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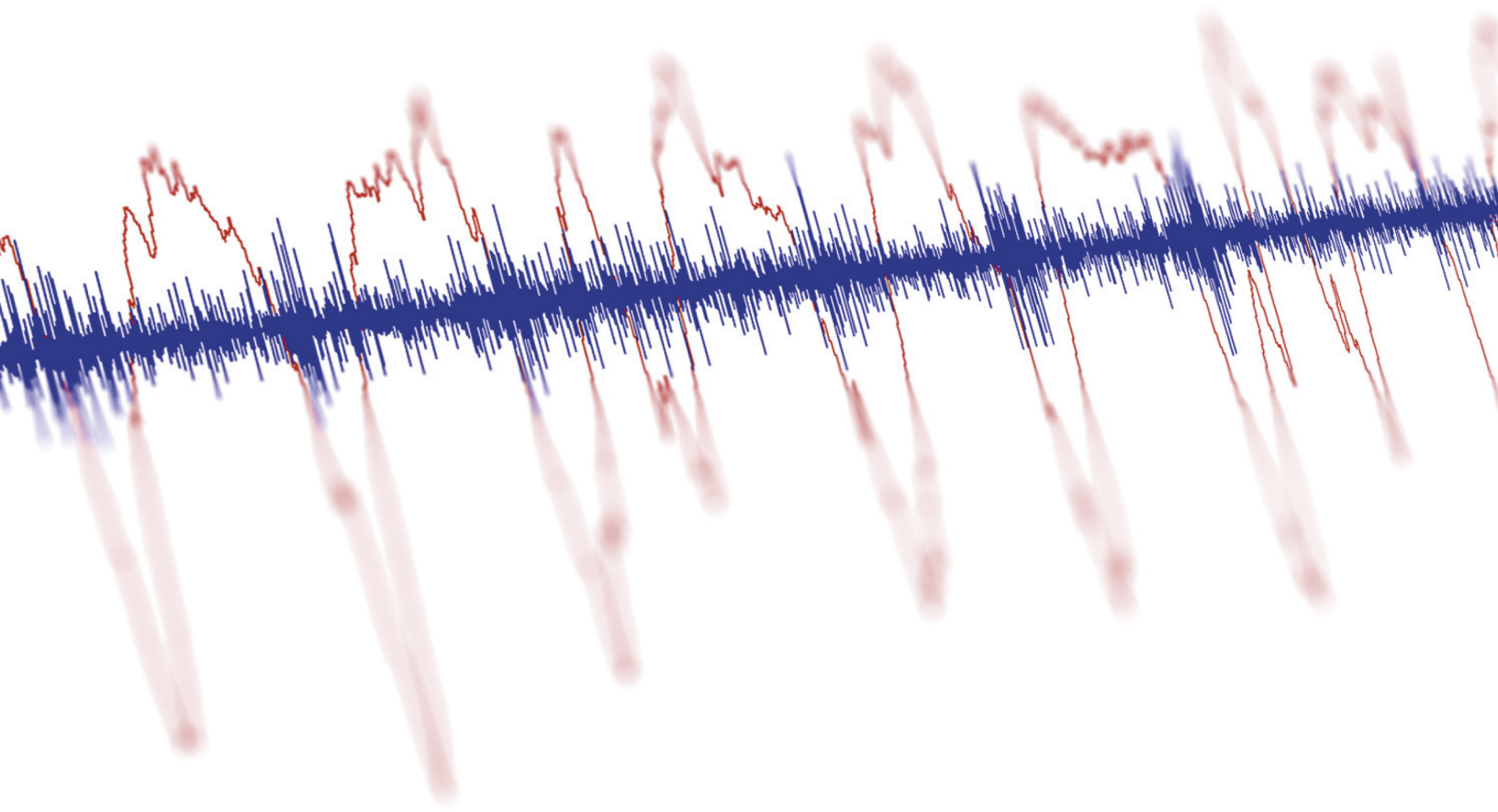
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20

Evolution of Sleep and Adaptive Sleeplessness

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I INTRODUCTION

Viewed as a behavior, sleep is a seemingly simple yet enigmatic state. A sleeping animal typically assumes a recumbent posture, remains inactive, and closes both eyes (at least in animals that have eyelids). During sleep, the intensity of stimulation required to evoke a response (the arousal threshold) is elevated (Neckelmann & Ursin, 1993). With sufficient stimulation, however, sleep can rapidly give way to wakefulness. This often-voluntary reduction of our awareness and associated increased vulnerability suggest that sleep serves an important function or functions (Lima, Rattenborg, Lesku, & Amlaner, 2005). Accordingly, sleep is also homeostatically regulated, such that an extended period of wakefulness increases the need for an extended period of sleep (Tobler, 2011). Taken together, this behavioral characterization of sleep distinguishes it from other quiescent states, including energy-saving torpor, and pathological conditions associated with illness. By doing so, it also allows us to search for sleep (or sleeplessness) in other animals, some of which may be quite different from ourselves.

The search is an important one. Such discoveries should reveal the origins and subsequent evolution of sleep. We might find that different types of animals sleep in different ways or that some animals have more than one kind of sleep, which could reflect the evolutionary gain (or loss) of sleep functions. If there is sufficient between-species (or interspecific) variation, then quantitative analyses can be used to examine possible explanations, which could even explain the purpose of sleep. Studies on how animals sleep in (what we might call) extreme environments might also reveal new adaptations, whereby animals resolve conflicts between sleep and competing demands. Such evolutionary solutions might inform our understanding of the biological targets for sleep-related processes. Lastly, comparative studies could reveal a world of undiscovered diversity in animals that can forgo sleep for long periods of time, or that naturally sleep very little, or even not at all.

Herein, we aim to provide a comprehensive review of sleep across the animal kingdom. Using a strong phylogenetic framework, we discuss studies of mammals, avian and nonavian reptiles, amphibians, bony and cartilaginous fishes, and invertebrates. It will be evident that much more is known about sleep in some groups than others. Where appropriate, we will highlight such gaps for future research. We will also review the growing contribution of studies on animals sleeping in the wild. Throughout, we relate ecological and evolutionary insights to a broader discussion on sleep functions.

II TERRESTRIAL MAMMALS

More is known about sleep in mammals than any other group of animals. Beyond being a profound behavioral shutdown, sleep is also a complex neurophysiological state involving distinct substates. This complexity is typically captured through recording various bioelectric signals, including brain waves with an electroencephalogram (EEG), skeletal muscle tone using the electromyogram (EMG), and eye movements via an electrooculogram (EOG). The EEG of an awake mammal shows low-amplitude (small), high-frequency (fast) waves and a hippocampal theta rhythm when engaged in exploratory behaviors. Muscle tone is present and high, and the EOG reflects intermittent and irregular saccades.

These characteristics of wakefulness stand in marked contrast to those of the sleep state first entered upon falling asleep: non-rapid eye movement (non-REM) sleep.

Hippocampal theta activity is replaced by hippocampal sharp waves and ripples. The small, fast waves of an alert mammal are replaced by large, slow waves (*circa* <4 Hz). Indeed, slow waves become the dominant waveform across much of the cortex (Massimini, Huber, Ferrarelli, Hill, & Tononi, 2004). For this reason, non-REM sleep is commonly referred to as slow-wave sleep (SWS) in non-human animals. At the level of an individual neuron, SWS is characterized by a slow (1 Hz) oscillation of the membrane potential, which alternates between hyperpolarized down states associated with neuronal quiescence and depolarized up states with action potentials (Vyazovskiy et al., 2009). The transition between down and up states is synchronized across neurons by synaptic connectivity (Hill & Tononi, 2005). In this way, the synchronous slow oscillation of neuronal membrane potentials underlying SWS manifests in the EEG as large, slow waves. These waves tend to originate in the prefrontal cortex and propagate in an anteroposterior direction across the sleeping mammalian neocortex as traveling waves (Kurth et al., 2017; Massimini et al., 2004). During SWS, the EEG also shows intermittent bursts of fusiform thalamocortical activity, called *sleep spindles*. The waxing-waning shape of sleep spindles is conserved across species, but their frequency is more species-specific, varying within the range of 6–15 Hz (Voirin et al., 2014). Brain temperature can drop upward of 0.5°C during an episode of SWS. SWS-related muscle tone is lower relative to wakefulness, and eye movements are largely absent; heart and respiratory rates are rhythmic.

REM sleep is the second sleep substate in mammals. REM sleep is characterized by a wake-like (or activated) EEG, including the return of a hippocampal theta rhythm (Peever & Fuller, 2017). For this reason, REM sleep is also known as paradoxical sleep, owing to an ostensibly awake brain in an unequivocally asleep body. Relative to SWS, REM sleep is also associated with an increased ability to process sensory information (Cote, Etienne, & Campbell, 2001; Nashida et al., 2000). Brain temperature likewise increases during REM sleep. Unlike wakefulness, however, skeletal muscle tone is either reduced or abolished. However, REM sleep-related muscle atony is periodically interrupted by twitches, which can occur in any muscle in the body, but is often most noticeable in the face and appendages. As the name suggests, REM sleep is associated with eye movements occurring under closed eyelids. REM sleep is also accompanied by cardiorespiratory arrhythmia and spontaneous penile erections. Interestingly, the behavioral generation and dissipation of heat through shivering and panting, respectively, ceases during REM sleep, owing to an unresponsive hypothalamic thermoregulatory system. Lastly, REM sleep is also the state in which the most vivid dreams are reported in humans; it is unknown whether nonhuman animals also dream.

In all mammals studied, REM sleep constitutes the minority of time spent asleep, at least in adults (Lesku, Roth, Rattenborg, Amlaner, & Lima, 2008). Conversely, in young, REM sleep is the major sleep state and then declines to a species-specific adult level. In mammals that birth young with relatively immature brains (or altricial species), this decrease occurs shortly after birth; in precocial species, the decline takes place primarily *in utero* (Jouvet-Mounier, Astic, & Lacote, 1970; Thurber, Jha, Coleman, & Frank, 2008). This ontogenetic shift toward less REM sleep, together with experimental work (Shaffery, Roffwarg, Speciale, & Marks, 1999), suggests that REM sleep is involved in early brain development (Roffwarg, Muzio, & Dement, 1966; see Chapter 27, this volume). Moreover, the persistence of REM sleep into adulthood suggests that this state serves functions beyond maturational processes for the central nervous system.

A Mammalian Sleep Homeostasis

Mammals deprived of sleep are able to recover lost sleep by sleeping longer and more intensely. For SWS, the size and incidence of slow waves can be quantified as low-frequency (typically 0.5–4.5 Hz) power density, known as slow-wave activity (SWA). The level of SWA during SWS depends on the duration (and intensity) of prior wakefulness (Lesku, Bark, et al., 2008; Tobler, 2011). SWA is highest following extended periods of wakefulness and decreases with time spent asleep. The initial level of SWA is higher still following short-term sleep loss. Conversely, daytime naps lower the initial level of SWA at night (Werth, Dijk, Achermann, & Borbély, 1996). The dependence of SWS-related SWA on prior sleep-wake history appears to be a conserved feature of mammalian SWS (Tobler, 2011). Furthermore, SWA can increase (Huber, Ghilardi, Massimini, & Tononi, 2004) and decrease (Huber et al., 2006) locally in the brain following local brain use and disuse, respectively, during prior wakefulness, a response called *local sleep homeostasis*. Moreover, the level of SWA correlates with arousal thresholds during SWS (Neckelmann & Ursin, 1993). Thus, SWS appears to be homeostatically regulated, with the level of SWA reflecting both SWS depth and the intensity of SWS-related functions (Tononi & Cirelli, 2014). REM sleep does not appear to have an intensity dimension. Instead, mammals increase the time spent in REM sleep following sleep loss, reflecting REM sleep homeostasis (Tobler, 2011).

B Monotremes

The presence of two kinds of sleep in mammals suggests that SWS and REM sleep serve different, or perhaps

complementary, functions (Vyazovskiy & Delogu, 2014). Unearthing the evolutionary history of these states might provide hints to their purpose, particularly if their evolutionary appearance corresponded to the appearance of other but functionally related behavioral and/or neurophysiological traits. To this end, studies on monotremes, represented only by the echidna and platypus, can be of value. Monotremes are mammals yet retain primitive traits, such as egg laying, and as such might retain primitive sleep traits that are more reflective of the common ancestor to all mammals.

