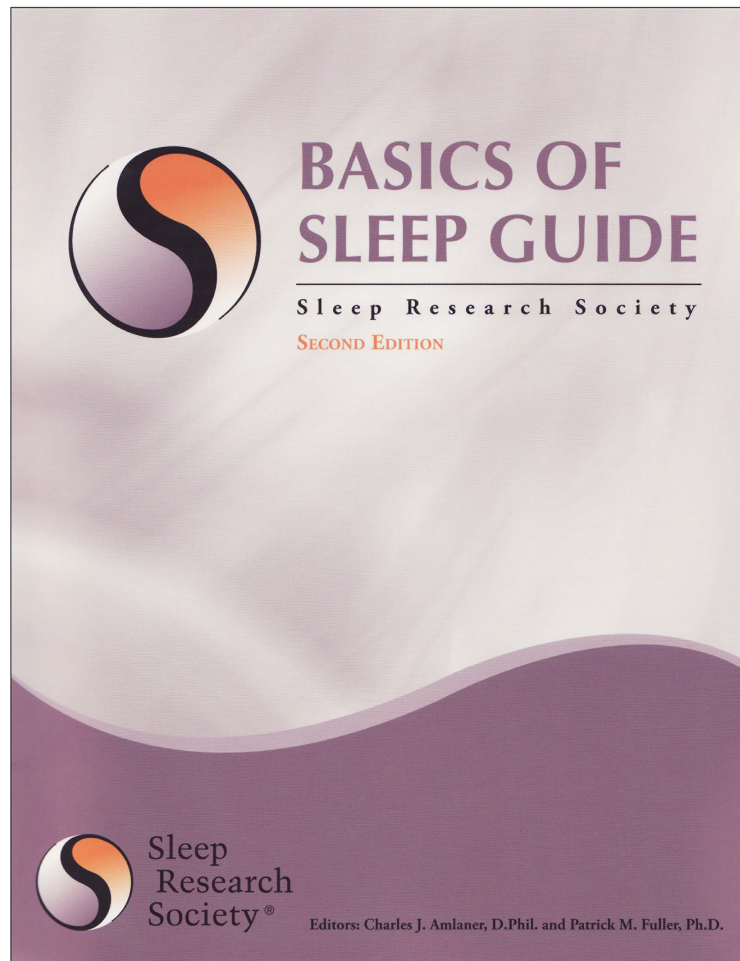


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CHAPTER 1

The Evolution of Sleep

Charles J. Amlaner Jr., DPhil¹; John A. Lesku, PhD²; Niels C. Rattenborg, PhD²

¹Department of Biology, Indiana State University, Terre Haute, IN

²Sleep and Flight Group, Max Planck Institute for Ornithology, Seewiesen, Germany

Corresponding author: Niels C. Rattenborg, PhD

Tel: +49 (0)8157 932 279

E-mail: rattenborg@orn.mpg.de

INTRODUCTION

The function(s) of sleep is an unresolved question in biology.¹ One approach to revealing the purpose of sleep is to trace its evolution. By identifying the type of animal in which sleep first appeared, we might identify the initial trait that caused a need for and presumably benefited from sleep. Furthermore, by tracing the subsequent evolution of sleep, we can determine if additional sleep functions evolved secondarily in conjunction with the evolution of new types of animals with new biological needs that could be fulfilled most effectively or exclusively during sleep. Indeed, our understanding of sleep in humans is likely to be incomplete until we identify both the initial, perhaps cellular function of sleep, and potential secondarily-derived functions linked to the changes in brain activity that occur during mammalian sleep.

Unfortunately, the sleeping brain does not fossilize. Hence, comparative neuroscientists must infer the evolutionary history of sleep from living animals. For instance, studies of fish may reveal clues to how the common ancestor to living amphibians, reptiles, birds, and mammals slept. A fundamental assumption of this approach, however, is that animals living today sleep in the same manner as their ancestors. Although it is impossible to test this assumption directly, in some groups fossilized endocasts of the cranial cavity reveal that gross brain anatomy has changed little over time. For instance, although the cerebrum expanded independently in the mammalian and avian lineages, the gross anatomy of the reptilian brain has changed little over time.² Consequently, depending on the degree to which the neurophysiological characteristics of sleep relate to gross brain anatomy, reptiles may thus provide clues to how early amniotes – the common ancestor to mammals, birds, and reptiles – slept (Figure 1). Ultimately, even if these assumptions are violated, comparisons of sleep across taxonomic groups with divergent neurophysiology, and those occupying unusual ecological

niches may nonetheless be of heuristic value for formulating hypotheses for the function of sleep in humans. For instance, the discovery of unihemispheric sleep in marine mammals (see *Mammalian sleep*) undoubtedly influenced the formulation of functional theories that posit a local role for sleep in synaptic maintenance in the neocortex.^{3,4} Moreover, even within a taxonomic group, such as mammals, where the basic characteristics of sleep are similar across species, relating interspecific variation in the time spent in, and presumably need for, sleep with specific traits might provide clues to the function of sleep. Here, we discuss our current understanding of the evolution of sleep. We also illustrate how understanding the evolutionary history of sleep can help us identify the biological target benefiting from sleep and thereby the functions of sleep.

