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Introduction

PATRICK MCNAMARA, CHARLES L. NUNN, AND ROBERT A. BARTON

Why do we and other animals sleep? When we are asleep, we are not performing activities that are important for reproductive success, such as locating food, caring for offspring, or finding mates. In the wild, sleep might make an animal more vulnerable to predation, and it certainly interferes with vigilance for predators. Sleep is found across the animal kingdom, yet it varies remarkably in its most fundamental characteristics across species. And for almost every pattern associated with sleep, exceptions can be found. For all of these reasons, sleep continues to be an evolutionary puzzle. Fortunately, sleep also has attracted much scientific interest, with many significant findings in the past 10 years.

The aim of this volume is to summarize recent advances in our understanding of the diversity of sleep patterns found in animals. Many of the chapters that follow examine sleep in different taxonomic groups, including insects, fish, reptiles, birds, and mammals. We take this “comparative approach” because it is one of the key ways in which biologists investigate the evolution of a trait (Harvey & Pagel, 1991). Indeed, the comparative method has long been used to investigate the evolution of sleep, particularly in mammals (e.g., Meddis, 1983; Zepelin, 1989). More recent comparative studies have capitalized on advances in the study of phylogenetic relationships to test hypotheses on the evolution of sleep (Capellini, Barton, Preston, et al., 2008a; Lesku, Roth, Amlaner, et al., 2006; Preston, Capellini, McNamara, et al., 2009; Roth, Lesku, Amlaner, et al., 2006). In mammals, these studies have revealed that species experiencing greater risk of predation at their sleep sites sleep less, that sleep duration correlates with immunocompetence across species, and that evolutionary increases in metabolic rate relative to body mass are associated with reductions in sleep. By incorporating phylogeny, a recent study also demonstrated that an apparent association between body mass and sleep is in fact a phylogenetic artifact (Capellini et al., 2008a; see also Lesku et al., 2006).

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Other chapters provide syntheses of new advances in our understanding of the physiology and genetics of sleep as well as advances in phylogenetic analysis and informatics. These chapters are essential for uncovering sleep functions because evolution works on the genome, and many aspects of animal biology constrain the types of physiological patterns of sleep that are found across species. For example, marine mammals must continuously come to the water's surface to breath air, and this limits the kind of sleep in which they can engage. Similarly, animals that lack highly developed forebrains will be unable to exhibit classically defined sleep, which includes both behavioral and electrophysiological criteria for mammals and birds. Importantly, the study of interspecies variation requires careful compilation of data collected under diverse conditions as well as the application of comparative methods that use phylogeny to study evolutionary patterns. All of these components are essential for making sense of the variation in sleep patterns across species, and thus also for uncovering the function – or functions – of sleep.

In most cases, chapters in this volume have integrated taxonomic perspectives and details on sleep physiology, natural history, and genetics. Such integration is essential to understand sleep and to stimulate future comparative and evolutionary studies of sleep. We see the need for new comparative studies in a broader phylogenetic perspective – as well as experimental research – as a way to assess the generality of sleep patterns and the factors that influence sleep. Much of this effort will require laboratory and fieldwork to obtain new quantitative data on sleep in relatively unstudied animals, such as fish, insects, and reptiles. Even in the case of mammals and birds, sleep has been quantified in remarkably few species and often on the basis of the availability of particular species rather than in relation to specific questions concerning sleep and its evolution. We hope that this volume will spur more research along these lines.

To help set the stage for what follows, it is helpful to briefly review basic characteristics of sleep that are essential for studying sleep in comparative perspective. An important starting point involves the definition of sleep. As summarized in Table I.1, sleep is composed of behavioral, physiological, and electrophysiological characteristics as well as evidence for homeostatic regulation (i.e., sleep rebound). Behavioral measures of sleep vary according to the biology of the species involved. These measures can include a species-specific body posture and sleeping site, reduced physical activity (quiescence), reduced muscle tone (especially neck/nuchal muscle tone in rapid-eye-movement [REM] sleep), and increased arousal threshold. To distinguish the quiescent state from other states, such as coma or hibernation, it is usually required that the animal shows rapid reversibility to wakefulness upon arousal. Electrophysiological measures of REM include low-voltage fast waves, rapid eye movements, theta rhythms in the hippocampus, and pontine-geniculo-occipital (PGO) waves. Electrophysiological measures of

Table I.1. *Criteria for the definition of sleep*[a]