There have been four electrophysiologically based studies of sleep in monotremes: three on the echidna (*Tachyglossus aculeatus*) and one on the platypus (*Ornithorhynchus anatinus*). Three of the studies, including the one on platypuses, reported cortical signs of SWS but not REM sleep (Allison, Van Twyver, & Goff, 1972; Siegel et al., 1999; Siegel, Manger, Nienhuis, Fahringer, & Pettigrew, 1996), suggesting that REM sleep evolved after the appearance of the marsupial + eutherian (or placental) mammal lineage. However, monotremes may have a rudimentary form of REM sleep present only at the level of the brain stem. In eutherian mammals, such as the cat and dog, brain stem neurons fire in an irregular burst-pause pattern of activity characterized by increased firing variability during REM sleep. The echidna brain stem exhibits this same pattern of activity during sleep; however, here, it is associated with cortical slow waves (Siegel et al., 1996). Although brain stem neurons were not studied in the platypus, sleeping platypuses showed phasic twitches of the appendages, along with eye movements under closed eyelids that were reminiscent of REM sleep (Siegel et al., 1999). REM sleep phenomena are controlled by the brain stem in eutherian mammals, such that the platypus appears to also exhibit a mixed sleep state characterized by cortical SWS-like slow waves concurrent with brain stem REM sleep-like activity. Moreover, the absence of EEG activation during REM sleep in monotremes appears to be due to an absence of hypothalamic cholinergic cells, which interrupts ascending projections from the brain stem to the forebrain (Manger, Fahringer, Pettigrew, & Siegel, 2002).

The form of REM sleep in monotremes may be less efficient than that of other mammals. When the amount of these ostensibly REM sleep-like phenomena were totaled in the platypus, it was found that these animals have more REM sleep than any other mammal studied (Siegel et al., 1999). A less efficient mechanism may require more time to complete the same function, or a rudimentary state may serve fewer functions, requiring less time to complete them. In either case, the integrated brain stem-forebrain REM sleep of marsupial and eutherian mammals might be an evolutionarily new (or derived) feature of REM sleep. If true, then it may support new sleep functions not found in monotremes or other animals lacking REM sleep-related EEG activation.

However, the third EEG-based study of sleeping echidnas is an exception to this evolutionary story. Nicol, Andersen, Phillips, and Berger (2000) reported alternating SWS and REM sleep (with EEG activation and reduced muscle tone). The expression of REM sleep was strongly temperature-dependent: ambient temperatures outside of their thermoneutral zone reduced or abolished the state. Interestingly, platypus housed in a naturalistic burrow system and exposed to natural ambient temperatures still failed to show REM sleep-related EEG activation (Siegel et al., 1999), such that the significance of the results from Nicol et al. (2000) is unclear.

C Marine Mammals

Mammals have made the evolutionary transition from a terrestrial existence to an aquatic habitat at least three times. Cetaceans (dolphins, porpoises, and whales) are most closely related to hippopotamuses; pinnipeds (seals and the walrus) and the sea otter (*Enhydra lutris*) are derived members of the Carnivora; sirenians (manatees and the dugong) are the sisters of elephants (Arnason et al., 2002). These animals sleep in the sea, but how? The question is not trivial, since these mammals must maintain their nares (or blowholes) above the surface of the water to respire atmospheric oxygen, yet also have to meet their biological requirements for sleep. The bottlenose dolphin (*Tursiops truncatus*), Amazonian river dolphin (*Inia geoffrensis*), harbor porpoise (*Phocoena phocoena*), beluga whale (*Delphinapterus leucas*), and presumably all other cetaceans obtain their daily amount of sleep by engaging in SWS with one-half of their brain at a time, or unihemispherically (Lyamin, Manger, Ridgway, Mukhametov, & Siegel, 2008; see Chapter 25, this volume). During unihemispheric SWS, one hemisphere shows slow waves, and the other shows wake-related EEG activation. Bihemispheric SWS has never been observed for more than a few seconds in cetaceans, such that unihemispheric SWS is the main form of sleep in these animals. In order for each hemisphere to obtain some sleep, both hemispheres are capable of being the one engaged in SWS. This asymmetry in brain state is mirrored by an asymmetry in eye state. The eye contralateral to the sleeping hemisphere is closed, while the other eye, which sends projections to the awake hemisphere, remains open. Unihemispheric SWS allows cetaceans to swim continuously and monitor the local environment with the open eye (Gnone, Moriconi, & Gambini, 2006). For instance, captive Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) and mother-calf pairs of bottlenose dolphin orient the open eye toward the other members of the pod, presumably to maintain group cohesion (Goley, 1999; Sekiguchi, Arai, & Kohshima, 2006).

Cetaceans might be the only mammals to have secondarily lost REM sleep (Lyamin et al., 2008). A REM sleep-like state has been reported just once, as a single bout, from a captive pilot whale (*Globicephala macrorhynchus*) and published as an abstract. Whether this episode truly reflected REM sleep or simply an awakening from sleep remains unknown, as all other EEG-based studies of cetacean sleep have not reported REM sleep. The continuous swimming of cetaceans might be incompatible with REM sleep, since REM sleep-related muscle atony would interfere with powered movement (but see Rattenborg et al., 2016). It is also possible that unihemispheric sleep removes the need for REM sleep. It has been proposed that a function of REM sleep is to warm the central nervous system, including the brain stem (Wehr, 1992). Animals that sleep only unihemispherically might maintain an optimal brain stem temperature from sustained (unihemispheric) wakefulness (Lyamin et al., 2018), although this idea has yet to be tested with measurements of brain stem temperature. A further possibility is that REM sleep exists only in a rudimentary form in cetaceans that has yet escaped detection. As discussed, sleeping monotremes show cortical slow waves occurring together with brain stem REM sleep-like activity (Siegel et al., 1996). For these reasons, there would be value in recording brain stem unit activity and temperature to shed light onto the presence (or extent) of REM sleep in cetaceans.

Although bihemispheric sleep is rare in cetaceans, behavioral observations from cetaceans without EEG electrodes raises the possibility that it does (or can) occur. Captive bottlenose dolphins, beluga, killer (*Orcinus orca*), and (juvenile) gray whales (*Eschrichtius robustus*) have been observed resting, either floating motionless at the water's surface or lying on the bottom of their pool. Similar reports exist for wild cetaceans, including horizontal logging in humpback whales (*Megaptera novaeangliae*) (Friedlaender, Tyson, Stimpert, Read, & Nowacek, 2013) and vertical logging in sperm whales (*Physeter macrocephalus*) (Miller, Aoki, Rendell, & Amano, 2008). Whether these animals are engaged in unihemispheric SWS, bihemispheric SWS, REM sleep or even wakefulness is unknown.

Seals can be divided into two mains group: otariid (or eared) seals and phocid (or earless) seals. These two types of seal sleep in different ways (Lyamin et al., 2008). Phocid seals retain the bihemispheric SWS (and REM sleep) of their terrestrial ancestors while sleeping on land or at sea. A study on wild Pacific northern elephant seals (*Mirounga angustirostris*) suggests that phocids can even sleep while diving (Mitani et al., 2010). This discovery was made by fitting elephant seals with a data logger that measured speed, depth, and three-dimensional acceleration. The animals were found to slowly drift downward following circular trajectories that resembled a falling leaf. During the descent, the seals wobbled slightly in the absence of flipper strokes. Interestingly, the animals could impact the sea bottom and remain immobile for many minutes, raising the possibility that they were asleep on the descent, unaware of the approaching sea floor.

In contrast to the obligatory bihemispheric sleep of phocid seals, otariid seals can engage in SWS both unihemispherically (like cetaceans) and bihemispherically (like phocid seals). The northern fur seal (*Callorhinus ursinus*) engages in bihemispheric and unihemispheric sleep on land and switches to sleeping mostly unihemispherically in the water (Lyamin et al., 2018). The use of unihemispheric SWS in seawater is apparently an adaptation to maintain their nares above the surface of the water to breathe (Lyamin et al., 2008). Specifically, the flipper sending projections to the awake hemisphere remains in the water, paddling, while the flipper contralateral to the asleep hemisphere is immobile. The amount of REM sleep drops substantially while sleeping in seawater (Lyamin et al., 2018). On land, seals engaged in 80 minutes of REM sleep per day but only 3 minutes per day in water. Some animals forgo REM sleep for days at a time. Not only was there a profound reduction in the amount of REM sleep over the 2 weeks in the water, but also the animals did not recover lost REM sleep when allowed to sleep on land. Lyamin et al. (2018) suggested that seals and other marine mammals may have no need for REM sleep when they are sleeping unihemispherically. If REM sleep functions to elevate brain stem temperature and unihemispheric wakefulness keeps the brain stem warm, then unihemispheric sleep while in the water would remove any need for REM sleep (see also Wehr, 1992). Sleep has also been studied in the walrus (*Odobenus rosmarus*). As a close relative of otariid seals, perhaps, it is not surprising that walruses engage in bihemispheric and unihemispheric SWS and a large reduction in the amount of REM sleep while sleeping in seawater (Lyamin et al., 2008).

The third group of marine mammals for which electrophysiologically defined sleep data exist is the sirenians, a group that includes manatees. Like otariid seals and the walrus, manatees (*Trichechus* spp.) have evolved the ability to engage in bihemispheric and unihemispheric SWS and small amounts of REM sleep (Lyamin et al., 2008).

Taken together, the convergent evolution of unihemispheric SWS in three groups of marine mammals—cetaceans, otariid seals and the closely related walrus, and manatees—suggests that it evolved to allow these aquatic animals to both sleep and respire at sea. Importantly, this also demonstrates that SWS must serve an inescapable function. Instead of evolving sleeplessness, these animals evolved an elegant mechanism to achieve their daily amount of SWS. Moreover, that these animals are able to continue paddling or swimming while asleep indicates that the biological target of sleep must lie within

the brain. Such research further suggests that sleep is fundamentally a local process, below the level of the whole brain (Oleksenko, Mukhametov, Polyakova, Supin, & Kovalzon, 1992), a view consistent with local sleep homeostasis (Huber et al., 2004, 2006; Lesku, Vyssotski, Martinez-Gonzalez, Wilzeck, & Rattenborg, 2011) and hypotheses for the function of SWS (Tononi & Cirelli, 2014). In contrast, the loss of REM sleep in cetaceans and fur seals sleeping in seawater for weeks suggests that the function of REM sleep either is less essential than that of SWS, is no longer needed, or can be fulfilled by some other mechanism.

D Variation in Mammalian Sleep Duration

The large quantity of mammalian sleep data has demonstrated the existence of substantial across-species variation in sleep duration. Toward the extremes in a comparative dataset of nearly 100 species, large hairy armadillo (*Chaetophractus villosus*) can sleep upward of 20 hours per 24 hour day, yet horses (*Equus caballus*) sleep fewer than 3 hours (Lesku, Roth, et al., 2008). Large variation also exists for each of the two basic types of sleep. This offers a unique opportunity for quantitative analyses to explain the reasons for the substantial interspecific variation in the amount and composition of sleep. The reasons might shed light on the purpose of these states, particularly if the amount of sleep reflects underlying variation in the need for sleep. If true, then factors that explain the variation would provide clues to their function. This line of investigation has been thoroughly explored over 50 years (reviewed in Lesku, Roth, Rattenborg, Amlaner, & Lima, 2009).

A downside to the earliest analyses was the assumption that each species is evolutionarily and statistically independent (Lesku et al., 2009). This assumption falters, however, as species share varying degrees of relatedness. A mouse is more closely related to a hamster than either is to an elephant. The problem is compounded by the unequal representation of the various groups of mammals in comparative sleep research. More than half of the species studied come from only two taxonomic orders, the rodents and primates. Failure to utilize modern phylogenetic comparative methods can lead to spurious conclusions about the evolutionary determinants of sleep in mammals (Lesku, Roth, et al., 2008). Consequently, shared evolutionary history must be taken into consideration when analyzing comparative data.

More recent analyses have controlled for evolutionary relatedness (Capellini, Barton, McNamara, Preston, & Nunn, 2008; Lesku, Roth, Amlaner, & Lima, 2006; Lesku, Roth, et al., 2008; Preston, Capellini, McNamara, Barton, & Nunn, 2009). Several relationships have been found to be robust to different analytic techniques. Larger

species tend to sleep less and engage in less SWS and REM sleep (Lesku et al., 2009), with the most recent data point further supporting this pattern. Using accelerometers implanted subcutaneously in the trunk, Gravett et al. (2017) found that African elephants (*Loxodonta africana*) appear to sleep only 2 hours per day. However, there are some exceptions to such large-scale correlations (Kruger et al., 2016). Beyond body size, animals with larger (absolute) brains and higher basal metabolic rates likewise engage in less sleep. Statistically controlling for the effects of size on sleep might actually reveal more biologically meaningful relationships. Brain size relative to body size is a purported measure of interspecific intelligence; it is conceptually similar to the encephalization quotient (Jerison, 2001). Primates and dolphins both have relatively large brains and are thought to possess advanced cognitive abilities (but see Manger, 2013). Since sleep is important for learning and the consolidation of memories, one might expect that evolutionary increases in encephalization predict increases in the amount of sleep or in the relative contribution of the two sleep states to total sleep time. Accordingly, species with relatively large brains allocate more time asleep to REM sleep (Lesku et al., 2006; Lesku, Roth, et al., 2008). Humans appear to be notable among primates for our higher proportion of REM sleep (Samson & Nunn, 2015). Other comparative lines of evidence point toward a neurological function for REM sleep. Species relatively immature at birth engage in more REM sleep, even as adults (Jouvet-Mounier et al., 1970). This holds true across mammals, as species with a relatively short gestation period (i.e., more altricial at birth) likewise have more REM sleep as adults (Capellini et al., 2008; Lesku et al., 2006). Such a relationship lends comparative support to the ontogenetic hypothesis for REM sleep (see Chapter 27, this volume).

