HHS Public Access

Author manuscript

Trends Neurosci. Author manuscript; available in PMC 2022 January 18.

Published in final edited form as:

Trends Neurosci. 2008 April ; 31(4): 208–213. doi:10.1016/j.tins.2008.02.001.

Do all animals sleep?

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Abstract

Some animals never exhibit a state that meets the behavioral definition of sleep. Others suspend or greatly reduce ‘sleep’ behavior for many weeks during the postpartum period or during seasonal migrations without any consequent ‘sleep debt.’ Rats die from one form of sleep deprivation, but sleep loss has not been shown to cause death in well-controlled studies in other vertebrate species. Some marine mammal species do not show evidence for REM sleep, and convincing evidence for this state in reptiles, fish and insects is lacking. The enormous variation in the nature of rest and sleep states across the animal kingdom and within the mammalian class has important implications for understanding the evolution and functions of sleep.

Introduction

An assumption made by many is that all animals sleep or that all animals with nervous systems sleep. A Google search for the phrase ‘all animals sleep’ brings up 3090 hits. A Google search for the phrase ‘do all animals sleep’ brings up only 327 hits, and many of these answer the question in the affirmative. Many neuroscientists and sleep researchers [1] have assumed (without, I would contend, good evidence) that all animals sleep. A further assumption is that sleep deprivation is lethal. Together, these two assumptions suggest that a universal, vital function is accomplished in sleep.

Defining sleep

We all understand what it means to be asleep, but it is not always obvious whether observed animals are experiencing the same state. Sleep must be distinguished from circadian changes in alertness controlled by the suprachiasmatic nucleus and other body clocks. Most animals need to adjust their activity to optimal conditions of prey availability, predator threat, sexual opportunities, temperature and other variables affecting survival that vary with time of day. Hence, even when completely sleep deprived, most animals exhibit a marked circadian rhythm of alertness and activity, and reduced responsiveness and inactivity. The presence of such periods of reduced activity and alertness cannot be assumed to be sleep. Sleep persists in animals in which circadian rhythms have been eliminated [2]. It is the summation of the circadian and homeostatically regulated sleep processes that determines our alertness [3]. Sleep must be distinguished from hibernation and torpor, states that have distinct

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physiological correlates. It is also very important to distinguish sleep from rest, a state of reduced activity without loss of consciousness or greatly reduced responsiveness.

Sleep is generally defined as a rapidly reversible state of immobility and greatly reduced sensory responsiveness. An important further criterion is that sleep is homeostatically regulated, namely that lost sleep is made up with an increased drive for sleep and a consequent ‘sleep rebound.’

It would appear to be highly maladaptive for animals to be driven to make up for lost sleep at a time of danger and stress unless some vital function was being subserved. Indeed, it has often been asked why some animals have not evolved a quiet waking state as a substitute for sleep. Surely it would be more adaptive to reduce activity and maintain vigilance. As we shall see, a survey of the literature reveals that evolution might well have produced species that have states that can be better described as quiet waking than as sleep.

Two types of sleep have been identified in mammals, non-REM sleep (slow-wave sleep) and REM sleep. At the neuronal level, non-REM sleep is characterized by greatly reduced activity in brainstem systems [4,5]. Forebrain neuronal activity rates are reduced below those of quiet waking, although the predominant change is from irregular discharge patterns to a rhythmic pattern of discharge. Reflecting this, high-voltage slow waves and spindles are present in the neocortex [6]. Cortical release of acetylcholine is minimal during non-REM sleep [7].

The human brain consumes more than 20% of the body’s energy usage in quiet waking, ten times the amount that would be predicted by its relative weight and not substantially less than it consumes while engaged in difficult cognitive tasks [8]. During non-REM sleep, forebrain metabolic activity is reduced far below the level in quiet waking [9]. This reduction in brain metabolic rate can make a significant contribution to reduction in the body’s overall energy consumption.

