periods — up to 300 days in the case of the European swift (*Apus apus*) [65] — might also sleep in flight [66]. Finally, in a lab-based study, Tisdale *et al.* showed that pigeons decrease the amount of REM sleep by one-third, and lighten the intensity of slow-waves during NREM sleep when sleeping on a low perch, presumably because they perceive a greater risk of predation when near the ground at night [26].

In some fishes, different populations belonging to the same species have adapted their sleeping time in relation to their ecology. The Mexican cavefish (*Astyanax mexicanus*) exists as surface-dwelling and numerous cave populations. Many cave populations, besides having convergently lost their eyes and pigmentation, have also evolved reduced sleeping times. This difference was recently shown to be accounted for by higher levels of hypocretin — a neuropeptide regulating wakefulness and arousal — present in the cave-living populations [67,68]. However, all measurements have been performed in controlled lab conditions, under 12:12 light:dark cycles. Given that the activity of blind cavefish increased during the light phase (indicating that they are responsive to light), it would be interesting to investigate how they sleep in the wild under natural constant darkness.

Some insects can temporarily suppress large amounts of sleep in favor of other behaviors, such as courtship and caring for young. Male fruit flies, for instance, prioritize mating behavior over sleep, without a subsequent sleep rebound [69–71]. The absence of such a rebound stands in contrast to the sleep rebound observed after male–male interactions that reduce sleep, or after mechanical sleep deprivation. In fruit flies, the temporary flexibility, particularly for suppressing the rebound in sleep, is driven by a general state of sexual arousal triggered by female pheromones [69]. Bumblebee (*Bombus terrestris*) workers sleep less to care for their brood [72]. As in fruit flies, the sleeplessness is thought to be driven by pheromones present in the cocoon. Additionally, in contrast to the sleep rebound observed after mechanical sleep deprivation, no rebound was recorded after brood-caring induced sleep loss.

The flexibility in sleep duration exhibited by many animals suggests that adaptive waking performance and health can be sustained on remarkably little sleep. The aforementioned studies show that some bird species are able to suspend large amounts of sleep in a real-world setting for periods of time that would lead to severe cognitive impairment in other animals [73–76], seemingly without any adverse short-term effect. They also show that some mammals and insects do not recover lost sleep in some (but not all) physiologically relevant contexts. Indeed, interspecific, intraspecific, and intraindividual variation in sleep duration seems to pose a profound challenge for any restorative theory for the function of sleep [77]. However, little is known about the potential long-term effects of sleeplessness. In addition, the mechanisms that protect adaptive waking performance in short-sleeping animals remain unknown [78]. Further work on such mechanisms may lead to new perspectives on the adaptive value of sleep.

Conflicts of interest statement

Nothing declared.

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