This approach has also found support for the idea that sleep maintains the immune system to better protect against infection (Imeri & Opp, 2009). Preston et al. (2009) found that species with more white blood cells (an index of investment into the immune system) engage in more sleep. Importantly, this relationship applied only to cell types involved in an immune response, including neutrophils, lymphocytes, eosinophils, and basophils. Conversely, red blood cells and platelets, which are not involved in an immune response, did not vary with sleep duration. Moreover, species that slept longer were also found to be parasitized less. Whether this was due to increased immune effectiveness or through lowering species' encounter rates with parasites is unclear. Nevertheless, these results are consistent with the idea that sleep reallocates energy to the immune system (Schmidt, 2014).

Ecological factors have also played a role in shaping sleep architecture. Species that sleep in more exposed environments engage in less sleep than those sleeping

in more secure locations, such as burrows (Lesku et al., 2006). Similarly, species with a more herbivorous diet (and subject to greater predation risk) engage in less sleep than those with a carnivorous diet. In both cases, reduced sleep arises largely from a reduction in the amount of REM sleep (Lesku et al., 2009). It should be noted, however, that these findings were often based on wild animals brought into the laboratory environment. Thus, instead of reflecting evolutionary changes in sleep in response to ecological forces, it could arise from plastic responses to a novel, potentially dangerous environment (see Section VIII). In either case, the risk of being eaten has played a role in shaping sleep in prey (Lesku, Bark, et al., 2008; Lesku, Roth, et al., 2008).

III BIRDS (AVIAN REPTILES)

Birds are a derived type of reptile that evolved from theropod dinosaurs. Birds and mammals last shared a common ancestor 300 million years ago. Despite the early divergence between avian and mammalian lineages, the sleeping brain activity of birds is remarkably similar to that of mammals (Lesku & Rattenborg, 2014). Like mammals, birds have two kinds of sleep, SWS and REM sleep. Avian SWS is similarly characterized by large, slow waves with elevated SWA; REM sleep is associated with (wake-like) small, fast waves. Like mammals, REM sleep in birds is accompanied by eye closure (even in birds that engage in SWS with one or both eyes open), rapid eye movements, reduced muscle tone, intermittent twitching, and a diminished capacity for thermoregulatory responses (e.g., panting). In many birds, the amount of REM sleep increases across the night, in a manner similar to humans (Martinez-Gonzalez, Lesku, & Rattenborg, 2008). In birds and mammals alike, the amount of REM sleep is highest in young and decreases across early, posthatch life until reaching an asymptote at an adult, species-specific level (Scriba et al., 2013), suggesting that REM sleep plays a similar role in brain maturation in both groups of animals. Sleep also plays a role in song learning in juvenile songbirds (for details, see Chapter 26, this volume).

SWS and REM sleep homeostasis manifests similarly in birds and mammals (Rattenborg, Martinez-Gonzalez, & Lesku, 2009). Following short-term periods of sleep loss, a compensatory increase in SWS-related SWA during recovery sleep has been observed in pigeons (*Columba livia*) (Lesku, Vyssotski, et al., 2011; Martinez-Gonzalez et al., 2008), white-crowned sparrows (*Zonotrichia leucophrys*) (Jones, Vyazovskiy, Cirelli, Tononi, & Benca, 2008), and great frigate birds (*Fregata minor*) (Rattenborg et al., 2016). SWA is also higher in short-sleeping pectoral sandpipers (*Calidris melanotos*) during the breeding season (Lesku et al., 2012). Like mammalian SWS, avian SWS is

regulated locally in the brain in response to brain use and disuse during prior wakefulness (Lesku, Vyssotski, et al., 2011). Thus, hypotheses for the function of SWS that rely on local sleep homeostasis apply to both mammals and birds. As is the case in mammals, the amount of REM sleep increases in birds following sleep deprivation, reflecting REM sleep homeostasis (Lesku, Vyssotski, et al., 2011; Martinez-Gonzalez et al., 2008; Newman, Paletz, Obermeyer, & Benca, 2009; Tobler & Borbély, 1988).

Birds have often been observed sitting with one eye open. Like marine mammals, this corresponds with the ability to sleep with one-half of the brain at a time (Rattenborg, Amlaner, & Lima, 2000). However, in most birds, the interhemispheric asymmetry in the level of SWA is less pronounced than in marine mammals (but see Rattenborg et al., 2016). There is some evidence that the open eye may be used to detect threats while sleeping. Mallard ducks (*Anas platyrhynchos*) switch from sleeping with both eyes closed to sleeping with one eye open in response to a perceived increase in the risk of predation and direct the open eye toward the potential threat (Rattenborg, Lima, & Amlaner, 1999). Similarly, frigate birds sleeping on the wing open the eye facing the direction of the turn, perhaps to prevent collisions with other birds (Rattenborg et al., 2016; see Section VIII.D). In contrast to the restriction of unihemispheric SWS to marine mammals, SWA-related interhemispheric asymmetries are common in birds and may be an ancestral trait (Kelly, Peters, Tisdale, & Lesku, 2015; Rattenborg et al., 2000).

Despite the similarities between avian and mammalian sleep, there are also interesting differences (Rattenborg & Martinez-Gonzalez, 2015). Birds do not show hippocampal sharp waves and ripples or sleep spindles; unlike mammalian REM sleep, avian REM sleep is not associated with a hippocampal theta rhythm, suggesting that the function these brain rhythms serve in mammals might be absent in birds. The duration of REM sleep episodes in birds is also short; REM sleep bouts can be tens of minutes long in mammals but are rarely longer than 16 seconds in birds (Lesku & Rattenborg, 2014). The short duration of REM sleep bouts does not arise from a need to maintain balance, since REM sleep episodes are equally short when birds are sitting with their heads supported on their backs (Dewasmes, Cohen-Adad, Koubi, & Le Maho, 1985). Lastly, birds seem to be cognitively more resilient in the face of chronic sleep restriction than are mammals (Newman et al., 2009; Rattenborg et al., 2004, see also Section VIII.D).

A Palaeognathae

Since SWS and REM sleep have been recorded in every avian species studied by sleep scientists (Roth, Lesku, Amlaner, & Lima, 2006), both states were likely present

in the most recent common dinosaur ancestor to extant birds. However, there is some evidence that REM sleep manifests differently in some palaeognath birds. Palaeognaths are primarily large and flightless birds, a group that includes the ostrich, emu, cassowary, rhea, and also the much smaller kiwi and volant tinamous. Palaeognaths diverged from neognaths (i.e., all other birds) in the mid-Cretaceous around 110 million years ago (Yonezawa et al., 2017). Sleep electrophysiology has been thoroughly studied in two species, the ostrich (*Struthio camelus*) and elegant crested tinamou (*Eudromia elegans*). Ostriches showed unequivocal SWS occurring with EEG slow waves, an absence of eye movements and stable muscle tone (Lesku, Meyer, et al., 2011). The birds had an unusual sleep posture, keeping the neck vertically extended and the eyes open, as if awake and alert. During REM sleep, the eyelids would close; the eyes would move; skeletal muscle tone would lessen; and behaviorally, the neck would give way to gravity, slowly falling forward. Meanwhile, however, the EEG showed either (i) small, fast waves characteristic of REM sleep in neognath birds and marsupial and eutherian mammals or (ii) SWS-like slow waves, reminiscent of monotremes. Indeed, this at-times heterogeneous REM sleep state with slow waves in the forebrain and signs of REM sleep in the brain stem was very similar to that of the platypus (Siegel et al., 1999). It was thought that REM sleep-related forebrain activation might have only been partially developed in palaeognath birds and, therefore, constitutes an ancestral condition to mammals and birds (Lesku, Meyer, et al., 2011). This also suggested that the evolution of REM sleep-related EEG activation followed similar evolutionary steps in early birds and again in mammals.

Such evolutionary stories, based on data from only a few species, should be viewed with caution, however. In contrast to the ostrich, a study on the elegant crested tinamou found no evidence of a mixed REM sleep state (Tisdale, Vyssotski, Lesku, & Rattenborg, 2017). Instead, tinamous showed two distinct sleep states—SWS and REM sleep. Thus, a mixed REM sleep state is not a common feature of sleep shared across all palaeognath birds. Further, recent genetic analysis suggests that the common ancestor to the Palaeognathae and Neognathae was more tinamou-like than ostrichlike; that is, it was small and capable of flight (Mitchell et al., 2014). The retention of these ancestral traits raises the possibility that flighted tinamous are more representative of the common ancestor to modern birds than are flightless ostriches. The absence of a monotreme/ostrichlike REM sleep state in tinamous could be explained by one of two evolutionary scenarios. One explanation is that there has been convergent evolution of REM sleep in tinamous and neognath birds, such that both now show REM sleep EEG activation. Alternatively, this state could represent an ancestral state already present in the common ancestor of all living birds. Why do ostriches then have an atypical REM sleep state? It is possible that this state arises from their unusual sleep posture, which is presumably used to detect approaching threats during SWS. Perhaps, they need to maintain some muscle tone during REM sleep to avoid free fall of the head atop a long neck, causing some features of SWS to infiltrate REM sleep. If true, then this state is an idiosyncrasy of ostrich sleep.

IV NONAVIAN REPTILES

A persistent question regarding the striking similarities between mammalian and avian sleep is as follows: Did these states evolve independently in birds and mammals, reflecting convergent evolution, or were they inherited from a common ancestor? The study of nonavian reptiles might shed light on this question. Mammals, birds, and nonavian reptiles make up the extant members of the amniote clade. However, mammals are members of the Synapsida, whereas birds and nonavian reptiles are both members of the Sauropsida. Synapsids and sauropsids last shared a common ancestor more than 300 million years ago. Studying the sleep patterns of nonavian reptiles should inform us on how the common ancestor to birds and nonavian reptiles slept, which could in turn shed light on the origins of SWS and REM sleep. For instance, the presence of SWS and/or REM sleep in nonavian reptiles would suggest that these states were present in the most recent common ancestor to all amniotes. Conversely, the absence of these states or the presence of a rudimentary form of one or both of these states would suggest that birds and mammals independently evolved similar sleep states.

Unfortunately, few nonavian reptiles and even fewer amphibians (the evolutionary outgroup to amniotes) have been studied (Libourel & Herrel, 2016). In addition, the available studies have yielded variable and often contradictory results, sometimes even in the same species. Looking within just the crocodilians—the closest living relatives to birds—provides an indication of the variation observed in the nonavian reptile sleep literature. An early study of caiman (*Caiman sclerops*) reported sleep-related EEG patterns containing periodic sharp waves overlying a low-voltage background (Flanigan, Wilcox, & Rechtschaffen, 1973). Other studies—on the same species—observed cortical slow waves reminiscent of mammalian and avian SWS (Meglasson & Huggins, 1979; Warner & Huggins, 1978). Furthermore, another study reported eye movements and phasic twitches during sleep (Peyrethon & Dusan-Peyrethon, 1969), while others did not (Flanigan et al., 1973). Finally, a study of the American alligator (*Alligator mississippiensis*) found no signs of behavioral sleep (Van Twyver, 1973). Similarly contradictory results can be found across other

nonavian reptile groups as well (Libourel & Herrel, 2016). It is unclear whether these results represent true intra-specific and interspecific variation in the EEG correlates of sleep or whether they reflect only technical differences between studies. Nevertheless, these inconsistencies make it difficult to interpret the electrophysiological correlates of sleep in these groups and therefore the evolution of SWS and REM sleep in amniotes.

Such inconsistencies aside, many EEG studies of sleeping nonavian reptiles have reported the presence of intermittent and irregular mono- and polyphasic high-amplitude deflections in the EEG, termed high-voltage sharp waves (HShW) (Flanigan et al., 1973; Libourel & Herrel, 2016; Shein-Idelson, Ondracek, Liaw, Reiter, & Laurent, 2016). While these signals appear to be associated with periods of sleep, how (if at all) HShW relate to sleep-related electrophysiological features in mammals and birds is a topic of debate. Based on phenomenological similarities, it has been suggested that reptilian HShW are homologous to mammalian hippocampal sharp waves (Hartse, 1994; Shein-Idelson et al., 2016). However, sharp waves are confined to the hippocampus in mammals, whereas reptilian HShW have been observed in several forebrain regions, including the dorsal ventricular ridge (Lorenzo, Macadar, & Velluti, 1999; Shein-Idelson et al., 2016). Interestingly, the dorsal ventricular ridge in birds also exhibits slow waves (Beckers, van der Meij, Lesku, & Rattenborg, 2014). In addition, sharp waves have not been observed in the avian hippocampus (Ookawa & Gotoh, 1965; Sugihara & Gotoh, 1973; Van Twyver & Allison, 1972); instead, slow waves have been reported throughout the avian pallium (Fuchs, Haney, Jechura, Moore, & Bingman, 2006; Martinez-Gonzalez et al., 2008; Szymczak, 1987). Collectively, this raises the possibility that reptilian HShW are evolutionarily homologous to mammalian and avian slow waves during SWS, rather than mammalian hippocampal sharp waves.