In contrast to non-REM sleep, REM sleep is characterized by a pattern of discharge that closely resembles that of waking in most brain regions. Brainstem neurons are highly active at rates often equal to or exceeding rates in active waking [5]. Cortical neurons also show a waking pattern of activity, with the electroencephalogram (EEG) in many species being indistinguishable from that of waking [4].

Therefore, mammalian sleep can be accompanied by either high- or low-voltage cortical activity. Conversely, although waking is usually characterized by low-voltage cortical activity, it can be accompanied by a high-voltage EEG similar to that seen in non-REM sleep [10]. Despite the similarity of REM sleep brain activity to the waking pattern, the loss of environmental awareness that characterizes non-REM sleep is also present in REM sleep. Although most neurons behave similarly in REM sleep and waking, noradrenergic, serotonergic and histaminergic neurons, which are tonically active throughout waking states, are silent in REM sleep. These cell groups also greatly reduce activity in non-REM sleep. The reduction in activity of the noradrenergic neurons has been linked to the reduction in muscle tone that occurs in REM sleep, whereas the reduction in activity of the histaminergic neurons has been related to the loss of consciousness occurring in sleep [11].

Sleepwalking and related pathological ‘dissociated states’ seen in humans are neither normal sleep nor normal waking [12]. They regularly lead to severe injuries if there is no intervention and would exert a substantial negative selection pressure in the wild.

The elevation of sensory thresholds that we use to define our sleep is not absolute. When we sleep, we are not aroused by household noises, tactile stimulation and smells that we would attend to during the day. However, we can often hear our baby cry, the opening of the front door and other significant sensory stimuli. Sensory response thresholds also vary within waking. We can be inattentive or immobile for long periods without being asleep. Vigorous exercise will tend to produce a ‘rebound’ of inactivity without being perceived by the subject or observers as sleep. Although eye closure is correlated with sleep, individuals can close their eyes for long periods of time with completely unimpaired consciousness. These phenomena must be kept in mind in evaluating evidence for sleep in animals.

Sleep deprivation

In a classic series of studies, Rechtschaffen and colleagues demonstrated that sleep deprivation in rats produces a consistent behavioral and physiological syndrome leading to death within 2–3 weeks [13]. The deprivation procedure did not completely eliminate sleep, but rather interrupted and reduced it by 70%–90% compared to controls who lost 30%–40% of their baseline sleep [14,15]. Deprivation greatly increased body temperature and food intake, but weight fell rapidly. A stereotyped pattern of fur discoloration and skin lesions occurred. Finally, body temperature fell and death followed. No similar syndrome has been described in mice or other mammals commonly observed in laboratories, or in rats’ sleep deprived by other means. Sleep deprivation in pigeons by the same technique used in rats is not lethal and produces none of the metabolic and thermoregulatory changes observed in rats [16]. Human sleep deprivation for as long as 11 days and chronic sleep restriction does not produce even the earliest signs of the autonomic changes seen in rats undergoing sleep deprivation by the ‘disk-over-water’ technique. Body temperature tends to fall in sleepy humans, rather than rising as it does in the initial stages of sleep deprivation in rats [17,18]. Humans whose sleep is reduced for long time periods tend to gain weight, rather than lose weight as rats do under 70%–90% sleep deprivation conditions [19]. Fatal familial insomnia, a rare genetic condition reported in humans, is not analogous to the disk-over-water method of sleep deprivation [13] because it is characterized by massive brain degeneration and autonomic dysregulation [20].

Sleep rebound

If we reduce our sleep for 1 or 2 h, we will be sleepy the next day and when allowed to sleep will repay this ‘sleep debt’ by significantly increasing sleep time. Most studies of human sleep deprivation have reported that this ‘rebound’ sleep is disproportionately made up by increased amounts of slow waves during sleep [21]. However, in rats and pigeons, the effects of long-term sleep deprivation can be completely reversed by a rebound made up almost entirely of REM sleep [13,16]. There appears to be some common function served by these two very different patterns of brain activity.