WHAT IS SLEEP?

Sleep is a behavioral state distinguishable from wakefulness by reduced responsiveness to stimulation.⁵ In contrast to other unresponsive states, such as hibernation, sleeping animals awaken rapidly when sufficiently stimulated. Although most animals are immobile during sleep, dolphins can swim while sleeping with only half of the brain at a time. Sleep behavior is associated with distinct changes in brain activity, although the exact features that correlate with sleep vary across taxonomic groups, and some groups show more than one type of sleep. Finally, following sleep deprivation, animals spend more time sleeping and sleep more deeply, indicating that sleep is homeostatically-regulated.

MAMMALIAN SLEEP

Sleep has been studied most extensively in mammals. Two distinct types of sleep occur in mammals, rapid eye movement (REM) sleep and non-REM sleep. When compared to the low-voltage, high-frequency (or

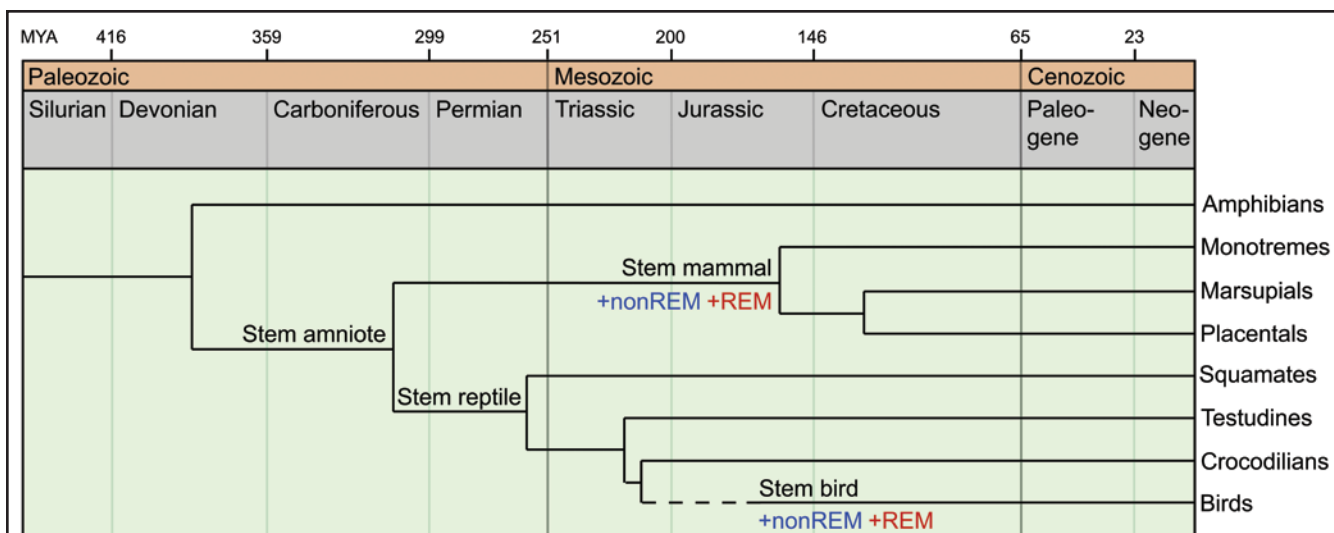


Figure 1: A cladogram for tetrapods showing the evolutionary appearance of non-REM and REM sleep. Time (millions of years ago, MYA) is given at the top of the plot above geological era (orange) and period (grey). Although the precise times of divergence among groups are somewhat ambiguous, the phylogenetic relationships are well-established. The dashed line at the start of the avian lineage reflects the extinct group of non-avian Dinosaurs from which birds evolved. Testudines is a group comprising turtles and tortoises; squamates includes lizards and snakes; the tuatara – the sister-group of Squamata – is not shown. Estimates of divergence times can be found at <http://wikipedia.org>.

activated) electroencephalogram (EEG) observed during wakefulness, non-REM sleep is characterized by high-voltage, low-frequency EEG activity (i.e., slow-waves), often quantified as slow-wave activity (SWA; 0.5 - 4.0 Hz spectral power density).⁵ EEG slow-waves reflect the bistable nature of neocortical neuronal membrane potentials during non-REM sleep.⁶ In contrast to wakefulness and REM sleep wherein neurons remain depolarized, the membrane potentials during non-REM sleep alternate on average once per second between a depolarized “up-state” with action potentials occurring at a rate comparable to wakefulness and a hyperpolarized “down-state” with no action potentials. Corticocortical connections, in conjunction with the corticothalamocortical loop, synchronize the alternation of membrane potentials of large populations of neurons, resulting in large-scale, slow network oscillations detectable as slow-waves in the EEG. The amount of SWA reflects sleep intensity, as it is harder to awaken an animal when SWA is high. Moreover, SWA increases and decreases as a function of time spent awake and in non-REM sleep, respectively, indicating that SWA reflects homeostatically-regulated processes.⁵ Interestingly, SWA can also increase locally in the neocortex in response to local activation during prior wakefulness,⁷ suggesting that SWA reflects restorative functions involved in synaptic maintenance that occur locally in the neocortex.^{3,4}

During REM sleep, the EEG reverts to an activated pattern similar to that observed during wakefulness. REM sleep is distinguished from wakefulness, primarily by reduced responsiveness and muscle atonia, al-

though rapid eye movements and other muscle twitching also occur intermittently. Given the simultaneous occurrence of EEG activation during an unresponsive state of paralysis, REM sleep has also been called paradoxical sleep. Finally, thermoregulatory responses are reduced during REM sleep when compared to wakefulness and non-REM sleep.