Unilateral eye closure—the behavioral correlate of unihemispheric SWS in marine mammals and some birds—has been observed in turtles and tortoises and lizards and crocodilians (Kelly et al., 2015; Mathews, Lesku, Lima, & Amlaner, 2006). As with cetaceans and birds, nonavian reptiles use their open eye adaptively. When presented with a potential threat, the animals engage in more unilateral eye closure and orient the open eye toward the perceived danger. The increase in unilateral eye closures comes at the expense of bilateral eye closure, raising the possibility that this is a form of sleep. However, it is unclear whether these animals are sleeping unihemispherically or engaged in another behavior (Kelly et al., 2015).

Do nonavian reptiles engage in REM sleep? Behavioral signs of REM sleep, including eye movements under closed eyelids and phasic twitches, have been observed in various reptiles (Libourel & Herrel, 2016). However, whether these REM sleep-like phenomena occur in a state characterized by REM sleep-like EEG activity is unclear. The green iguana (*Iguana iguana*) engages in REM sleep-like behaviors, in conjunction with an (electrophysiological) sleep state that might reflect REM sleep (Ayala-Guerrero & Mexicano, 2008). However, other studies have found that these ostensibly REM sleep-like behaviors occur across all sleep (Stropes, 1971, 1975) or without any change in the EEG (Tauber, Roffwarg, & Weitzman, 1966). Indeed, most studies on nonavian reptiles have reported an absence of REM sleep-related EEG activity (Hartse, 1994). Interestingly, a recent study has described REM sleep-like EEG activity in cortical regions and the dorsal ventricular ridge, occurring in conjunction with rapid eye movements in bearded dragons (*Pogona vitticeps*) (Shein-Idelson et al., 2016). Another recent study also described a second sleep state, reminiscent of REM sleep, in the Argentine tegu (*Salvator merianae*) (Libourel et al., 2017). In contrast to the second sleep state described in bearded dragons, behavioral indicators of REM sleep in tegus occurred in conjunction with a beta frequency (12–18 Hz) oscillation. These data would seem to indicate that at least some squamate lizards engage in a second sleep state that is potentially homologous to mammalian and avian REM sleep. This also suggests, however, that the electrophysiological correlates of REM sleep may not be fixed across lizards or nonavian reptiles in general.

There is a need to determine whether putative REM sleep states in nonavian reptiles feature other key characteristics of REM sleep. For example, it is currently unknown whether these putative REM sleep states are associated with higher arousal thresholds, are more prevalent in the young, rebound following deprivation, and can be modulated with pharmaceuticals that influence the amount of REM sleep in mammals. Furthermore, in mammals, rapid eye movements and twitches are generated by the brain stem. During REM sleep in eutherian mammals, brain stem units increase discharge variability (Siegel et al., 1996). Eye movements and twitches similar to those seen during mammalian REM sleep have been observed in chelonian reptiles, but these occur in the absence of increased neuronal firing variability (Eiland, Lyamin, & Siegel, 2001), suggesting that these phenomena reflect something other than REM sleep in nonavian reptiles, for example, saccadic eye oscillations (Eiland et al., 2001; Ott, 2001; Pettigrew, Wallman, & Wildsoet, 1990). To unequivocally confirm the presence of REM sleep, further behavioral and electrophysiological correlates of REM sleep-like states must be linked to behaviorally defined sleep.

V AMPHIBIANS

Amphibians exhibit periods of behavioral quiescence associated with increased arousal thresholds that are indicative of sleep. Unlike the EEG that shows HShW

accompanying sleep behavior in nonavian reptiles, the majority of electrophysiological sleep studies of amphibians have not observed HShW (Libourel & Herrel, 2016). Instead, most studies have reported lower voltage and slower EEG with the onset of behavioral restfulness, as compared with wakefulness (Fang, Chen, Cui, & Tang, 2012; Hobson, Goin, & Goin, 1968; Huntley, Donnelly, & Cohen, 1978; Lazarev, 1978, see also Shine et al., 2015). Neither behavioral nor electrophysiological evidence of REM sleep in amphibians has been obtained, suggesting that these states evolved only after the appearance of amniotes.

VI BONY AND CARTILAGINOUS FISHES

Fish are the most species-rich group of vertebrates, and yet, their sleep is perhaps the least understood of all vertebrate taxa. What little is known comes from behavioral studies on the presence or absence of sleep; however, the data are often anecdotal or an incomplete characterization of sleep. For instance, bluehead wrasse (*Thalassoma bifasciatum*) and Spanish hogfish (*Bodianus rufus*), along with other wrasse of the family Labridae, could be lifted to the water surface by researchers at night, perhaps owing to elevated arousal thresholds associated with sleep (Tauber, 1974; Tauber & Weitzman, 1969). The existence of sleep was more convincingly demonstrated with the convict cichlid (*Cichlasoma nigrofasciatum*) and goldfish (*Carassius auratus*). Deprivation of nighttime inactivity was followed by increased restfulness, suggestive of a homeostatic sleep rebound after extended wakefulness (Tobler & Borbély, 1985). Zebrafish (*Danio rerio*) have recently emerged as a new animal model for studying sleep (see Chapter 24, this volume). Zebrafish are diurnal and, like goldfish, show a sleep rebound following sleep loss (Yokogawa et al., 2007). Moreover, hypnotic agents that induce sleep in humans (e.g., melatonin, diazepam, and sodium pentobarbital) likewise promote sleep in zebrafish (Zhdanova, 2011). Thus, the neurochemical pathways regulating sleep appears to be conserved across distantly related vertebrates.

Very few studies have focused on the electrophysiological correlates of sleep behavior in bony fish. A study on the tench (*Tinca tinca*) found no evidence for a distinctive EEG pattern following sleep onset (Peyrethon & Dusan-Peyrethon, 1967). Conversely, EEG spikes and slow waves have been observed from the mid- and forebrain in catfish (*Ameiurus nebulosus*), accompanied by cardiac arrhythmia (Karmanova & Belich, 1983; Karmanova, Belich, & Lazarev, 1981). Although fishes cannot close their eyes, Bermuda reef fish have eye movements during periods of sustained quiescence, raising the possibility of a REM sleep state (Tauber & Weitzman, 1969). However, this observation has not consistently been reported (Peyrethon & Dusan-Peyrethon, 1967; Shapiro & Hepburn, 1976). More study is needed to characterize the EEG correlates of sleep behavior and possible sleep states in fishes.

Other fishes appear to have greatly reduced their sleep. Some reef fish spend the night fanning their symbiotic coral by increasing fin stroke frequency while maintaining a sleeplike posture (Goldshmid, Holzman, Weihs, & Genin, 2004). Whether they are awake or asleep during this time is unclear. Early research on sightless cavefish suggested these animals might be sleepless, owing to continuous swimming and the absence of circadian rhythmicity (Pavan, 1946; Poulson & Jegla, 1969). More recent studies have shown that cavefish do, in fact, sleep but only very little (Duboué, Keene, & Borowsky, 2011; Yoshizawa et al., 2015). There have been multiple transitions from a surface-living to cave-dwelling existence in cavefish and among these populations the transition to cave life was associated with great reductions in sleep. Such convergence might have arisen from reduced food availability in the caves and the consequent need to spend more time foraging (Jaggard et al., 2018). Alternatively, if cave living is less neurologically demanding than surface living, then reduced sleep among cave populations might reflect reduced sleep need arising from less intense forms of wakefulness. The latter possibility could be somewhat akin to the local decreases in sleep intensity that have been observed in the human cortex following reduced brain use during prior wakefulness (Huber et al., 2006).

A Sharks and Rays

Cartilaginous fishes (e.g., sharks and rays) are the simplest of modern jawed vertebrates, in that the most recent common ancestor to all jawed vertebrates was almost certainly more sharklike than fishlike. Fossilized sharks from sediments 450 million years old reveal that their gross morphology has changed little (Kavanau, 2004). Mechanisms for ventilation separate cartilaginous fishes into two groups. Buccal pumping sharks lower the floor of their buccal cavity to draw oxygenated water into the mouth and then raise the floor to push the oxygen-rich water over their gills. This mechanism is also used by many bony fishes and allows the animal to remain immobile for extended periods of time (Carlson & Parsons, 2001), some of which is thought to reflect time asleep (Compagno, 1988). In contrast, ram ventilators must maintain forward motion to push oxygenated water over their gills (Heyman, Graham, Kjerfve, & Johannes, 2001). Such obligate swimming species do not show conspicuous periods of inactivity, which has led some to assume that these animals do not sleep (Kavanau, 1998). As with the sensory-impoverished environment of cavefish, it has been suggested that the barren landscape of the open

ocean does not tax the brain sufficiently to generate a need for the beneficial effects of sleep (Kavanau, 1998). Many sharks, however, including pelagic species, have excellent visual acuity (Sabbah, Laria, Gray, & Hawryshyn, 2010) and exhibit complex navigation and predatory (Lisney, Theiss, Collin, & Hart, 2012) and communicative (Hart, Lisney, & Collin, 2006) behaviors, along with an ability to learn (Fuss, Bleckmann, & Schluessel, 2014), making this idea unlikely.

Many species of buccal pumping shark have been observed to have a sleeplike state in the wild or aquaria. Some have been reported to be predominantly nocturnal, including the Port Jackson shark (*Heterodontus portusjacksoni*) (McLaughlin & O'Gower, 1971), the leopard shark (*Triakis semifasciata*) (Baronio, 2012), the zebra shark (*Stegostoma fasciatum*) (Dudgeon, Lanyon, & Semmens, 2013), and the dogfish (*Scyliorhinus canicula*) (Sims, Nash, & Morritt, 2001). The whitetip reef shark (*Triaenodon obesus*) has been observed resting on the seafloor during the day and foraging during the night (Barnett, Payne, Semmens, & Fitzpatrick, 2016; Fitzpatrick, Abrantes, Seymour, & Barnett, 2011), with a lower metabolic rate during the day (Whitney, Papastamatiou, Holland, & Lowe, 2007). An early study by Weber (1961) described sleep behavior of the large-spotted dogfish (*S. stellaris*) and nurse shark (*Ginglymostoma cirratum*) in an aquarium. Both species were observed to spend much of the 24 hour-day immobile near the bottom of the tank in a "rest" posture. In the dogfish, its eyelids were partially closed during this time. The nurse shark appeared to have elevated arousal thresholds when engaged in the rest posture; the animals would not respond outwardly to scuba divers until physical contact was made, eliciting an escape response. Two other benthic sharks, the horn shark (*Heterodontus francisci*) and swell shark (*Cephaloscyllium ventriosum*), are nocturnal, with night swimming and feeding beginning with the onset of darkness. The swell shark maintained this rhythm even in the absence of photoperiodic cues, whereas the horn shark did not (Nelson & Johnson, 1970).

Ram-ventilating species show more modest (if any) activity patterns. Gray nurse sharks (*Carcharias taurus*) spend up to 85% of the day "milling" (Baronio, 2012; Smith, Scarr, & Scarpaci, 2010), a low level of swimming activity at slow speeds with frequent directional changes to maintain the animal in the same area. This might reflect a form of sleep swimming, but the shark can rapidly escape when provoked. A telemetry study of a single, juvenile great white shark (*Carcharodon carcharias*) monitored muscle temperature, location, and depth, but found no circadian changes of any variable (Carey et al., 1982). The scalloped hammerhead (*Sphyrna lewini*) has a state of relative inactivity during the day, at which time the animals do not feed and swim around a seamount (Klimley, Butler, Nelson, & Stull, 1988). The hammerhead will even ignore the presence of prey fish during this time, but it is unclear whether the hammerhead (or prey fish) is asleep during this time. Although extended periods of quiescence have not been observed in ram-ventilating sharks, many species show vertical movement through the water column, with the animals spending more time closer to the surface by day and in deeper waters at night (Andrews et al., 2009). Nevertheless, the absence of a clear sleeplike behavior does not preclude the possibility that the animals sleep while swimming (Lyamin et al., 2008). Going forward, a systematic investigation of the existence of sleep is needed for both buccal pumping and ram-ventilating sharks, preferably using a combination of behavioral assays and electrophysiological recordings.