Sleep in simple organisms

To my knowledge, there has been no claim of sleep occurrence in unicellular organisms. However, there is ample evidence that some cyanobacteria, protists, euglenozoa and dinoflagellates show circadian rhythms of activity [22]. There are more than 400 000 unicellular species [23].

Sleep in insects

It has been shown that cockroaches, bees and scorpions have quiescent behaviors with elevated arousal thresholds (reviewed in Refs. [24,25]). Rest deprivation, studied in cockroaches, did not produce a significant or consistent increase in rest time during the recovery period [25], although it did produce increases in metabolic rate, with all effects being critically dependent on the exact parameters of the stimulation used to arouse them [26]. Circadian changes in sensory response thresholds have been documented in bees [27,28]. Changes in certain movement parameters were reported after disturbance of the quiescent state in bees, although no increase in rest duration was noted [28]. *Drosophila* appear to show a behavioral state which satisfies all the behavioral criteria of sleep [29,30]. In this case, as in the other non-mammalian species, it is unclear whether the *Drosophila* state that meets criteria for sleep is homologous or analogous to the sleep state experienced by humans. Clearly the anatomical and some of the neurochemical properties of sleep cannot exist in insects, because of the differences in the structure of their nervous systems. No claims of insect REM sleep have been made. There are more than 700 000 insect species [23].

Sleep in fish

There are more than 30 000 species of fish [23]. They vary in size, diet and ecological specialization. Fewer than 10 fish species have been examined for rest or sleep behavior in laboratory studies.

In studies of rest/sleep-like activity of the zebrafish (*Danio rerio*), circadian variations in responsiveness and activity and decreased response to stimuli were seen after rest deprivation, leading the authors to conclude it was a ‘sleep-like’ state [31,32]. The state characterized as ‘sleep’ could be completely blocked for long periods by light, with no evidence of subsequent rebound [31]. Zebrafish with a null mutation of the receptor for the peptide hypocretin have a substantial decrease in sleep behavior, the opposite of the syndrome seen with loss of this receptor in mammals [33]. The anatomy of systems known to have a major role in sleep–waking control in mammals is radically different in zebrafish [31].

Activation of the perch (*Cichlosoma nigrofasciatum*) by light during the normally inactive period produced an increase in rest behavior during the subsequent 12 h period [34]. As the authors point out, these effects could be due to the stimulatory effects of light rather than the induced motor activation. No evidence for elevated response threshold during the ‘rest’ state in baseline or rebound conditions was presented and the authors do not claim to have demonstrated the presence of sleep. In another study, activity of a school of *Tilapia*

mossambica was monitored and a smaller response to electrical stimulation was noted during inactive periods. A study of several species of coral reef teleosts reported continuous daytime activity and continuous nighttime activity termed ‘sleep swimming’ [35].

Sleep in amphibians

A detailed study of activity and responsiveness in the bullfrog *Rana catesbeiana* (Figure 1), a diurnally active species, concluded that although levels of activity varied in a circadian pattern, the animals were *more* responsive during periods of inactivity than when they were active. It was suggested that these animals, which are highly vulnerable to predation, ‘have survived only because they rest without loss of vigilance,’ and it was concluded that they do not sleep [36]. By contrast, a similar study of the tree frog *Hyla septentrionalis* by the same investigator concluded that this species slept [37]. No evidence of REM sleep was seen in either species. In both species of frogs, forebrain EEG is at maximum voltage during alert active states and at minimum voltage during rest states, reminding us that rest and sleep states are not universally associated with high-voltage cortical activity and must ultimately be defined behaviorally. There are more than 6000 amphibian species.

Sleep in reptiles

There have been several reports claiming to see a REM sleep-like state in reptiles, but other reports have come to the opposite conclusion even after studies of the same species [38-43]. These discrepancies might be a result of the difficulty of equating observable physiological changes in reptiles with those in mammals, so that in some cases it has been concluded that REM sleep exists in the absence of eye movement or muscle tone suppression. In these and other cases, it was unclear whether episodes labeled REM sleep were adequately distinguished from waking.