Non-REM and REM sleep have been recorded in all placental and marsupial (or therian) species investigated, with the possible exception of cetaceans (dolphins, porpoises and whales; see below).⁸ Although the time spent in each state varies across species, the general characteristics of non-REM and REM sleep are remarkably consistent, suggesting that both states were present in the common ancestor to therian mammals. Studies of sleep in monotremes, a group of egg-laying mammals that last shared a common ancestor with therian mammals 163 to 186 million years ago, provide a window on the early evolution of sleep in mammals. Interestingly, an early EEG-based study found that the echidna (*Tachyglossus aculeatus*) only exhibited non-REM sleep, and thereby suggested that REM sleep evolved after the appearance of the therian lineage.⁹ However, a more recent study suggests that sleeping echidnas exhibit brainstem neuronal activity characteristic of REM sleep in placental mammals, concurrent with neocortical EEG activity characteristic of non-REM sleep.¹⁰ Similarly, during sleep in another species of monotreme – the duck-billed platypus (*Ornithorhynchus anatinus*) – REM sleep-like rapid eye movements and twitching occurred in conjunction with non-REM sleep-

related EEG activity.¹⁰ Although brainstem neuronal activity was not recorded in the platypus, these studies suggest that early mammals exhibited a single heterogeneous sleep state, combining features of REM sleep in the brainstem with features of non-REM sleep in the neocortex, that subsequently became temporally segregated into two distinct sleep states, non-REM sleep and REM sleep with cortical activation. However, a subsequent study reported distinct non-REM and REM sleep (with cortical activation) occurring in the neocortex of sleeping echidnas when they were exposed to ambient temperatures comparable to those experienced in the wild.¹¹ The authors suggested that unnatural temperatures used in the earlier studies prevented those echidnas from exhibiting typical features of REM sleep in therian mammals. This explanation may not fully explain the discrepancy, however, given that the platypus might have exhibited the heterogeneous sleep state when housed under natural temperatures. Moreover, some controversy persists over whether the episodes of REM sleep with cortical activation reported in the echidna reflect REM sleep or quiet wakefulness instead, as arousal thresholds and eye state (open or closed) were not assessed during putative REM sleep.¹¹ Clearly, additional studies are needed to fully characterize sleep in monotremes, and thereby the early stages of mammalian sleep evolution. Regardless, the available evidence indicates that REM sleep in some form was present in the ancestor of all mammals (Figure 1).

Marine mammals exhibit several interesting adaptations to sleeping in the water.¹² Notably, cetaceans, seals in the Family Otariidae, and manatees can engage in non-REM sleep with one cerebral hemisphere at a time, while the other hemisphere remains awake (Figure 2), a trait that evolved independently in each group. In cetaceans, unihemispheric non-REM sleep is the primary type of sleep. Although seals can also engage in unihemispheric non-REM sleep, they usually only show an interhemispheric asymmetry in the level of SWA or bilaterally symmetrical non-REM sleep. Cetaceans can swim and surface to breathe in a coordinated manner during unihemispheric non-REM sleep, and the eye contralateral to the awake hemisphere remains open, thereby allowing cetaceans to visually monitor their environment during sleep.¹² For instance, while swimming continuously along side their mother during the first weeks postpartum, neonatal dolphins (*Tursiops truncatus*) maintain close proximity with their mothers by keeping the eye toward her open, while the other eye is closed. Presumably, unilateral eye closure in neonatal cetaceans is also associated with unihemispheric non-REM sleep, as it is in adults, although this has not been established with neurophysiological recordings.