VII INVERTEBRATES

Most animals are invertebrates. Of the 36 (or so) animal phyla, 35 are wholly invertebrates, yet our understanding of sleep is probably poorest in these ubiquitous animals. Sleep has been convincingly demonstrated in just five invertebrate phyla, including several species of arthropod (Klein, Klein, Wray, Mueller, & Seeley, 2010; Tobler, 2011) and mollusk (Stephenson & Lewis, 2011; Vorster, Krishnan, Cirelli, & Lyons, 2014) and one species of nematode roundworm (Nichols, Eichler, Latham, & Zimmer, 2017), platyhelminth (flatworm) (Omond et al., 2017), and jellyfish (Nath et al., 2017). The presence of sleep across distantly related invertebrates of varying complexities suggests that sleep appeared very early in the evolution of animals. Accordingly, even brainless jellyfish sleep, indicating that a brain is not a prerequisite for sleep to evolve. Nonetheless, there is a dearth of sleep data for the other animal phyla, and coverage within a group is nearly as minimal. Thus, there is an urgent need for more research into the phylogenetic breadth of sleep among invertebrates to shed light on the origin(s) of sleep and sleep functions (Lesku & Ly, 2017).

Brain activity has been recorded from several sleeping invertebrates. During the night, a time when honey bee (*Apis mellifera*) foragers are often asleep, optomotor interneurons in the optic lobes show lowered sensitivity than during the day (Kaiser & Steiner-Kaiser, 1983). Interestingly, sleep deprivation impaired the ability of foragers to perform the waggle dance, thus interfering with an individual's ability to communicate the direction and distance of food resources to others in the colony (Klein et al., 2010). Thus, neurobehavioral performance is reduced following sleep deprivation in humans (Van Dongen, Maislin, Mullington, & Dinges, 2003) and bees alike. Similar to bees, crayfish (*Procambarus clarkii*) have sleep-dependent brain activity, although the specific patterns involved are less clear (Mendoza-Angeles,

Hernández-Falcón, & Ramón, 2010). Activity in the fruit fly (*Drosophila melanogaster*) medial brain (between the mushroom bodies) is reduced relative to that occurring in awake flies (Nitz, van Swinderen, Tononi, & Greenspan, 2002). Furthermore, flies might have two types of sleep. Yap et al. (2017) identified a second sleep stage characterized by a 7–10 Hz oscillation in the central brain during spontaneous sleep or sleep induced by activating sleep-promoting neurons in the dorsal fan-shaped body (see Chapter 22). Cuttlefish might also have two sleep states. Restful cuttlefish have REM sleep-like phasic twitches of the arms, accompanied by eye movements and chromatophore activity, resulting in changes in body coloration (Frank, Waldrop, Dumoulin, Aton, & Boal, 2012). Additional study is needed to fully appreciate the similarities (and possible homologies) between sleep states in flies, cuttlefish, and perhaps other invertebrates with that of mammals and birds.

VIII WILD SLEEP

Sleep has been studied most extensively in the laboratory. The laboratory environment offers many advantages, particularly for investigating the underlying mechanisms of sleep (Aulsebrook, Jones, Rattenborg, Roth, & Lesku, 2016; Daan, 2011). Laboratory environments can be controlled and manipulated, allowing researchers to isolate the effects of individual variables. Laboratory studies can utilize selectively bred strains of animals that are genetically similar to each other; this allows environmental and genetic influences to be disentangled. Laboratory model animals, notably rodents and increasingly fruit flies, are also easy to breed in captivity and readily available. These factors facilitate the use of large sample sizes, replication of research, and comparison of results between laboratory studies—all of which are good scientific practice. Sleep research has also historically been restricted to the laboratory, due to technological limitations. Until relatively recently, recording the EEG required electrodes on an animal's brain to be connected to a computer. This protocol, in which an animal must be tethered, does not easily lend itself to sleep research in natural settings. Only in the past decade, with the development of miniature data loggers for recording EEG, has sleep research in the wild even become possible.

The first study of sleep in a wild animal was on the brown-throated three-toed sloth (*Bradypus variegatus*) in a Panamanian rainforest (Rattenborg et al., 2008). A previous study on sloths sleeping in captivity had observed around 16 hours of sleep each day, reinforcing their slothful reputation. However, when recording the sleep of wild sloths, researchers found a surprise: wild sloths slept less than 10 hours per day (Rattenborg et al., 2008; Voirin et al., 2014). This discovery provided a hint

that sleep in captivity is not necessarily representative of sleep in real-world contexts. This brings into question previous comparisons of sleep across species, which had been based entirely on laboratory research (Lesku et al., 2009). So, why is there a difference in sleep between captivity and the wild?

A Environmental and Ecological Considerations

The natural environment is complex, variable, and often risky. Animals typically need to compete for resources and mates, cope with changes in the environment, and avoid starvation and predation. Consequently, the same factors that are advantageous for laboratory experiments make the laboratory context very different from a natural context. Even in more naturalistic captive environments, food is usually freely available, there is no risk of predation (although animals may perceive humans to be threats), the environment is relatively simple, and animals cannot move as freely as they would in the wild. These environmental factors can have substantial effects on sleep. An analogy might be that the amount, continuity, and composition of sleep humans obtain on overnight airplane flights are quite unlike that observed in the comfort of their own bedroom.

There are other advantages of studying sleep in the wild. The natural world, with all of its complexity, is where sleep evolved. Individuals are different from one another. Studying between-individual variation in sleep can help us understand how sleep evolved (and might continue to evolve) in wild populations. Thus, wild sleep research is a necessary complement for sleep research in the laboratory. Laboratory studies have given rise to many predictions for the origins and functions of sleep; the natural environment is the ideal context in which to test these predictions.

B Sleeping Is Dangerous

The risk of being eaten is one factor predicted to affect the duration, composition, and timing of sleep (Acerbi & Nunn, 2011; Lesku, Bark, et al., 2008; Lesku, Roth, et al., 2008; Lima et al., 2005; Rattenborg et al., 1999). During sleep, animals are less aware of changes in their environment and, therefore, more vulnerable to predators (Lima et al., 2005). This is particularly true during REM sleep, when animals can have a particularly high arousal threshold. For large animals, the danger is compounded by the loss of muscle tone during REM sleep, which often necessitates the animal to lay on the ground (Gravett et al., 2017; Ruckebusch, 1972). With increasing risk, animals are predicted to spend less time sleeping and allocate less time asleep to REM sleep (Lesku, Bark, et al., 2008; Lesku et al., 2009; Lesku, Roth, et al., 2008).

These predictions have received some support from experimental studies (Lesku, Bark, et al., 2008) and comparisons between mammals, albeit studied in the laboratory (Lesku et al., 2009). Prior to the miniaturization of EEG technology, these ideas had not been tested in the wild.

The pygmy three-toed sloth (*B. pygmaeus*) is a sister species of *B. variegatus*, and both are found in Panama. While brown-throated sloths are exposed to nocturnal predators on the mainland, pygmy sloths live on a predator-free island. Researchers found that, although the two species shared a similar sleep duration, their timing of sleep differed. On the mainland, the brown-throated sloths slept predominantly at night, whereas the pygmy sloths showed no preference for sleeping during the night or day. These findings contradicted predictions: if animals are more vulnerable when sleeping, it appears counterintuitive that sloths sleep more at night when exposed to nocturnal predators. However, it is important to consider the ecology of the species. Sloths have very few physical defenses against predators; often, they will not even react to humans unless physically touched (Voirin et al., 2014). Moreover, they are depredated by visually orientating predators, including arboreal ocelots and harpy eagles. Sloths rely almost exclusively on crypsis to avoid being detected by predators, with the algae in their hair making them difficult to distinguish from surrounding foliage. Unlike most species, sloths might be much more vulnerable when they are active than when they are sleeping. For the brown-throated three-toed sloth, a preference for sleeping at night may have evolved as a strategy to minimize predation risk. This system illustrates the value in considering ecology in studies on wild sleep.

C Human Impacts

Understanding the evolution and functions of sleep has practical implications. Humans are altering the natural environment on a global scale. Increasing urbanization is contributing to habitat loss and unprecedented levels of noise and artificial light at night. Sleep is rarely considered when trying to understand and mitigate these threats to wildlife. However, human impacts on sleep could have detrimental outcomes for behavior, development, health, and survival. Sleep loss could well be an underappreciated factor in the decline of species. To confront this potential problem, researchers first need to measure human impacts on sleep and then investigate the extent to which species can cope or adapt.

Artificial light at night has gained attention as an anthropogenic factor that might impact sleep (Aulsebrook, Jones, Mulder, & Lesku, 2018). Sleep evolved under a predictable, 24 hour cycle of light and darkness. One common characteristic of sleep is that it has a circadian rhythm,

which optimizes the timing of sleep and wakefulness (Fisher, Foster, & Peirson, 2013). However, with the increasing presence of artificial light, many places no longer experience true darkness at night (Falchi et al., 2016). Light can affect sleep via multiple pathways, including the suppressive effect of light on the production of melatonin (Dijk & Archer, 2009). Laboratory research has demonstrated that artificial light can disrupt sleep, and studies of wild animals indicate that light at night can alter the daily timing of behavior (Da Silva, Samplonius, Schlicht, Valcu, & Kempenaers, 2014; Russ, Rüger, & Klenke, 2014). Experimental field studies have also found evidence for impacts of artificial light at night on sleep behavior (Raap, Pinxten, & Eens, 2015, 2016; Sun, Raap, Pinxten, & Eens, 2017). However, to gain a comprehensive understanding of the real-world impacts, research will need to investigate the impacts of artificial light on the sleep neurophysiology of wild animals (Aulsebrook et al., 2016). With recent and ongoing technological developments, researchers are now able to conduct studies in the ecological context where sleep has evolved. Such research has implications not only for our understanding of sleep but also for our broader understanding of animal behavior and the ability of animals to cope or adapt to a changing world.

D Adaptive Sleeplessness

Some species naturally sleep very little. For instance, although most rodents sleep a lot, typically between 12 and 20 hours per day (Lesku, Roth, et al., 2008), captive Cape mole rats (*Georychus capensis*) sleep less than 9 hours (Kruger et al., 2016). More remarkably, wild African elephants sleep less than 2 hours per day, based on trunk immobility (Gravett et al., 2017). Further, the elephants could seemingly go without any sleep for up to 46 hours and, like northern fur seals (Lyamin et al., 2018), might not engage in REM sleep each night.

Other species show reduced sleep or substantial variation in their amount of sleep in the face of competing demands. Pectoral sandpipers (*C. melanotos*) are shorebirds that migrate each year from the southern hemisphere to above the arctic circle to breed in a short, intense mating period under the continuous sunlight of the polar summer. Males try to mate with as many females as possible while defending their territories, chasing rivals, avoiding predators, and courting females. On the other hand, females are more discriminating about which male will sire her only clutch of the season. How do males sleep in this environment where competition for access to females is intense? Activity recordings from males on their territories on the tundra revealed that some males had a capacity to become almost sleepless (Lesku et al., 2012). The most active males are moving 95% of the time for 3 weeks. EEG recordings of wild

sandpipers showed that they transitioned rapidly from active wakefulness to sleep without engaging in quiet wakefulness, such that inactivity and activity are valid proxies for sleep and wakefulness, respectively, in this context; this also implies that intrasex variation in activity levels among males reflects intrasex variation in sleep (range 2.4–7.7 hours). Despite sleeping very little, the males that slept the least interacted with the most females and ultimately sired the most offspring. Thus, sleep loss can be evolutionarily adaptive.

A more recent study on the sleep EEG of wild animals focused on great frigate birds. Frigate birds are seabirds, yet, owing to a preen oil with a low-lipid content, cannot alight on the sea without quickly becoming waterlogged. Consequently, to forage at sea, they rely on subsurface predators to drive prey near or above the surface of the water. However, this type of food resource is temporally and spatially heterogeneous, such that the birds must cover large distances to meet their energetic requirements, spending up to 9 weeks at sea (Weimerskirch, Bishop, Jeanniard-du-Dot, Prudor, & Sachs, 2016). Rattenborg et al. (2016) equipped frigate birds with EEG and accelerometery data loggers, along with small GPS units to see how sleep responded to these periods at sea. It was found that the frigate birds were able to sleep on the wing, engaging in bihemispheric and unihemispheric SWS and REM sleep in flight. Although the birds were able to nap in the air, they slept very little in flight. On the nest, frigate birds would sleep 13 hours per day, but in the air, this value dropped to less than 1 hour per day. Thus, like the sandpipers, frigate birds are able to greatly reduce their sleep for days or weeks.