1. Behavioral
    - Typical body posture
    - Specific sleeping site
    - Behavioral rituals before sleep (e.g., circling, yawning)
    - Physical quiescence
    - Elevated threshold for arousal and reactivity
    - Rapid state reversibility
    - Circadian organization of rest–activity cycles
    - Hibernation/torpor
2. Electrophysiological
    EEG
        NREM: high-voltage slow waves (quiet sleep)
            - spindles in some animals
            - K-complexes in some primates
        REM: low-voltage fast waves (REM, Paradoxical sleep or AS [active sleep])
            - hippocampal theta; PGO waves
    Electro-oculogram (EOG)
        NREM: absence of eye movements or slow, rolling eye movements
        REM: rapid eye movements
    EMG
        - Progressive loss of muscle tone from Wake→NREM→REM
3. Physiological
    - REM: instabilities in heart rate, breathing, body temperature, etc.; penile tumescence
    - NREM: reduction in physiologic/metabolic processes; reduction of about 2°C in body temp
4. Homeostatic regulation
    - enhancement of sleep time
    - intensification of the sleep process (e.g., enhanced EEG power in the Delta range)

[a] Adapted from Moorcroft, 2003; Campbell & Tobler, 1984.

non-rapid eye movement (NREM) include high-voltage slow waves (HVSW), spindles, and K-complexes. Functional indices of sleep include increased amounts of sleep after sleep deprivation, and increased sleep intensity after sleep deprivation. Physiologic indices of sleep include significant reductions in temperature and metabolism during NREM and significant lability in autonomic nervous system (ANS), cardiovascular, and respiratory measures during REM, along with increases in metabolism. Lastly, as noted earlier, sleep typically involves a rebound effect, in which a sleep-deprived animal must make up for lost sleep by sleeping longer or more deeply.

For most animals, sleep can be identified only via measurement of its behavioral and functional sleep traits, as their nervous systems do not support what has become known as full polygraphic sleep – that is, electrophysiological measures of both REM and NREM sleep identified via the electroencephalogram or EEG. It has become common, however, to use the term "full polygraphic sleep" to refer to an animal that exhibits most or all of the other three major components of sleep in addition to the electrophysiologic measures. When an animal exhibits all four major components of sleep – including the behavioral, electrophysiological, physiological, and functional components – then it is said to have full polygraphic sleep. Full polygraphic sleep in this sense has so far been documented only in mammals and in birds. Although REM and NREM have been identified in 127 mammalian species representing 46 families across 17 orders (McNamara, Capellini, Harris, et al., 2008), NREM in most of these species cannot be differentiated into distinct "light" and "deep" stages as it is in several primate species. We estimate that REM and NREM sleep states have also been documented in about 36 avian species.

Overview of the volume

Krueger's chapter focuses on the neural basis of sleep. He suggests that core sleep characteristics are a property of small groups of neurons, and he summarizes the accumulating evidence that sleep is a network-emergent property of any viable group of interconnected neurons. Many biochemical sleep-regulatory events are shared by insects and mammals, suggesting that they evolved from metabolic regulatory events and that sleep is a local use-dependent process. Relationships between sleep and tumor necrosis factor (TNF) are used to examine the local use-dependent sleep hypothesis. Krueger argues that the need for sleep is derived from the experience-driven changes in neuronal microcircuitry that necessitate the stabilization of synaptic networks to maintain physiological regulatory networks and instinctual and acquired memories.

Hartse provides an overview of sleep in insects. Her work necessarily probes the definition of sleep while also giving some context to natural sleeping patterns in insects. An important discovery in the past two decades is that insects can serve as a model organism for studying sleep. She reviews the literature on sleep in *Drosophila* and the role of such studies in understanding sleep as a general phenomenon. Many insects, in fact, display all of the standard behavioral phenomena of sleep, such as periodic reduction in activity, increase in arousal threshold when quiescent, and rebound or increased rest–sleep durations after sleep deprivation.

Tucci and Nolan review the genetics of sleep in mice. They highlight the importance of understanding the genetic mechanisms of sleep – for example, by identifying functional genes. Mouse models of sleep disorders are also extremely useful for probing potential functional effects of sleep-related genes. Current progress

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in mouse functional genetics promises to increase the rate of discovery of sleep-related genes. There can be little doubt that basic sleep processes are influenced by genes, and it may be that separate sets of genes regulate expression of REM and NREM in mammals.