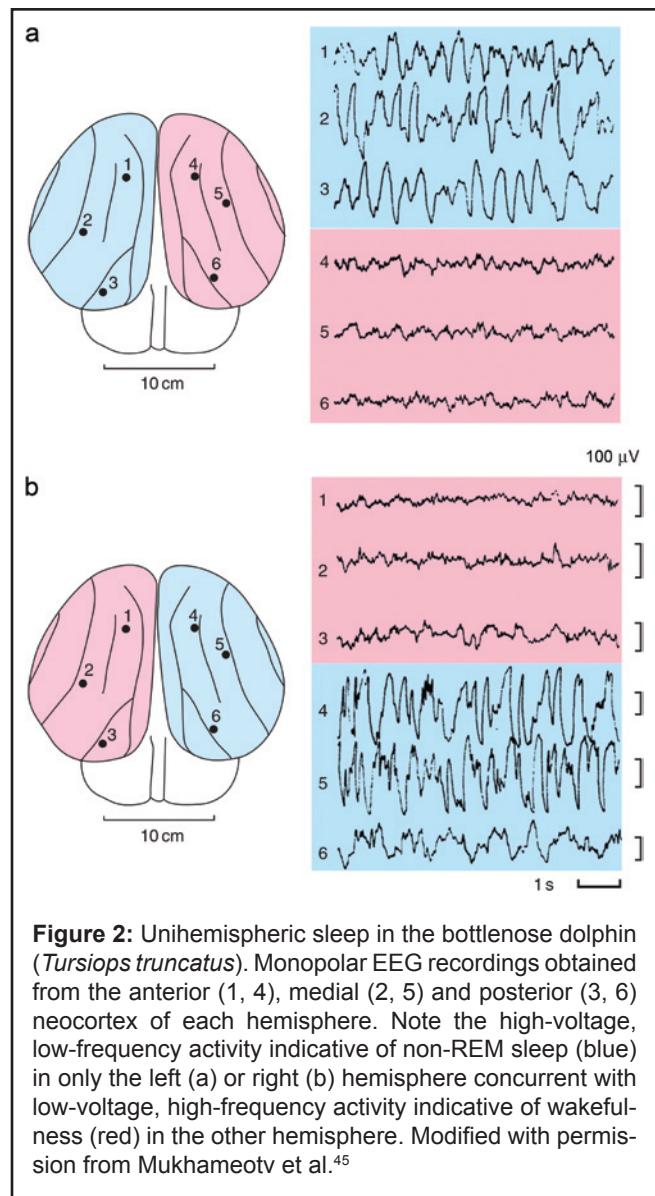


Figure 2: Unihemispheric sleep in the bottlenose dolphin (*Tursiops truncatus*). Monopolar EEG recordings obtained from the anterior (1, 4), medial (2, 5) and posterior (3, 6) neocortex of each hemisphere. Note the high-voltage, low-frequency activity indicative of non-REM sleep (blue) in only the left (a) or right (b) hemisphere concurrent with low-voltage, high-frequency activity indicative of wakefulness (red) in the other hemisphere. Modified with permission from Mukhameotv et al.⁴⁵

In contrast to non-REM sleep, REM sleep is not known to occur unihemispherically in any animal. Interestingly, whereas REM sleep has been recorded in all seals and manatees studied, unequivocal REM sleep has not been found in cetaceans, despite extensive efforts to identify this state.¹² Nonetheless, when sleeping motionless under water, cetaceans show infrequent twitches similar to those observed in terrestrial mammals during REM sleep. Consequently, REM sleep may occur in small amounts or in a modified manner that does not manifest as EEG activation. As previously mentioned, neonatal dolphins swim continuously during their first weeks of life, a time when altricial terrestrial mammals show the most REM sleep.⁸ Assuming that REM sleep does not occur while swimming, this observation seemingly questions whether REM sleep plays a role in early brain development in cetaceans similar to that demonstrated experimentally in terrestrial mammals.¹³ However, REM sleep may still have a role

in early brain development in cetaceans if it occurs primarily *in utero*.

INSIGHTS FROM PHYLOGENETIC ANALYSES OF MAMMALIAN SLEEP

More EEG-based sleep data exist on mammals than any other group of animals. A compendium of this data shows that there is great variation in the time spent in non-REM and REM sleep across species.¹⁴ For example, large hairy armadillos (*Chaetophractus villosus*) spend 16 hours per day in non-REM sleep, whereas horses (*Equus caballus*) spend just 2 hours. A similar range of interspecific variation occurs with the time spent in REM sleep: Virginia opossums (*Didelphis virginiana*) engage in REM sleep for more than 7 hours per day, but sheep (*Ovis aries*) spend just half an hour. If we assume that such interspecific variation reflects underlying differences in the need for sleep, then identifying the evolutionary factors responsible for maintaining such variation should provide insight into the functions of sleep. In addition to identifying unexpected relationships between sleep and various traits, this comparative approach can also be used to evaluate whether the results from experiments obtained from a single or few species can be applied to a broader taxonomic group.

Many studies have used the comparative approach to evaluate theories for the function of sleep.^{14,15} For example, experimental evidence indicates that non-REM and REM sleep play a role in processing memories.¹⁶ However, studies have been performed only on mammalian species of limited phylogenetic diversity (mainly rodents and primates). Thus, it is unclear whether sleep across mammals in general is important in memory processing. If memory processing is a universal function for mammalian sleep (irrespective of the specific mechanism), then species possessing greater cognitive abilities might be expected to engage in more sleep. Indeed, in recent comparative analyses that controlled for pseudoreplication stemming from the inclusion of closely-related species with similar sleep trait values (a confound in earlier analyses), species with greater encephalization – a possible index of interspecific intelligence² – were found to allocate a higher percentage of time spent asleep to REM sleep than those with lower encephalization¹⁴ (but see¹⁷). Although non-REM sleep has also been implicated experimentally in memory processing,⁷ a similar relationship between encephalization and non-REM sleep has not been identified in comparative studies. However, the “time” spent in this state may not be the most neurophysiologically-meaningful metric for non-REM sleep; a combination of time in *and* intensity of non-REM sleep (i.e., cumulative

SWA) may be the more relevant measure. Unfortunately, non-REM sleep intensity has been reported for only a few species. Nevertheless, the relationship between REM sleep and encephalization demonstrates the potential usefulness of comparative analysis as a complement to experimentation.