Sleep loss causes neurobehavioral impairments, including lapses in attention, motivation, and memory, along with reduced coordination and increased emotional reactivity in humans (Van Dongen et al., 2003). Such impairments are costly to society and to the individual (Hillman et al., 2018). How pectoral sandpipers and great frigate birds are able to retain the ability to perform well on little sleep is unknown. Nonetheless, additional studies of sleeping animals in their natural environments will only enhance our appreciation of the plasticity, function, and ecological relevance of sleep in the lives of wild animals.

IX CONCLUSIONS

Do all animals sleep? Sleep has been observed in all species studied by sleep scientists. There is a temptation to conclude that all animals sleep; however, no data exist for most animal groups. Around 30 animal phyla have yet to be tested for the presence of sleep (Lesku & Ly, 2017). Even within studied phyla, the phylogenetic coverage is often poor. This is true for invertebrates and also fishes and amphibians. That said, the existence of sleep in very simple animals, such as flatworms (Omond et al., 2017) and jellyfish (Nath et al., 2017), indicates that sleep evolved early in the lineage of animals. Whether it has persisted in all species over evolutionary time is unclear. Nonetheless, the apparent evolutionary longevity of sleep suggests that it fulfills a fundamental and inescapable need. This fundamental need is further revealed by (i) the persistence of sleep, despite the inherent vulnerability associated with this state (Lima et al., 2005); (ii) the evolution of unihemispheric SWS in marine mammals and birds (Lyamin et al., 2008; Rattenborg et al., 2000); and (iii) animals that can greatly reduce (but not eliminate) sleep when other demands favor sustained performance (Lesku et al., 2012; Rattenborg et al., 2016). It seems likely that sleep serves many functions, some of which might be evolutionarily "ancient," present in jellyfish, flatworms, and vertebrates (Nath et al., 2017), while others might be evolutionarily new and present only in derived species (Lesku, Vyssotski, et al., 2011).

When did SWS and REM sleep appear? The relatively low number of studies and variability of observations in the nonavian reptiles impedes firm conclusions about the homology of sleep states across amniotes. With this caveat in mind, fully formed SWS and REM sleep states have been unequivocally observed only in birds and mammals. The absence of clear electrophysiological indicators of SWS and REM sleep in nonavian reptiles and amphibians suggests that these states were absent from the most recent common ancestor to amniotes (mammals, avian, and nonavian reptiles) and anamniotes (amphibians). Instead, features of SWS likely appeared in the common ancestor to the amniote clade with the appearance of HShW, as observed in many nonavian reptiles. Given that nonavian reptilian HShW and avian slow waves share a similar distribution across forebrain structures, along with the absence of hippocampal sharp waves and ripples in the avian brain, HShW are likely a homologous electrophysiological signal to avian and mammalian slow waves, potentially representing the neurophysiological correlate of a rudimentary form of avian and mammalian SWS. Moreover, the dorsal ventricular ridge is involved in the propagation of avian slow waves (Beckers et al., 2014) and nonavian reptilian HShW (Shein-Idelson et al., 2016; Tisdale, Lesku, Beckers, & Rattenborg, 2018) further strengthening this interpretation. Additional studies describing the distribution and characteristics of HShW will provide a clearer picture of any potential relationship between HShW and avian and mammalian slow waves. Perhaps, with the shift from ectothermy to endothermy and/or more interconnected brains arising from increased neuronal and astrocyte densities, HShW became a synchronized and sustained slow oscillation across the brain in birds and mammals (Rattenborg et al., 2009). In this way, SWS (and REM sleep) in

mammals and birds arose from convergent evolution in the immediate ancestor to each group. The mixed SWS/REM sleep states observed in monotremes might represent an early form of fully differentiated SWS and REM sleep, characterized by the presence of brain stem-regulated components of REM sleep, in conjunction with slow waves in the forebrain. This evolutionary model suggests that SWS and REM sleep perform derived or evolutionarily new sleep functions not found in more basal animals. Alternatively, sleep might perform similar functions across the animal kingdom, with SWS and REM sleep offering new, more efficient mechanisms for achieving those functions in animals with highly interconnected brains (Rattenborg et al., 2009).

This hypothesis must be tempered, however, by observations of multiple sleep states in lizards (Libourel et al., 2017; Shein-Idelson et al., 2016), cuttlefish (Frank et al., 2012), and fruit flies (Yap et al., 2017). If and how these states resemble mammalian and avian REM sleep needs to be further explored. Indeed, much work remains to be done until our understanding of the evolution of sleep states and functions is complete. To this end, we must have an integration of disciplines that includes behavior, electrophysiology, pharmacology, and genetics to glean how sleep states appeared over evolutionary time. Only such an endeavor will fully reveal the origin(s), evolution, and functions of sleep.

References

Acerbi, A., & Nunn, C. L. (2011). Predation and the phasing of sleep: an evolutionary individual-based model. *Animal Behaviour*, *81*, 801–811.

Allison, T., Van Twyver, H., & Goff, W. R. (1972). Electrophysiological studies of the echidna, *Tachyglossus aculeatus*. I. Waking and sleep. *Archives Italiennes de Biologie*, *110*, 145–184.

Andrews, K. S., Williams, G. D., Farrer, D., Tolimieri, N., Harvey, C. J., Bargmann, G., et al. (2009). Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. *Animal Behaviour*, *78*, 525–536.

Arnason, U., Adegoke, J. A., Bodin, K., Born, E. W., Esa, Y. B., Gullberg, A., et al. (2002). Mammalian mitogenomic relationships and the root of the eutherian tree. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 8151–8156.

Aulsebrook, A. E., Jones, T. M., Mulder, R. A., & Lesku, J. A. (2018). Impacts of artificial light at night on sleep: a review and prospectus. *Journal of Experimental Zoology Part A*, *329*(8-9), 409–418. https://doi.org/10.1002/jez.2189.

Aulsebrook, A. E., Jones, T. M., Rattenborg, N. C., Roth, T. C., & Lesku, J. A. (2016). Sleep ecophysiology: integrating neuroscience and ecology. *Trends in Ecology & Evolution*, *31*, 590–599.

Ayala-Guerrero, F., & Mexicano, G. (2008). Sleep and wakefulness in the green iguanid lizard (*Iguana iguana*). *Comparative Biochemistry and Physiology—Part A*, *151*, 305–312.

Barnett, A., Payne, N. L., Semmens, J. M., & Fitzpatrick, R. (2016). Ecotourism increases the field metabolic rate of whitetip reef sharks. *Biological Conservation*, *199*, 132–136.

Baronio, M. (2012). *The use of a micro remotely operated vehicle as a tool for studies of shark behavior and diver impact.* Lismore: Southern Cross University.

Beckers, G. J. L., van der Meij, J., Lesku, J. A., & Rattenborg, N. C. (2014). Plumes of neuronal activity propagate in three dimensions through the nuclear avian brain. *BMC Biology*, *12*, 16.

Capellini, I., Barton, R. A., McNamara, P., Preston, B. T., & Nunn, C. L. (2008). Phylogenetic analysis of the ecology and evolution of mammalian sleep. *Evolution*, *62*, 1764–1776.

Carey, F. G., Kanwisher, J. W., Brazier, O., Gabrielson, G., Casey, J. G., & Pratt, H. L. (1982). Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia*, *1982*, 254–260.

Carlson, J. K., & Parsons, G. R. (2001). The effects of hypoxia on three sympatric shark species: physiological and behavioral responses. *Environmental Biology of Fishes*, *61*, 427–433.

Compagno, L. J. (1988). *Sharks of the order Carcharhiniformes.* 486. Princeton: Princeton University Press.

Cote, K. A., Etienne, L., & Campbell, K. B. (2001). Neurophysiological evidence for the detection of external stimuli during sleep. *Sleep*, *24*, 791–803.

Da Silva, A., Samplonius, J. M., Schlicht, E., Valcu, M., & Kempenaers, B. (2014). Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. *Behavioral Ecology*, *25*, 1037–1047.

Daan, S. (2011). How and why? The lab versus the field. *Sleep and Biological Rhythms*, *9*, 1–2.

Dewasmes, G., Cohen-Adad, F., Koubi, H., & Le Maho, Y. (1985). Polygraphic and behavioral study of sleep in geese: existence of nuchal atonia during paradoxical sleep. *Physiology & Behavior*, *35*, 67–73.

Dijk, D. J., & Archer, S. N. (2009). Light, sleep, and circadian rhythms: together again. *PLoS Biology*, *7*, e1000145.

Duboué, E. R., Keene, A. C., & Borowsky, R. L. (2011). Evolutionary convergence on sleep loss in cavefish populations. *Current Biology*, *21*, 671–676.

Dudgeon, C. L., Lanyon, J. M., & Semmens, J. M. (2013). Seasonality and site fidelity of the zebra shark, *Stegostoma fasciatum*, in southeast Queensland, Australia. *Animal Behaviour*, *85*, 471–481.

Eiland, M. M., Lyamin, O. I., & Siegel, J. M. (2001). State-related discharge of neurons in the brainstem of freely moving box turtles, *Terrapene carolina major*. *Archives Italiennes de Biologie*, *139*, 23–36.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C., Elvidge, C. D., Baugh, K., et al. (2016). The new world atlas of artificial night sky brightness. *Science Advances*, *2*, e1600377.

Fang, G., Chen, Q., Cui, J., & Tang, Y. (2012). Electroencephalogram bands modulated by vigilance states in an anuran species: a factor analytic approach. *Journal of Comparative Physiology A*, *198*, 119–127.

Fisher, S. P., Foster, R. G., & Peirson, S. N. (2013). The circadian control of sleep. *Handbook of Experimental Pharmacology*, *217*, 157–183.

Fitzpatrick, R., Abrantes, K. G., Seymour, J., & Barnett, A. (2011). Variation in depth of whitetip reef sharks: does provisioning ecotourism change their behavior? *Coral Reefs*, *30*, 569–577.

Flanigan, W. F., Wilcox, R. H., & Rechtschaffen, A. (1973). The EEG and behavioral continuum of the crocodilian, *Caiman sclerops*. *Electroencephalography and Clinical Neurophysiology*, *34*, 521–538.

Frank, M. G., Waldrop, R. H., Dumoulin, M., Aton, S., & Boal, J. G. (2012). A preliminary analysis of sleep-like states in the cuttlefish *Sepia officinalis*. *PLoS One*, *7*, e38125.

Friedlaender, A. S., Tyson, R. B., Stimpert, A. K., Read, A. J., & Nowacek, D. P. (2013). Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*, *494*, 281–289.

Fuchs, T., Haney, A., Jechura, T. J., Moore, F. R., & Bingman, V. P. (2006). Daytime naps in night-migrating birds: behavioral adaptation to seasonal sleep deprivation in the Swainson's thrush, *Catharus ustulatus*. *Animal Behaviour*, *72*, 951–958.

Fuss, T., Bleckmann, H., & Schluessel, V. (2014). Visual discrimination abilities in the gray bamboo shark (*Chiloscyllium griseum*). *Zoology*, *117*, 104–111.

Gnone, G., Moriconi, T., & Gambini, G. (2006). Sleep behavior: activity and sleep in dolphins. *Nature*, *441*, E10–E11.

Goldshmid, R., Holzman, R., Weihs, D., & Genin, A. (2004). Aeration of corals by sleep-swimming fish. *Limnology and Oceanography*, *49*, 1832–1839.

Goley, P. D. (1999). Behavioral aspects of sleep in Pacific white-sided dolphins (*Lagenorhynchus obliquidens*, Gill 1865). *Marine Mammal Science*, *15*, 1054–1064.

Gravett, N., Bhagwandin, A., Sutcliffe, R., Landen, K., Chase, M. J., Lyamin, O. I., et al. (2017). Inactivity/sleep in two wild free-roaming African elephant matriarchs: does large body size make elephants the shortest mammalian sleepers? *PLoS One*, *12*, e0171903.

Hart, N. S., Lisney, T. J., & Collin, S. P. (2006). Visual communication in elasmobranchs. In F. Ladich, S. P. Collin, P. Moller, & B. G. Kapoor (Eds.), *Communication in fishes* (pp. 337–392). Enfield: Science Publishers.

Hartse, K. M. (1994). Sleep in insects and nonmammalian vertebrates. In M. H. Kryger, T. Roth, & W. C. Dement (Eds.), *Principles and practice of sleep medicine* (2nd ed., pp. 95–104). Philadelphia: Saunders.

Heyman, W. D., Graham, R. T., Kjerfve, B., & Johannes, R. E. (2001). Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series*, *215*, 275–282.

Hill, S., & Tononi, G. (2005). Modeling sleep and wakefulness in the thalamocortical system. *Journal of Neurophysiology*, *93*, 1671–1698.

Hillman, D., Mitchell, S., Streatfeild, J., Burns, C., Bruck, D., & Pezzullo, L. (2018). The economic cost of inadequate sleep. *Sleep*, *41*, zsy083.

Hobson, J. A., Goin, O. B., & Goin, C. J. (1968). Sleep behavior of frogs in field. *Psychophysiology*, *5*, 202.