Chapters by Zhdanova and Kavanau review the literature on sleep in fishes. Fish are an ancient lineage and exhibit extensive variation in behavior and ecology. Resting behavior in fish shares several similarities with mammalian sleep. The behavioral criteria for sleep, such as periodic reduction in activity, increase in arousal threshold, and rebound after sleep deprivation are common in fish. Similarly, the principal neuronal structures involved in mammalian sleep, with the notable exception of the cerebral cortex, are conserved in fish and have neurochemical composition similar to that of higher vertebrates. In her studies of zebra fish, Zhdanova demonstrated both increased duration of sleep and changes in plasticity and behavioral performance following sleep deprivation.

Kavanau focuses on the phenomenon of schooling in fishes and the effects of schooling on sleep. Kavanau points out that by virtue of the rich variety and great permissiveness of aquatic habitats, some fish appear never to have encountered selective pressures for sleep. It is remarkable that three continuously active states of perpetual vigilance exist in these fishes, in which they achieve comparable, and even greater, benefits than accrue to animals that sleep. Even some continuously active but nonschooling fishes (some “pelagic cruisers”) probably achieve highly efficient brain operation at all times, illustrating the exceptional demands of pelagic environments (open oceans).

Rial et al. review sleep processes in reptiles. While behavioral signs of sleep are clearly observable in reptiles, correlations between these behavioral signs of sleep and selected EEG indices are difficult to evaluate, given the complexities of recording sleep EEGs from the reptilian scalp and brain. Early studies of reptilian sleep reported an association between behavioral sleep and intermittent high-voltage spikes and sharp waves recorded from various brain structures in crocodilians, lizards, and turtles. Other investigators found no such association between behavioral sleep and high-amplitude spikes and sharp waves in the same animals. Rial et al. propose that mammalian sleep is a residual of reptilian waking states that were shunted aside when new cortical-based waking states became possible in early mammals.

Because birds and mammals exhibit electrophysiological signs of both REM and NREM while reptiles do not, sleep processes in birds and mammals may reflect common descent from a reptilian ancestor with similar sleep patterns. Alternatively, similar sleep processes of birds and mammals may be due to convergent evolution. Convergent evolution would suggest that similar sleep patterns of birds and mammals occur because these animals developed a similar solution to a common problem. Both birds and mammals are endothermic species. Sleep processes are implicated in temperature regulation, at least in mammals, and therefore the evolution of similar REM and NREM sleep processes in birds and mammals may be due to the emergence of the need for complex thermoregulatory processes to support endothermy in these animals.

Rattenborg and Amlaner review the literature on sleep in birds. As in mammals, birds can either sleep with a monophasic pattern (one consolidated period of sleep per day) or a polyphasic pattern (several short episodes of sleep per day). Birds also appear to exhibit a special form of slow-wave activity (SWA) and very little REM-like sleep. As in aquatic mammals, unilateral eye closure and unihemispheric slow-wave sleep (USWS) also occur in birds. Rattenborg and Amlaner first describe the basic changes in brain activity and physiology that accompany avian SWS and REM sleep. The unihemispheric nature of avian sleep is emphasized and reduction in sleep expression in migratory birds is considered. Rattenborg and Amlaner note that SWS-related spindles and hippocampal spikes, and the hippocampal theta rhythm that occurs during mammalian REM sleep, have not been observed in birds, even though they are readily detectable in epidural EEG recordings from the mammalian neocortex. They propose that the evolution of similar sleep states in mammals and birds is linked to the convergent evolution of relatively large and highly interconnected brains capable of complex cognition in each group.

Thakkar and Datta review the evolution of REM sleep. There is no evidence to suggest that REM sleep is present in invertebrates. Within the vertebrates, there is no evidence that supports the presence of REM sleep in fishes or amphibians. Some weak evidence exists to indicate the presence of REM sleep in reptiles, but further detailed studies are necessary before it can be concluded with any certainty that REM sleep is present in reptiles. REM sleep is definitely found in birds, marsupials, and mammals. However, major differences exist between avian and mammalian REM sleep. As compared to mammals, for example, REM bouts are shorter and the total amount of time spent in REM sleep is much smaller in birds than in mammals. These differences between birds and mammals may provide clues about the function of REM sleep.