In the turtle, behavioral quiescence is accompanied by a 29% reduction in response probability and a 0.44 s increase in response latency, and the EEG correlates of quiescent behavior increased after disruption of quiescent states [44]. In a direct search for the neuronal activity pattern defining REM sleep, we recorded neuronal activity in turtles. There was no periodic activation of brainstem neuronal activity during quiescence resembling that seen in REM sleep [5,45]. Rather, there was a general and marked reduction in neuronal activity immediately upon cessation of waking activity, with little further reduction during extended periods of inactivity. Although 30–80 ms duration EEG spikes were sometimes seen during quiescent states, no forebrain slow waves were reported in any of these studies. There are more than 8000 reptile species.

Sleep in birds

Birds have been reported to have both REM and non-REM sleep as defined by electrographic criteria, although REM sleep periods tend to be shorter than those in most mammals [46]. A study of seasonal EEG and activity patterns in the white-crowned sparrow (Figure 1) showed that even when confined to cages, EEG and behaviorally defined sleep were reduced by two-thirds during the seasons when they would have migrated in the wild.

This was not accompanied by any reduction in accuracy or performance on a repeated acquisition task. There were no signs of the pathologies seen in sleep-deprived rats and no sleep rebound at the end of the period [47]. There are more than 10 000 bird species [23].

Sleep in land mammals

There are more than 4000 mammalian species [23]. Most systematic studies of mammalian sleep have been conducted in only a few domesticated species [48] including rats, mice, cats, dogs and monkeys. It is clear that these species meet, and indeed created, the conventional definition of sleep. More interesting would be studies of sleep under naturalistic conditions in animals that appear to sleep relatively little. This would include the large herbivores such as the giraffe and elephant. These species have been observed to migrate for large distances over periods of weeks. Although excellent behavioral studies of sleep and rest behavior have been performed on these animals, they have generally been done in zoos where food is in constant supply, predator threats are nonexistent and migrations are impossible [49,50]. Furthermore, sensory response threshold measurement, sleep deprivation and rebound tests and the recording of physiological variables are not generally possible in zoos, making it difficult to distinguish quiet waking states from true sleep. The vulnerability of the large herbivores in the wild suggests that it would be highly maladaptive for them to have the greatly reduced sensory responsiveness that defines sleep. On the basis of the behavioral observations that have been conducted, we cannot say with confidence that all herbivores meet the standard criteria for sleep throughout their lifespan. Hunger, a normal condition in the wild, has been found to greatly reduce sleep in the rat [51], and it might be expected to do so in other species under conditions where waking would increase the probability of feeding. Conversely, when no food is likely to be found, increased sleep is the best survival strategy. REM sleep is present in all terrestrial mammals so far examined, occupying the greatest amount of the 24 h cycle in the egg-laying mammal platypus [52]. The properties of sleep vary substantially across mammalian land species that have been studied (Box 1).

Sleep in marine mammals

The standard criteria defining sleep have often been modified for descriptions of sleep in marine mammals. Thus, it has been said that marine mammals can sleep with one-half of the brain at a time and that they can swim while sleeping. Two unusual forms of this behavior have been described: sleep in otariids, such as the fur seal and sea lion, and sleep in cetaceans, such as the bottlenose dolphin and beluga whale.

On land, sleep in the fur seal generally resembles that in most terrestrial mammals. The EEG is bilaterally synchronized and the animal closes both eyes, appears unresponsive and cycles between REM and non-REM sleep. By contrast, when the fur seal is in the water, it usually shows an asymmetrical pattern of behavior, with one of the flippers being active in maintaining body position while the other flipper is inactive. The fur seal can have slow waves in one hemisphere with the contralateral eye being closed. The other eye is generally open or partially open. Therefore, it appears that half of the brain and body might be ‘asleep’ and the other half ‘awake.’ REM sleep time is greatly reduced in the water and little or no

rebound of lost REM sleep is seen when the fur seal returns to land, even after several weeks in the water [53].