Huber, R., Ghilardi, M. F., Massimini, M., Ferrarelli, F., Riedner, B. A., Peterson, M. J., et al. (2006). Arm immobilization causes cortical plastic changes and locally decreases sleep slow wave activity. *Nature Neuroscience*, *9*, 1169–1176.

Huber, R., Ghilardi, M. F., Massimini, M., & Tononi, G. (2004). Local sleep and learning. *Nature*, *430*, 78–81.

Huntley, A., Donnelly, M., & Cohen, H. (1978). Sleep in the western toad *Bufo boreas*. *Sleep Research*, *7*, 141.

Imeri, L., & Opp, M. R. (2009). How (and why) the immune system makes us sleep. *Nature Reviews Neuroscience*, *10*, 199–210.

Jaggard, J. B., Stahl, B. A., Lloyd, E., Prober, D. A., Duboue, E. R., & Keene, A. C. (2018). Hypocretin underlies the evolution of sleep loss in the Mexican cavefish. *eLife*, *7*, e32637.

Jerison, H. J. (2001). The study of primate brain evolution: where do we go from here? In D. Falk & K. Gibson (Eds.), *Evolutionary anatomy of the primate cerebral cortex* (pp. 305–337). Cambridge: Cambridge University Press.

Jones, S. G., Vyazovskiy, V. V., Cirelli, C., Tononi, G., & Benca, R. M. (2008). Homeostatic regulation of sleep in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *BMC Neuroscience*, *9*, 47.

Jouvet-Mounier, D., Astic, L., & Lacote, D. (1970). Ontogenesis of the states of sleep in rat, cat, and guinea pig during the first postnatal month. *Developmental Psychobiology*, *2*, 216–239.

Kaiser, W., & Steiner-Kaiser, J. (1983). Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature*, *301*, 707–709.

Karmanova, H., & Belich, A. (1983). Temporal organization of "wakefulness-primary sleep" cycle in the dwarf catfish *Ictalurus nebulosus*. *Journal of Evolutionary Biochemistry and Physiology*, *19*, 131–136.

Karmanova, H., Belich, A. I., & Lazarev, S. G. (1981). An electrophysiological study of wakefulness and sleep-like states in fish and amphibians. In P. R. Laming (Ed.), *Brain mechanisms of behavior in lower vertebrates* (pp. 181–202). Cambridge: Cambridge University Press.

Kavanau, J. (1998). Vertebrates that never sleep: implications for sleep's basic function. *Brain Research Bulletin*, *46*, 269–279.

Kavanau, J. (2004). Sleep researchers need to bring Darwin on board: elucidating functions of sleep via adaptedness and natural selection. *Medical Hypotheses*, *62*, 161–165.

Kelly, M. L., Peters, R. A., Tisdale, R. K., & Lesku, J. A. (2015). Unihemispheric sleep in crocodilians? *The Journal of Experimental Biology*, *218*, 3175–3178.

Klein, B. A., Klein, A., Wray, M. K., Mueller, U. G., & Seeley, T. D. (2010). Sleep deprivation impairs precision of waggle dance signaling in honey bees. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 22705–22709.

Klimley, A., Butler, S., Nelson, D., & Stull, A. (1988). Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* Griffith and Smith, to and from a seamount in the Gulf of California. *Journal of Fish Biology*, *33*, 751–761.

Kruger, J. L., Gravett, N., Bhagwandin, A., Bennett, N. C., Archer, E. K., & Manger, P. R. (2016). Sleep in the Cape mole rat: a short-sleeping subterranean rodent. *Brain, Behavior and Evolution*, *87*, 78–87.

Kurth, S., Riedner, B. A., Dean, D. C., O'Muircheartaigh, J., Huber, R., Jenni, O. G., et al. (2017). Traveling slow oscillations during sleep: a marker of brain connectivity in childhood. *Sleep*, *40*, zsx121.

Lazarev, S. G. (1978). Electroencephalographic analysis of wakefulness and the primary form of sleep in the frog, *Rana temporaria*. *Journal of Evolutionary Biochemistry and Physiology*, *14*, 379–384.

Lesku, J. A., Bark, R. J., Martinez-Gonzalez, D., Rattenborg, N. C., Amlaner, C. J., & Lima, S. L. (2008). Predator-induced plasticity in sleep architecture in wild-caught Norway rats (*Rattus norvegicus*). *Behavioural Brain Research*, *189*, 298–305.

Lesku, J. A., & Ly, L. M. T. (2017). Sleep origins: restful jellyfish are sleeping jellyfish. *Current Biology*, *27*, R1060–R1062.

Lesku, J. A., Meyer, L. C. R., Fuller, A., Maloney, S. K., Dell'Omo, G., Vyssotski, A. L., et al. (2011). Ostriches sleep like platypuses. *PLoS One*, *6*, e23203.

Lesku, J. A., & Rattenborg, N. C. (2014). Avian sleep. *Current Biology*, *24*, R12–R14.

Lesku, J. A., Rattenborg, N. C., Valcu, M., Vyssotski, A. L., Kuhn, S., Kuemmeth, F., et al. (2012). Adaptive sleep loss in polygynous pectoral sandpipers. *Science*, *337*, 1654–1658.

Lesku, J. A., Roth, T. C., Amlaner, C. J., & Lima, S. L. (2006). A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *The American Naturalist*, *168*, 441–453.

Lesku, J. A., Roth, T. C., Rattenborg, N. C., Amlaner, C. J., & Lima, S. L. (2008). Phylogenetics and the correlates of mammalian sleep: a reappraisal. *Sleep Medicine Reviews*, *12*, 229–244.

Lesku, J. A., Roth, T. C., Rattenborg, N. C., Amlaner, C. J., & Lima, S. L. (2009). History and future of comparative analyses in sleep research. *Neuroscience and Biobehavioral Reviews*, *33*, 1024–1036.

Lesku, J. A., Vyssotski, A. L., Martinez-Gonzalez, D., Wilzeck, C., & Rattenborg, N. C. (2011). Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? *Proceedings of the Royal Society B*, *278*, 2419–2428.

Libourel, P. A., Barillot, B., Arthaud, S., Massot, B., Morel, A. L., Beuf, O., Herrel, A., & Luppi, P. H. (2017). Identification of two sleep states in the tegu lizard, *Salvator merianae*. Program No. 241.06/KK34. Neuroscience Meeting Planner. Washington, DC: Society for Neuroscience, Online.

Libourel, P. A., & Herrel, A. (2016). Sleep in amphibians and reptiles: a review and a preliminary analysis of evolutionary patterns. *Biological Reviews*, *91*, 833–866.

Lima, S. L., Rattenborg, N. C., Lesku, J. A., & Amlaner, C. J. (2005). Sleeping under the risk of predation. *Animal Behaviour*, *70*, 723–736.

Lisney, T. J., Theiss, S. M., Collin, S. P., & Hart, N. S. (2012). Vision in elasmobranchs and their relatives: 21st century advances. *Journal of Fish Biology*, *80*, 2024–2054.

Lorenzo, D., Macadar, O., & Velluti, J. C. (1999). Origin and propagation of spontaneous electrographic sharp waves in the *in vitro* turtle brain: a model of neuronal synchronization. *Clinical Neurophysiology, 110*, 1535–1544.

Lyamin, O. I., Kosenko, P. O., Korneva, S. M., Vyssotski, A. L., Mukhametov, L. M., & Siegel, J. M. (2018). Fur seals suppress REM sleep for very long periods without subsequent rebound. *Current Biology, 28*, 2000–2005.

Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M., & Siegel, J. M. (2008). Cetacean sleep: an unusual form of mammalian sleep. *Neuroscience and Biobehavioral Reviews, 32*, 1451–1484.

Manger, P. R. (2013). Questioning the interpretations of behavioral observations of cetaceans: is there really support for a special intellectual status for this mammalian order? *Neuroscience, 250*, 664–696.

Manger, P. R., Fahringer, H. M., Pettigrew, J. D., & Siegel, J. M. (2002). The distribution and morphological characteristics of cholinergic cells in the brain of monotremes as revealed by ChAT immunohistochemistry. *Brain, Behavior and Evolution, 60*, 275–297.

Martinez-Gonzalez, D., Lesku, J. A., & Rattenborg, N. C. (2008). Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons (*Columba livia*): evidence for avian sleep homeostasis. *Journal of Sleep Research, 17*, 140–153.

Massimini, M., Huber, R., Ferrarelli, F., Hill, S., & Tononi, G. (2004). The sleep slow oscillation as a traveling wave. *The Journal of Neuroscience, 24*, 6862–6870.

Mathews, C. G., Lesku, J. A., Lima, S. L., & Amlaner, C. J. (2006). Asynchronous eye closure as an anti-predator behavior in the western fence lizard (*Sceloporus occidentalis*). *Ethology, 112*, 286–292.

McLaughlin, R., & O'Gower, A. (1971). Life history and underwater studies of a heterodont shark. *Ecological Monographs, 41*, 271–289.

Meglasson, M. D., & Huggins, S. E. (1979). Sleep in a crocodilian, *Caiman sclerops. Comparative Biochemistry and Physiology—Part A, 63A*, 561–567.

Mendoza-Angeles, K., Hernández-Falcón, J., & Ramón, F. (2010). Slow waves during sleep in crayfish: origin and spread. *The Journal of Experimental Biology, 213*, 2154–2164.

Miller, P. J., Aoki, K., Rendell, L. E., & Amano, M. (2008). Stereotypical resting behavior of the sperm whale. *Current Biology, 18*, R21–R23.

Mitani, Y., Andrews, R. D., Sato, K., Kato, A., Naito, Y., & Costa, D. P. (2010). Three-dimensional resting behavior of northern elephant seals: drifting like a falling leaf. *Biology Letters, 6*, 163–166.

Mitchell, K. J., Llamas, B., Soubrier, J., Rawlence, N. J., Worthy, T. H., Wood, J., et al. (2014). Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird evolution. *Science, 344*, 898–900.

Nashida, T., Yabe, H., Sato, Y., Hiruma, T., Sutoh, T., Shinozaki, N., et al. (2000). Automatic auditory information processing in sleep. *Sleep, 23*, 821–828.

Nath, R. D., Bedbrook, C. N., Abrams, M. J., Basinger, T., Bois, J. S., Prober, D. A., et al. (2017). The jellyfish *Cassiopea* exhibits a sleep-like state. *Current Biology, 27*, 2984–2990.

Neckelmann, D., & Ursin, R. (1993). Sleep stages and EEG power spectrum in relation to acoustical stimulus arousal threshold in the rat. *Sleep, 16*, 467–477.

Nelson, D. R., & Johnson, R. H. (1970). Diel activity rhythms in the nocturnal, bottom-dwelling sharks, *Heterodontus francisci* and *Cephaloscyllium ventriosum. Copeia, 1970*, 732–739.

Newman, S. M., Paletz, E. M., Obermeyer, W. H., & Benca, R. M. (2009). Sleep deprivation in pigeons and rats using motion detection. *Sleep, 32*, 1299–1312.

Nichols, A. L. A., Eichler, T., Latham, R., & Zimmer, M. (2017). A global brain state underlies *C. elegans* sleep behavior. *Science, 356*, eaam6851.

Nicol, S. C., Andersen, N. A., Phillips, N. H., & Berger, R. J. (2000). The echidna manifests typical characteristics of rapid eye movement sleep. *Neuroscience Letters, 283*, 49–52.

Nitz, D. A., van Swinderen, B., Tononi, G., & Greenspan, R. J. (2002). Electrophysiological correlates of rest and activity in *Drosophila melanogaster. Current Biology, 12*, 1934–1940.

Oleksenko, A. I., Mukhametov, L. M., Polyakova, I. G., Supin, A. Y., & Kovalzon, V. M. (1992). Unihemispheric sleep deprivation in bottlenose dolphins. *Journal of Sleep Research, 1*, 40–44.

Omond, S., Ly, L. M. T., Beaton, R., Storm, J. J., Hale, M. W., & Lesku, J. A. (2017). Inactivity is nycthemeral, endogenously generated, homeostatically regulated, and melatonin modulated in a free-living platyhelminth flatworm. *Sleep, 40*, zsx124.

Ookawa, T., & Gotoh, J. (1965). Electroencephalogram of the chicken recorded from the skull under various conditions. *The Journal of Comparative Neurology, 124*, 1–14.

Ott, M. (2001). Chameleons have independent eye movements but synchronise both eyes during saccadic prey tracking. *Experimental Brain Research, 139*, 173–179.

Pavan, C. (1946). Observations and experiments on the cave fish *Pimelodella kronei* and its relatives. *The American Naturalist, 80*, 343–361.

Peever, J., & Fuller, P. M. (2017). The biology of REM sleep. *Current Biology, 27*, R1237–R1248.