In addition to its role in memory processing in adults, REM sleep may also serve a role in the development of the central nervous system (CNS). This hypothesis stems from the observation that altricial species – those born relatively immature and dependent on their parents (e.g., cats) – engage in higher amounts of REM sleep at birth when compared to precocial species (e.g., guinea pigs), a pattern that continues in adults.⁸ Specifically, this hypothesis suggests that brain activation occurring during REM sleep provides endogenous stimulation necessary for the normal development of the CNS, including the neocortex.¹⁸ In addition to being supported by experimental evidence,¹³ this hypothesis finds some comparative support in that species more altricial at birth have more REM sleep as adults than more precocial species,¹⁴ although it remains unclear why this difference, most evident at birth, persists into adulthood.

Another noteworthy relationship has bearing on several metabolically-based hypotheses for the function of sleep. Specifically, it has been suggested that the function of non-REM sleep is to reduce energy expenditure by enforcing inactivity and lowering the metabolic rate of an animal.⁸ Indeed, this was one of the early ideas for why mammals and birds, as homeotherms with high energetic demands, are the only animals known to exhibit non-REM sleep¹⁹ (see *Avian sleep*). This hypothesis would seem to predict that species with relatively high metabolic rates should engage in more non-REM sleep. Although this predicted positive relationship has been observed,¹⁵ it is merely a consequence of an ineffective statistical control of body mass. In determining “relative” metabolic rate, some studies used a mass-specific ratio (i.e., basal metabolic rate / body mass); yet this mass-specific value still correlates significantly with body mass indicating an ineffective control.¹⁴ When one re-visits the relationship using a more appropriate residual-based approach, the relationship between relative metabolic rate and the time spent in non-REM sleep is *negative*.^{14,17} Consequently, species with higher relative metabolic rates actually engage in *less* non-REM sleep, a relationship that does not provide broad phylogenetic support for an energy conservation role for sleep or other metabolically-based hypotheses.

A recent comparative study suggests that sleep may influence immune function. Preston et al. found that mammalian species that sleep longer show enhanced

immune defenses and lower rates of parasitism.²⁰ Preston et al. suggest that when compared to short sleeping species, those that sleep longer are able to allocate more energy to maintaining the immune system.

Ecological pressures, such as the risk of predation, can also influence the evolution of sleep.²¹ Indeed, early ecological hypotheses for the adaptive significance of sleep proposed that sleep functions to immobilize animals during times of the day when they cannot safely interact with the environment. However, experimental evidence suggests that the reduction in responsiveness that (in part) defines sleep actually renders animals more vulnerable to predation.^{22,23} Moreover, comparative analyses show that species sleeping in riskier (more open) environments in the wild engage in less REM sleep in the laboratory.¹⁴ This reduction of REM sleep in more vulnerable species might reflect an evolutionary strategy to minimize sleep-related risk, as arousal thresholds can be highest during REM sleep. Alternatively, species more sensitive to disturbance may habituate poorly to the novel laboratory conditions and thus show reduced REM sleep. Regardless of whether this relationship reflects a fixed evolutionary pattern¹⁴ or a plastic physiological response,²² the selective reduction of REM sleep suggests that it is a particularly dangerous state, presumably with benefits that outweigh the risk of predation.

Due to prior technological constraints, the relationships outlined above were based on sleep durations obtained from captive animals. The recent development of techniques for recording the EEG from animals sleeping in the wild will allow researchers to determine whether these relationships also occur in animals sleeping in the ecological context in which sleep evolved.²⁴

AVIAN SLEEP

Despite being more closely related to crocodiles and other reptiles than to mammals, birds exhibit sleep patterns more similar to their distant mammalian relatives. Birds are the only non-mammalian group to exhibit non-REM and REM sleep²⁵ (Figure 1). Non-REM and REM sleep have been found in all species studied (representing 11 taxonomic Orders), although the neurophysiological correlates of sleep have not been examined in paleognaths (ostriches, emus, tinamous, etc.), the most evolutionarily ancient (or basal) lineage of living birds. As in mammals, non-REM sleep is characterized by high-voltage, low-frequency EEG activity. Despite this similarity in non-REM sleep-related brain activity, initial studies in pigeons (*Columba livia*) did not detect a compensatory increase in SWA following long-term sleep deprivation, and thereby suggested that