The situation in the dolphin (Figure 1) and other cetaceans is quite different. These animals show only unihemispheric slow waves (USW). They never show high-voltage waves bilaterally. Sometimes they float at the surface while showing USW. However, often they swim with USW. When they swim while having USW, there is no asymmetry in their motor activity, in contrast to the behavior seen in the fur seal. Regardless of which hemisphere is showing slow wave activity, they tend to circle in a counterclockwise direction (in the northern hemisphere [54]). Mukhametov states that 'the sleep behavior of these animals is indistinguishable from that of quiet waking' [55]. No evidence has been presented for elevated sensory response thresholds contralateral to the hemisphere that has slow waves. Indeed, it seems that a substantial elevation of sensory thresholds on one side of the body would be quite maladaptive given the danger of collisions while moving. Similarly, brain motor systems must be bilaterally active to maintain the bilaterally coordinated movement. Therefore, forebrain and brainstem activity must differ radically from that seen in terrestrial mammals during sleep. The one study of USW rebound after USW deprivation in dolphins produced very variable results, with little or no relation between the amount of slow waves lost in each hemisphere and the amount of slow waves recovered when the animals were subsequently left undisturbed [55]. In another study it was shown that dolphins are able to maintain continuous vigilance for 5 days with no decline in accuracy. At the end of this period there was no detectable decrease of activity or evidence of inattention or sleep rebound such as would be expected of a sleep-deprived animal [56].

In some smaller cetaceans, such as the harbor porpoise [57] and Commerson's dolphin [58] (Figure 1), motor activity is essentially continuous from birth to death, that is, they never float or sink to the bottom and remain still. They move rapidly, and it is evident that they must have accurate sensory and motor performance and associated brain activation to avoid collisions. It is difficult to accept this behavior as sleep without discarding all aspects of the behavioral definition of sleep offered above.

A remarkable behavior is seen in newborn dolphins, killer whales and their mothers. All land mammals show maximal sleep and maximal immobility at birth, behaviors that have been assumed to be required for brain and body development. However, newborn killer whales and dolphins are continuously active, in the manner seen in adults of small dolphin species, for 4–6 weeks after birth. Although some USW might be present at these times, the eyes are open bilaterally when they surface at average intervals of less than 1 min, indicating that any slow wave pattern could not last longer than this period [59]. Sleep interruption at such intervals is lethal to rats [13], and human sleep is not restorative if interrupted on such a schedule [60]. The cetacean mothers also cease eye closure and floating behavior during the postpartum period. No rebound of lost immobility is seen. Rather, the neonate and mother gradually return to the adult pattern over a 1–2 month period. In many cetacean species, migration occurs during the postpartum period. In all cetaceans, the neonatal period is the time of greatest danger from predation because of the small size of the calf, necessitating the mother and calf to be maximally alert. One could describe the maternal and neonatal pattern as sleep with well-coordinated motor activity, accurate sensory processing, alert observation

of and response to threats in the environment and without the likelihood of any EEG slow waves or eye closure lasting more than 60 s [61,62]. However, this does not comport with the behavioral definition of sleep [63].

Do all animals sleep?

The evidence that all animals have a state that meets the accepted definitions of sleep is quite poor. Indeed, fewer than 50 of the nearly 60 000 vertebrate species [23] have been tested for all of the criteria that define sleep. Of those, some do not meet the criteria for sleep at any time of their lives and others appear able to greatly reduce or go without sleep for long periods of time. Many marine mammals, terrestrial animals and birds that migrate for long distances and large herbivores and animals with exposed sleeping sites might not show the periods of greatly reduced awareness, or the rebound after deprivation that defines sleep, during certain periods of their lives. It remains questionable whether all species that do meet the behavioral definitions of sleep, sleep for the same reason.