Pettigrew, J. D., Wallman, J., & Wildsoet, C. F. (1990). Saccadic oscillations facilitate ocular perfusion from the avian pecten. *Nature, 343*, 362–363.

Peyrethon, J., & Dusan-Peyrethon, D. (1967). Etude polygraphique du cycle veille-sommeil d'un téléosteen (*Tinca tinca*). *Comptes Rendus des Seances de la Societe de Biologie et de Ses Filiales, 161*, 2533–2536.

Peyrethon, J., & Dusan-Peyrethon, D. (1969). Polygraphic study of the sleep-wake cycle in 3 genera of reptiles. *Comptes Rendus des Seances de la Societe de Biologie et de Ses Filiales, 163*, 181–186.

Poulson, T., & Jegla, T. (1969). Circadian rhythms in cave animals. In: *Proceedings of the 4th international congress of speleology*, pp. 4–5.

Preston, B. T., Capellini, I., McNamara, P., Barton, R. A., & Nunn, C. L. (2009). Parasite resistance and the adaptive significance of sleep. *BMC Evolutionary Biology, 9*, 7.

Raap, T., Pinxten, R., & Eens, M. (2015). Light pollution disrupts sleep in free-living animals. *Scientific Reports, 5*, 13557.

Raap, T., Pinxten, R., & Eens, M. (2016). Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environmental Pollution, 215*, 125–134.

Rattenborg, N. C., Amlaner, C. J., & Lima, S. L. (2000). Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neuroscience and Biobehavioral Reviews, 24*, 817–842.

Rattenborg, N. C., Lima, S. L., & Amlaner, C. J. (1999). Half-awake to the risk of predation. *Nature, 397*, 397–398.

Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M., et al. (2004). Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biology, 2*, e212.

Rattenborg, N. C., & Martinez-Gonzalez, D. (2015). Avian versus mammalian sleep: the fruits of comparing apples and oranges. *Current Sleep Medicine Reports, 1*, 55–63.

Rattenborg, N. C., Martinez-Gonzalez, D., & Lesku, J. A. (2009). Avian sleep homeostasis: convergent evolution of complex brains, cognition and sleep functions in mammals and birds. *Neuroscience and Biobehavioral Reviews, 33*, 253–270.

Rattenborg, N. C., Voirin, B., Cruz, S. M., Tisdale, R., Dell'Omo, G., Lipp, H. P., et al. (2016). Evidence that birds sleep in mid-flight. *Nature Communications, 7*, 12468.

Rattenborg, N. C., Voirin, B., Vyssotski, A. L., Kays, R. W., Spoelstra, K., Kuemmeth, F., et al. (2008). Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest. *Biology Letters, 4*, 402–405.

Roffwarg, H. P., Muzio, J. N., & Dement, W. C. (1966). Ontogenetic development of the human sleep-dream cycle. *Science, 152*, 604–619.

Roth, T. C., Lesku, J. A., Amlaner, C. J., & Lima, S. L. (2006). A phylogenetic analysis of the correlates of sleep in birds. *Journal of Sleep Research, 15*, 395–402.

Ruckebusch, Y. (1972). The relevance of drowsiness in the circadian cycle of farm animals. *Animal Behaviour, 20*, 637–643.

Russ, A., Rüger, A., & Klenke, R. (2014). Seize the night: European blackbirds (*Turdus merula*) extend their foraging activity under artificial illumination. *Journal für Ornithologie, 156*, 123–131.

Sabbah, S., Laria, R. L., Gray, S. M., & Hawryshyn, C. W. (2010). Functional diversity in the color vision of cichlid fishes. *BMC Biology, 8*, 133.

Samson, D. R., & Nunn, C. L. (2015). Sleep intensity and the evolution of human cognition. *Evolutionary Anthropology, 24*, 225–237.

Schmidt, M. H. (2014). The energy allocation function of sleep: a unifying theory of sleep, torpor, and continuous wakefulness. *Neuroscience and Biobehavioral Reviews, 47*, 122–153.

Scriba, M. F., Ducrest, A. L., Henry, I., Vyssotski, A. L., Rattenborg, N. C., & Roulin, A. (2013). Linking melanism to brain development: expression of a melanism-related gene in barn owl feather follicles covaries with sleep ontogeny. *Frontiers in Zoology, 10*, 42.

Sekiguchi, Y., Arai, K., & Kohshima, S. (2006). Sleep behavior: sleep in continuously active dolphins. *Nature, 441*, E9–E10.

Shaffery, J. P., Roffwarg, H. P., Speciale, S. G., & Marks, G. A. (1999). Ponto-geniculo-occipital-wave suppression amplifies lateral geniculate nucleus cell-size changes in monocularly deprived kittens. *Developmental Brain Research, 114*, 109–119.

Shapiro, C., & Hepburn, H. (1976). Sleep in a schooling fish, *Tilapia mossambica*. *Physiology & Behavior, 16*, 613–615.

Shein-Idelson, M., Ondracek, J. M., Liaw, H. P., Reiter, S., & Laurent, G. (2016). Slow waves, sharp waves, ripples, and REM in sleeping dragons. *Science, 352*, 590–595.

Shine, R., Amiel, J., Munn, A. J., Stewart, M., Vyssotski, A. L., & Lesku, J. A. (2015). Is "cooling then freezing" a humane way to kill amphibians and reptiles? *Biology Open, 4*, 760–763.

Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M., & Pettigrew, J. D. (1996). The echidna *Tachyglossus aculeatus* combines REM and non-REM aspects in a single sleep state: implications for the evolution of sleep. *The Journal of Neuroscience, 16*, 3500–3506.

Siegel, J. M., Manger, P. R., Nienhuis, R., Fahringer, H. M., Shalita, T., & Pettigrew, J. D. (1999). Sleep in the platypus. *Neuroscience, 91*, 391–400.

Sims, D., Nash, J., & Morritt, D. (2001). Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioral strategies and apparent sexual segregation. *Marine Biology, 139*, 1165–1175.

Smith, K., Scarr, M., & Scarpaci, C. (2010). Grey nurse shark (*Carcharias taurus*) diving tourism: tourist compliance and shark behavior at Fish Rock, Australia. *Environmental Management, 46*, 699–710.

Stephenson, R., & Lewis, V. (2011). Behavioral evidence for a sleep-like quiescent state in a pulmonate mollusc, *Lymnaea stagnalis* (Linnaeus). *The Journal of Experimental Biology, 214*, 747–756.

Stropes, S. (1971). *Electrographic and behavioral correlates of sleep in the Colorado Desert Fringe-toed Lizard, Uma Notata*. San Diego University.

Stropes, S. (1975). *Sleep behavior in reptiles*. University of Arizona.

Sugihara, K., & Gotoh, J. (1973). Depth-electroencephalograms of chickens in wakefulness and sleep. *The Japanese Journal of Physiology, 23*, 371–379.

Sun, J., Raap, T., Pinxten, R., & Eens, M. (2017). Artificial light at night affects sleep behavior differently in two closely related songbird species. *Environmental Pollution, 231*, 882–889.

Szymczak, J. T. (1987). Distribution of sleep and wakefulness in 24-h light-dark cycles in the juvenile and adult magpie, *Pica pica*. *Chronobiologia, 14*, 277–287.

Tauber, E. S. (1974). Phylogeny of sleep. *Advanced Sleep Research, 1*, 133–172.

Tauber, E. S., Roffwarg, H. P., & Weitzman, E. D. (1966). Eye movements and electroencephalogram activity during sleep in diurnal lizards. *Nature, 212*, 1612–1613.

Tauber, E. S., & Weitzman, E. D. (1969). Eye movements during behavioral inactivity in certain Bermuda reef fish. *Communications in Behavioral Biology, 3*, 131–135.

Thurber, A., Jha, S. K., Coleman, T., & Frank, M. G. (2008). A preliminary study of sleep ontogenesis in the ferret (*Mustela putorius furo*). *Behavioural Brain Research, 189*, 41–51.

Tisdale, R. K., Lesku, J. A., Beckers, G. J. L., & Rattenborg, N. C. (2018). Bird-like propagating brain activity in anesthetized Nile crocodiles. *Sleep, 41*, zsy105.

Tisdale, R. K., Vyssotski, A. L., Lesku, J. A., & Rattenborg, N. C. (2017). Sleep-related electrophysiology and behavior of tinamous (*Eudromia elegans*): tinamous do not sleep like ostriches. *Brain, Behavior and Evolution, 89*, 249–261.

Tobler, I. (2011). Phylogeny of sleep regulation. In M. H. Kryger, T. Roth, & W. C. Dement (Eds.), *Principles and practice of sleep medicine* (5th ed., pp. 112–125). Philadelphia: Saunders.

Tobler, I., & Borbély, A. A. (1985). Effect of rest deprivation on motor activity of fish. *Journal of Comparative Physiology A, 157*, 817–822.

Tobler, I., & Borbély, A. A. (1988). Sleep and EEG spectra in the pigeon (*Columba livia*) under baseline conditions and after sleep-deprivation. *Journal of Comparative Physiology A, 163*, 729–738.

Tononi, G., & Cirelli, C. (2014). Sleep and the price of plasticity: from synaptic and cellular homeostasis to memory consolidation and integration. *Neuron, 81*, 12–34.

Van Dongen, H. P., Maislin, G., Mullington, J. M., & Dinges, D. F. (2003). The cumulative cost of additional wakefulness: dose-response effects on neurobehavioral functions and sleep physiology from chronic sleep restriction and total sleep deprivation. *Sleep, 26*, 117–126.

Van Twyver, H. (1973). Sleep and wakefulness of the American alligator. *Sleep Research, 2*, 87.

Van Twyver, H., & Allison, T. (1972). A polygraphic and behavioral study of sleep in the pigeon (*Columba livia*). *Experimental Neurology, 35*, 138–153.

Voirin, B., Scriba, M. F., Martinez-Gonzalez, D., Vyssotski, A. L., Wikelski, M., & Rattenborg, N. C. (2014). Ecology and neurophysiology of sleep in two wild sloth species. *Sleep, 37*, 753–761.

Vorster, A. P., Krishnan, H. C., Cirelli, C., & Lyons, L. C. (2014). Characterization of sleep in *Aplysia californica*. *Sleep, 37*, 1453–1463.

Vyazovskiy, V. V., & Delogu, A. (2014). NREM and REM sleep: complementary roles in recovery after wakefulness. *The Neuroscientist, 20*, 203–219.

Vyazovskiy, V. V., Olcese, U., Lazimy, Y. M., Faraguna, U., Esser, S. K., Williams, J. C., et al. (2009). Cortical firing and sleep homeostasis. *Neuron, 63*, 865–878.

Warner, B. F., & Huggins, S. E. (1978). An electroencephalographic study of sleep in young caimans in a colony. *Comparative Biochemistry and Physiology—Part A, 59*, 139–144.

Weber, V. E. (1961). Uber ruhelagen von fischen. *Zeitschrift für Tierpsychologie, 18*, 517–533.

Wehr, T. A. (1992). A brain-warming function for REM sleep. *Neuroscience and Biobehavioral Reviews, 16*, 379–397.

Weimerskirch, H., Bishop, C., Jeanniard-du-Dot, T., Prudor, A., & Sachs, G. (2016). Frigate birds track atmospheric conditions over months-long transoceanic flights. *Science, 353*, 74–78.

Werth, E., Dijk, D. J., Achermann, P., & Borbély, A. A. (1996). Dynamics of the sleep EEG after an early evening nap: experimental data and simulations. *The American Journal of Physiology, 271*, R501–R510.

Whitney, N. M., Papastamatiou, Y. P., Holland, K. N., & Lowe, C. G. (2007). Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks, *Triaenodon obesus. Aquatic Living Resources, 20*, 299–305.

Yap, M. H. W., Grabowska, M. J., Rohrscheib, C., Jeans, R., Troup, M., Paulk, A. C., et al. (2017). Oscillatory brain activity in spontaneous and induced sleep stages in flies. *Nature Communications, 8*, 1815.

Yokogawa, T., Marin, W., Faraco, J., Pézeron, G., Appelbaum, L., Zhang, J., et al. (2007). Characterization of sleep in zebrafish and insomnia in hypocretin receptor mutants. *PLoS Biology, 5*, e277.

Yonezawa, T., Segawa, T., Mori, H., Campos, P. F., Hongoh, Y., Endo, H., et al. (2017). Phylogenomics and morphology of extinct paleognaths reveal the origin and evolution of the ratites. *Current Biology, 27*, 68–77.

Yoshizawa, M., Robinson, B. G., Duboué, E. R., Masek, P., Jaggard, J. B., O'Quin, K. E., et al. (2015). Distinct genetic architecture underlies the emergence of sleep loss and prey-seeking behavior in the Mexican cavefish. *BMC Biology, 13*, 15.

Zhdanova, I. (2011). Sleep and its regulation in zebrafish. *Reviews in the Neurosciences, 22*, 27–36.