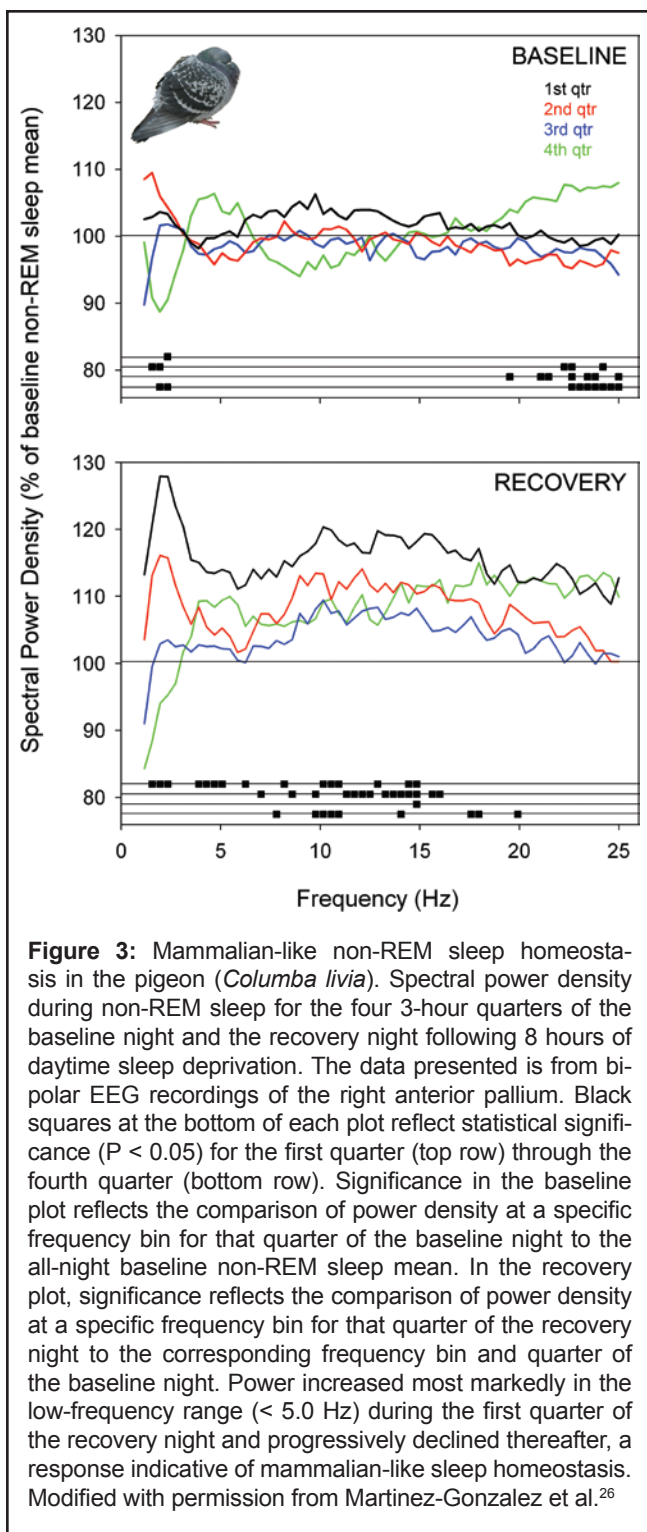
avian non-REM sleep is not homeostatically-regulated, as it is in mammals. However, a recent study of pigeons demonstrated for the first time that SWA during non-REM sleep increases following short-term sleep deprivation in birds²⁶ (Figure 3). Thus avian non-REM sleep is homeostatically-regulated in a manner similar to that observed in mammals, and therefore may serve a similar function in both groups.²⁷

Birds often keep one eye open during non-REM sleep.²⁸ This sleep behavior has been observed in several avian orders, and may predate the evolution of birds, as reptiles can also sleep with one eye open. In birds, unilateral eye closure is associated with an inter-hemispheric asymmetry in SWA, with the hemisphere contralateral to the open eye showing SWA intermediate between the high level occurring in the hemisphere contralateral to the closed eye and the low level that occurs during wakefulness. Birds sleeping in riskier situations increase the time spent sleeping with only one eye open, and direct the open eye toward potential threats.²³ In addition to serving a predator detection function, sleeping with one eye open may allow birds that fly continuously for days, weeks or longer to sleep in flight, although this has not been confirmed with EEG recordings.²⁹

As in placental and marsupial mammals, avian REM sleep is characterized by EEG activation similar to that observed during wakefulness.²⁵ Rapid eye movements, twitching and reduced thermoregulatory responses also occur during avian REM sleep. Although electro-myogram recordings only rarely show mammalian-like hypotonia or atonia during REM sleep, behavioral signs of reduced tone, such as head drooping, often occur. In contrast to mammals, individual episodes of REM sleep are short, typically lasting less than ten seconds. Birds tend to have less overall REM sleep than mammals, although recent studies suggest that songbirds may have more REM sleep than previously recognized.^{30,31} In some, but not all birds, the incidence and duration of REM sleep episodes increases across the main period of sleep, a pattern similar to that observed in mammals.²⁶ Also, as in mammals, avian REM sleep increases following sleep deprivation.²⁷