It might well be more accurate to view sleep as a behavior whose presence, quality, intensity and functions vary between species and across the lifespan. Different animals have used sleep to maximize energy savings by reducing body and brain energy consumption, increasing survival by seeking out a safe sleeping site, releasing hormones and conducting a variety of recuperative processes. Some species appear to be able to accomplish these processes during the waking state. This view contrasts with the idea that sleep is a universal state with the same underlying vital function in all species [64,65].

Acknowledgements

This work was supported by the Medical Research Service of the VA, NS14610, HL41370, MH64109 and NSF0234687. I thank Oleg Lyamin and Dennis McGinty for helpful comments on an earlier version of this manuscript.

References

1. Allison T et al. (1977) A behavioral and polygraphic study of sleep in the shrews *Suncus murinus, Blarina brevicauda*, and *Cryptotis parva*. Behav. Biol 20, 354–366 [PubMed: 889556]
2. Bergmann BM et al. (1987) Period-amplitude analysis of rat electroencephalogram: stage and diurnal variations and effects of suprachiasmatic nuclei lesions. Sleep 10, 523–536 [PubMed: 3432854]
3. Borbely AA and Achermann P (2005) Sleep homeostasis and models of sleep regulation. In Principles and Practice of Sleep Medicine (4th edn) (Kryger MH et al., eds), pp. 405–417, Elsevier Saunders
4. Siegel JM (1990) Mechanisms of sleep control. J. Clin. Neurophysiol 7, 49–65 [PubMed: 2406284]
5. Siegel JM (2005) REM sleep. In Principles and Practice of Sleep Medicine (4th edn) (Kryger MH et al., eds), pp. 120–135, Elsevier Saunders
6. Steriade M (2005) Brain electrical activity and sensory processing during waking and sleep. In Principles and Practice of Sleep Medicine (4th edn) (Kryger MH et al., eds), pp. 101–119, Elsevier Saunders
7. Lapierre JL et al. (2007) Cortical acetylcholine release is lateralized during asymmetrical slow wave sleep in northern fur seals. J. Neurosci 27, 11999–12006 [PubMed: 17978041]
8. Raichle ME and Mintun MA (2006) Brain work and brain imaging. Annu. Rev. Neurosci 29, 449–476 [PubMed: 16776593]