The chapters by Capellini et al. and Nunn et al. utilize recent advances in phylogenetic methods in their analyses of the adaptive function of sleep in mammals and primates, respectively. Phylogenetic comparative analyses provide a means to reconstruct ancestral states, examine correlated evolution, and identify variation in how traits change over time. Capellini et al. review their work on the links between ecology and sleep in mammals. They show that predation pressure, trophic niche, and energy demands can, in part, explain patterns of interspecific variation in mammalian sleep architecture. Thus, the ecological niche that animals inhabit can exert significant evolutionary pressure on sleep durations as well

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as on how sleep is organized across the daily cycle. Nunn et al. focus on primate sleep, using a taxonomic subset of data that was analyzed by Capellini et al. They reconstruct the evolutionary history of primate sleep, use the data to investigate the function of sleep in primates, and pinpoint species in need of further research. In one new finding, Nunn et al. show that nocturnal species have longer sleep durations than do diurnal species.

McNamara and Auerbach discuss evolutionary medicine as a relatively new field of inquiry that attempts to apply findings and principles of evolutionary anthropology and biology to medical disorders. Although several medical disorders have been explored from the perspective of evolutionary medicine (see the collection of papers in Trevathan, Smith, & McKenna, 1999, 2007), sleep disorders have not so far been among them. This gap should be seen as an opportunity, as application of evolutionary theory to problems of sleep disorders may yield significant new insights into both causes and solutions of major sleep disorders. McNamara and Auerbach note that natural selection operates on the intensity dimension of sleep and thus that insomnia can be construed as resistance to homeostatic drive. Disorders involving excessive amounts of sleep, on the other hand, appear to be the result of chronic immune system activation.

Lacunae

A single volume cannot possibly cover all the dimensions of sleep across the tree of life or in the context of new advances in understanding sleep genetics and physiology. It is worth mentioning two areas that are not covered in this book: sleep in aquatic mammals and the phenomena of hibernation and torpor.

Sleep in aquatic mammals was recently the focus of a comprehensive review (Lyamin, Manger, Ridgeway, et al., 2008) and so is not covered here. Aquatic mammals include cetaceans (dolphins, porpoises, and whales), carnivores (seals, sea lions, and otters), and sirenians (manatees). These species are important because they depart from the typical patterns of mammalian sleep, for the obvious reason that they must come to the surface to breathe. Cetaceans exhibit a clear form of unihemispheric SWS (USWS). EEG signs of REM are absent, but cetaceans show other behavioral signs of REM, including rapid eye movements, penile erections, and muscle twitching. The two main families of pinnipeds, Otariidae (sea lions and fur seals) and Phocidae (true seals), show both unihemispheric and bihemispheric forms of sleep. Phocids sleep underwater (obviously holding their breaths) while both hemispheres exhibit either REM or SWS. Amazonian manatees (*Trichechus inunguis*) also sleep underwater, exhibiting three sleep states: bihemispheric REM, bihemispheric SWS, and USWS. Both hemispheres awaken when the animal surfaces to breathe.

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Departures from the typical mammalian pattern provide an opportunity to test specific functions of sleep. For example, sleep deprivation in an animal exhibiting unihemispheric sleep has been shown to result in unihemispheric sleep rebound, prompting some authorities to claim that sleep serves a primary function for the brain rather than the body. The data on unihemispheric sleep in marine mammals also suggest that REM and NREM serve distinct functions, as animals without full polygraphic REM can survive. In addition, when REM occurs in marine mammals, it is always bihemispheric. The bilateral nature of REM may be considered one of its costs, and the brain structure of certain marine mammals, apparently, cannot bear these costs.

Hibernation and torpor are not typically considered part of the definition of behavioral sleep – yet intuitively most investigators feel that hibernation and torpor are states closely related to sleep. Several orders of mammals contain hibernating species or species that enter torpor, including the monotremes (echidna), the marsupials (mouse opposum), insectivores (hedgehog), bats (brown bat), primates (dwarf lemur), and some rodents (Kilduff, Krilowicz, Milsom, et al., 1993). Contrary to popular belief, bears are not true hibernators. During winter their body temperature does not decrease beyond the level of normal sleep, and the bear remains alert and active in its den. Typically it is the pregnant female who retires to the den for the entire winter. She gives birth to her cubs and nourishes them, often while in a state of sleep. To accomplish this feat, she bulks up during the feeding season and lives off fat reserves during the winter.