REPTILES, AMPHIBIANS AND FISH

As the closest living relatives to birds, one might predict that crocodilian reptiles would exhibit similar sleep states (Figure 1). However, crocodilians and other reptiles exhibit sleep states largely unlike those in birds or mammals. Although some controversy persists,^{32,33} studies in crocodilians, turtles, and lizards report an association between sleep behavior and the occurrence



of high-voltage, spikes arising from a background EEG with voltages similar to, or lower than, that occurring during alert wakefulness. Arousal thresholds are higher when spikes are more frequent, indicating that spikes reflect sleep intensity. Moreover, the incidence of spikes increases during recovery following sleep deprivation, suggesting that spikes reflect homeostatically-regulated sleep processes. Pharmacological studies suggest that the spikes observed in sleeping reptiles resemble the hippocampal spikes that occur during non-REM sleep in

mammals. Indeed, recent studies have shown that reptilian spikes originate in the hippocampus and propagate to the dorsal cortex where the EEG is typically recorded in studies of sleep in reptiles. In this respect, reptilian sleep may be evolutionarily homologous with mammalian non-REM sleep. However, sleeping reptiles appear to lack the large-scale, slow synchronous neuronal activity that is the hallmark of non-REM sleep in mammals and birds. This may reflect differences in cortical cytoarchitecture.²⁷ In contrast to the six-layered mammalian neocortex, the three-layered reptilian dorsal cortex lacks the layers with extensive corticocortical connectivity (i.e., layers II and III of the mammalian neocortex) known to be involved in the genesis of slow-waves in mammals. Moreover, the avian hyperpallium (the developmental homologue of the neocortex) also exhibits extensive interconnectivity when compared to the reptilian dorsal cortex. Interestingly, neurons with extensive corticocortical (or palliopallial) connectivity evolved independently in mammals and birds. These differences in interconnectivity may thus explain why mammals and birds, but not reptiles, exhibit high-voltage, slow-waves during sleep.²⁷

The presence of REM sleep in mammals and birds suggests that a similar state might occur in reptiles.³² Although some studies report REM sleep in reptiles – based on the occurrence of eye and limb movements during sleep – it remains unclear whether such behaviors reflect REM sleep-related twitching similar to that observed in mammals and birds, or simply brief arousals from sleep. Moreover, sleeping turtles do not show patterns of neuronal activity in the brainstem comparable to that observed during REM sleep in mammals.³⁴ Consequently, given the available data, reptiles do not appear to exhibit REM sleep. Assuming that reptiles do in fact lack REM sleep, then REM sleep apparently evolved independently in the respective ancestors of mammals and birds (Figure 1).

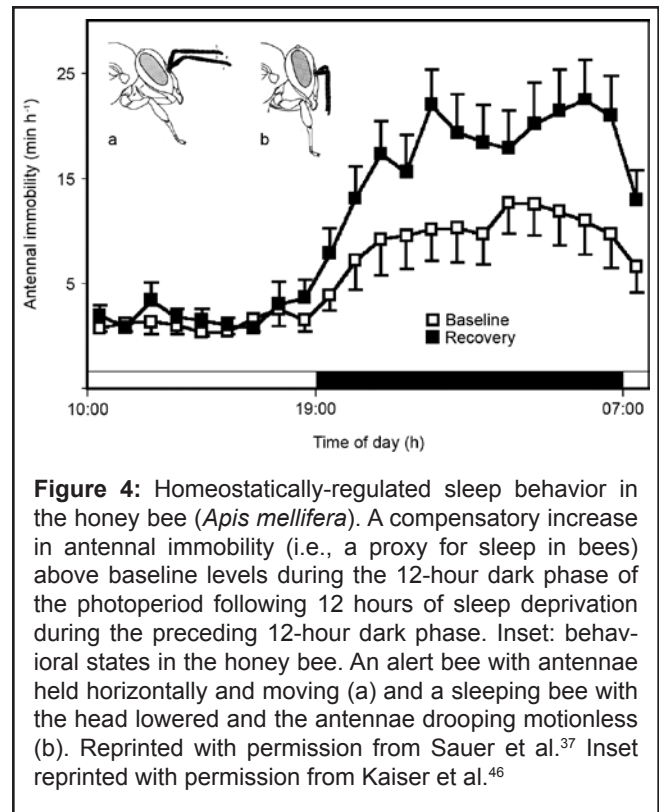
The majority of studies of sleep in amphibians have been done on frogs and toads.³² With the exception of the bullfrog (*Rana catesbeiana*), all studies found behavioral evidence for sleep. The absence of behavioral or neurophysiological signs of sleep in the bullfrog may reflect poor adaptation to the recording environment. The neurophysiological correlates of sleep vary greatly among the other studies on amphibians. Unfortunately, it is unclear whether this variability reflects interspecific differences in sleep or simply methodological differences, such as electrode placement and adaptation to the laboratory. Additional studies are therefore needed to clarify the neurophysiological correlates of sleep in amphibians.

Although relatively few studies have examined sleep in fish, it is clear that at least some species sleep.³² For

instance, zebrafish (*Danio rerio*) exhibit homeostatically-regulated periods of quiescence with reduced responsiveness at night.³⁵ Unfortunately, as in amphibians, the few studies that have investigated the neurophysiological correlates of sleep in fish have revealed conflicting results. Although REM sleep has been reported in some fish based on the occurrence of eye movements during sleep, as in reptiles, it is unclear whether this behavior reflects REM sleep or an unrelated phenomenon. Finally, although it has been suggested that fish that swim continuously do not sleep,³⁶ this has not been confirmed with neurophysiological recordings; they may swim and sleep simultaneously in a manner similar to that observed in cetaceans.

INVERTEBRATES

The development of the fruit fly (*Drosophila melanogaster*) as a genetic model for revealing sleep mechanisms and functions has renewed interest in the study of sleep in invertebrates (see Chapter 11). Early studies identified behavioral signs of sleep, including a compensatory response to sleep deprivation in arthropods, such as cockroaches (*Leucophaea maderae*) and scorpions (Family Scorpionidae).⁵ Subsequently, similar homeostatically-regulated sleep behaviors were reported in *Drosophila* (see Chapter 20) and honey bees³⁷ (*Apis mellifera*; Figure 4). Honey bees are particularly interesting, because they pass through a series of castes (each associated with a specific task in the hive) as they age. A recent study demonstrated that, as in mammals, young bees (cell cleaners) observed within a hive slept longer than older bees (nurses, food storers, and foragers).³⁸ Among arthropods, the neurophysiological correlates of sleep have been investigated in honey bees, *Drosophila* and crayfish. In honey bees, optomotor interneurons showed reduced spontaneous firing rates and reduced responsiveness to visual stimulation at night when the animals exhibited sleep behavior³⁹; this study was the first to characterize sleep-wake changes in CNS activity in an invertebrate. In *Drosophila*, sleep behavior was associated with a decrease in spectral power across all frequencies in local field potential (LFP) recordings obtained from the brain.⁴⁰ This was due largely to the disappearance of high-voltage spikes that occurred during wakefulness. Sleep behavior in crayfish (*Procambarus clarkii*) is associated with a reduction in high-frequency (30–45 Hz) spectral power in brain LFP recordings.⁴¹ Sleep behavior has also been observed in the octopus (*Octopus vulgaris*), although the neurophysiological correlates of sleep in cephalopods remain unclear.⁴² Recently, a sleep-like state has been described in the roundworm (*Caenorhabditis el-*



egans) that occurs primarily during specific stages of development called lethargus.⁴³

SLEEPLESS ANIMALS?

Perhaps the most straightforward approach to understanding the initial evolution and function of sleep would be to identify animals that do not sleep and determine how they differ from animals that do. For instance, theories that propose a role for sleep in synaptic plasticity predict that animals with a non-plastic CNS should not sleep. Although truly sleepless animals have not been described, the report of a sleep-like state that only occurs in *C. elegans* during lethargus, the only time when synaptic plasticity is observed in their simple nervous system, is consistent with this notion.⁴³ Nonetheless, additional studies of animals with simple nervous systems, as well as those lacking a nervous system altogether, are needed to evaluate this and other theories for the initial evolution of sleep.

DISCUSSION

Sleep is ubiquitous among the animals studied to date. This suggests that sleep serves a fundamental function for all animals.¹ Indeed, recent genetic work in *Drosophila* indicates that some sleep-related cellular processes may be highly conserved (see Chapter 11). During the course of evolution, however, it is likely that sleep acquired new functions. Moreover, such

secondarily-derived functions were probably tailored to the specific needs of certain taxonomic groups. In this regard, it is interesting to note that the changes in brain activity that accompany sleep vary across and, in some cases, within taxonomic groups. While it is certainly possible that these differences in sleep-related brain activity simply reflect differences in the manifestation of a functionally similar sleep state, arising from differences in neuroanatomy, they may also reflect differences in the functions of sleep. Consider reptiles, which lack the high-voltage, slow-waves that characterize mammalian and avian non-REM sleep. On the one hand, reptilian sleep might be functionally homologous to non-REM sleep in mammals and birds; the absence of high-voltage, slow-waves may simply reflect the lack of sufficient cortical interconnectivity to generate large-scale, slow network oscillations. However, it is also possible that the slow, network oscillations that emerge from this interconnectivity serve a new function in mammals and birds that does not occur in reptiles. For instance, in addition to evolving non-REM sleep and REM sleep independently from mammals, birds also independently evolved large (relative to body mass), heavily interconnected brains capable of orchestrating complex cognition, in some cases comparable to that exhibited by primates.⁴⁴ Consequently, non-REM and REM sleep may serve functions involved in maintaining adaptive cognition in animals with complex brains.²⁷ The point here is not to evaluate the merits of this specific hypothesis, but rather to simply illustrate how differences in sleep-related brain activity could reflect differences in the functions of sleep. Ultimately, a challenge for future comparative sleep researchers will be to integrate comparative work on the neurophysiological correlates of sleep in vertebrates with that on invertebrates aimed at identifying conserved cellular processes occurring during sleep. Our understanding of the functions of sleep in humans is likely to be incomplete until such a synthesis is realized.

ABBREVIATIONS

CNS = central nervous system
 EEG = electroencephalogram
 MYA = millions of years ago
 REM = rapid eye movement
 SWA = slow-wave activity

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