Interestingly, a hibernation bout is entered through slow-wave sleep (SWS), which thus suggests that some links exist to physiological processes involved in sleep. Body temperature drifts to ambient temperature until it is below 10°C. Metabolism shifts to lipid catabolism in a kind of slow starvation. Both REM sleep and wakefulness are suppressed. Interestingly, animals arouse from hibernation and promptly go into SWS, suggesting to some investigators that the hibernating animal is in fact sleep-deprived! Whatever the function of hibernation, the fact that the hibernator regularly arouses to go into SWS suggests that the function of SWS may not simply be to conserve energy, as hibernation would be a more efficient way to conserve energy.

Future directions

Further comparative and field research are needed to improve our understanding of sleep. In particular, it remains unclear whether ecological correlates of sleep durations found in well-studied groups, such as mammals, also account for patterns of sleep in other groups, such as birds, insects, reptiles, and fish. Similarly, more studies are needed on the links between sleep cycles, number of sleep bouts per day, and ecology as well as whether consolidating sleep into a single uninterrupted time period provides more efficient acquisitions of the benefits of sleep (Capellini, Nunn, McNamara, et al., 2008b). Other gaps in our knowledge include the effects of environmental seasonality on circadian rhythms and sleep, the links between sleep and infection in wild animals, quantification of the "opportunity costs" of sleep, and better understanding of how ecological factors constrain sleep. In the latter case, for example, could it be that the great energy requirements of some of the largest dinosaurs would have eliminated their opportunity for sleep? Models of sleep ecology coupled with digestive physiology could help to shed light on this question.

Another critical area for future research involves measures of sleep intensity. This could be achieved by tabulating those studies that provide quantitative data on SWA. Intensity indexes physiological need and is thus a target of natural selection. Avian sleep is similar to mammalian sleep in many ways except that SWA alone may not index sleep intensity in avian species as accurately as it does in mammalian species. Thus, a comparison of intensity expression in mammals versus birds may reveal potential additional sleep factors (e.g., depth or length of the sleep cycle) that are required for restorative effects of sleep in birds. Similarly, there is currently little understanding of what can be termed the evolutionary architecture of sleep: how variations in the physiological intensity of sleep, the length of sleep cycles, the length of sleep bouts and daily sleep durations, all interrelate. The determination of this architecture should lead to greater understanding of how constraints on overall sleep durations are accommodated at a physiological level.

Sleep function remains an enigma of modern biology. This is especially surprising in view of the substantial time animals and humans spend in this distinct physiological state, major similarities in its behavioral manifestations observed in different species, and typically deleterious effects of sleep deprivation on behavioral, autonomic, and cognitive functions. Although all this attests to sleep being a basic necessity, the question of whether sleep function is single and universal among diverse taxa remains to be determined. To reveal such common function requires in-depth investigation of the sleep processes in phylogenetically distant organisms that are adapted to different environments.

The study of variation in sleep expression among human populations also needs attention. It is likely that sleep duration, sleep phasing, and sleep expression varies dramatically across cultures, yet very few reliable data exist on this matter. Sleep of hunter-gatherers likely differs substantially from sleep of city dwellers in industrialized nations, for example. Surely ecologic conditions of a culture impacts sleep expression in that culture.

One last critical area for future research involves the collection of new data on sleep from wild mammals and birds. Most of the data in existing comparative

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databases comes from laboratory animals subjected to conditions different from those in the wild. Just as we might imagine that our own sleep would vary considerably if we were forced to sleep in the wild without shelter, easy access to food, or clothing, so can we imagine that animals will sleep differently when brought into conditions that are both more stressful (e.g., in terms of restraints or constant lighting) and less stressful (e.g., with constant access to food). Recent advances in EEG data loggers are providing new opportunities to collect data from wild animals that are ranging freely in their natural habitats (Rattenborg, Martinez-Gonzalez, & Lesku, 2009; Rattenborg, Martinez-Gonzalez, Lesku, et al., 2008; Rattenborg, Voirin, Vyssotski, et al., 2008). As these breakthrough methods are applied to more species of animals, we are likely to code at least some species as having different sleep durations. It will be interesting to see if new estimates of sleep from wild animals lead to different conclusions in comparative tests.

In summary, the study of sleep is at an exciting stage. Together with advances in the genetics and physiology of sleep, our understanding of sleep in different taxonomic groups is finally providing some answers to the question: Why do we sleep? Future research will undoubtedly build on the research synthesized here and elsewhere, and perspectives on functional aspects of sleep expression will change as this field of research develops.

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