9. Nofzinger EA (2006) Neuroimaging of sleep and sleep disorders. Curr. Neurol. Neurosci. Rep 6, 149–155 [PubMed: 16522269]
10. Vanderwolf CH (2000) Are neocortical gamma waves related to consciousness? Brain Res 855, 217–224 [PubMed: 10677593]
11. John J et al. (2004) Cataplexy-active neurons in the posterior hypothalamus: implications for the role of histamine in sleep and waking behavior. Neuron 42, 619–634 [PubMed: 15157423]
12. Mahowald MW and Schenck CH (2005) Insights from studying human sleep disorders. Nature 437, 1279–1285 [PubMed: 16251953]
13. Rechtschaffen A and Bergmann BM (2002) Sleep deprivation in the rat: an update of the 1989 paper. Sleep 25, 18–24 [PubMed: 11833856]
14. Everson CA et al. (1989) Sleep deprivation in the rat: III. Total sleep deprivation. Sleep 12, 13–21 [PubMed: 2928622]
15. Ramanathan L et al. (2002) Sleep deprivation decreases superoxide dismutase activity in rat hippocampus and brainstem. Neuroreport 13, 1387–1390 [PubMed: 12167758]
16. Newman SM et al. (2008) Sleep deprivation in the pigeon using the disk-over-water method. Physiol. Behav 93, 50–58 [PubMed: 17765274]
17. Krauchi K et al. (2006) Challenging the sleep homeostat does not influence the thermoregulatory system in men: evidence from a nap vs. sleep-deprivation study. Am. J. Physiol. Regul. Integr. Comp. Physiol 290, R1052–R1061 [PubMed: 16306164]
18. Ross JJ (1965) Neurological findings after prolonged sleep deprivation. Arch. Neurol 12, 399–403 [PubMed: 14264871]
19. Knutson KL et al. (2007) The metabolic consequences of sleep deprivation. Sleep Med. Rev 11, 163–178 [PubMed: 17442599]
20. Schenkein J and Montagna P (2006) Self management of fatal familial insomnia. Part 1: what is FFI? MedGenMed 8, 65
21. Campbell IG and Feinberg I (2005) Homeostatic sleep response to naps is similar in normal elderly and young adults. Neurobiol. Aging 26, 135–144 [PubMed: 15585353]
22. Wijnen H and Young MW (2006) Interplay of circadian clocks and metabolic rhythms. Annu. Rev. Genet 40, 409–448 [PubMed: 17094740]
23. University of Michigan Museum of Zoology, (2007) Animal Diversity Website (http://animaldiversity.ummz.umich.edu)
24. Hartse KM (1989) Sleep in insects and nonmammalian vertebrates. In Principles and Practice of Sleep Medicine (Kryger MK et al., eds), pp. 95–104, W.B. Saunders
25. Tobler I and Neuner-Jehle M (1992) 24-h variation of vigilance in the cockroach Blaberus giganteus. J. Sleep Res 1, 231–239 [PubMed: 10607056]
26. Stephenson R et al. (2007) Prolonged deprivation of sleep-like rest raises metabolic rate in the Pacific beetle cockroach, *Diploptera punctata* (Eschscholtz). J. Exp. Biol 210, 2540–2547 [PubMed: 17601958]
27. Kaiser W and Steiner-Kaiser J (1983) Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. Nature 301, 707–709 [PubMed: 6828153]
28. Sauer S et al. (2004) Sleep deprivation in honey bees. J. Sleep Res 13, 145–152 [PubMed: 15175094]
29. Hendricks JC et al. (2000) Rest in *Drosophila* is a sleep-like state. Neuron 25, 129–138 [PubMed: 10707978]
30. Shaw PJ et al. (2000) Correlates of sleep and waking in *Drosophila melanogaster*. Science 287, 1834–1837 [PubMed: 10710313]
31. Yokogawa T et al. (2007) Characterization of sleep in zebrafish and insomnia in hypocretin receptor mutants. PLoS Biol 5, 2379–2397
32. Zhdanova IV et al. (2001) Melatonin promotes sleep-like state in zebrafish. Brain Res 903, 263–268 [PubMed: 11382414]
33. Siegel JM (2004) Hypocretin (orexin): role in normal behavior and neuropathology. Annu. Rev. Psychol 55, 125–148 [PubMed: 14744212]

34. Tobler I and Borbely AA (1985) Effect of rest deprivation on motor activity of fish. J. Comp. Physiol. A 157, 817–822 [PubMed: 3837116]
35. Nilsson GE et al. (2007) Tribute to P. L. Lutz: respiratory ecophysiology of coral-reef teleosts. J. Exp. Biol 210, 1673–1686 [PubMed: 17488931]
36. Hobson JA (1967) Electrographic correlates of behavior in the frog with special reference to sleep. Electroencephalogr. Clin. Neurophysiol 22, 113–121 [PubMed: 4163680]
37. Hobson JA et al. (1968) Electrographic correlates of behavior in tree frogs. Nature 220, 386–387 [PubMed: 5684884]
38. Ayala-Guerrero F and Huitron-Resendiz S (1991) Sleep patterns in the lizard *Ctenosaura pectinata*. Physiol. Behav 49, 1305–1307 [PubMed: 1896516]
39. De Vera L et al. (1994) Reptilian waking EEG: slow waves, spindles and evoked potentials. Electroencephalogr. Clin. Neurophysiol 90, 298–303 [PubMed: 7512911]
40. Flanigan WF Jr et al. (1973) The EEG and behavioral continuum of the crocodilian, *Caiman sclerops*. Electroencephalogr. Clin. Neurophysiol 34, 521–538 [PubMed: 4121324]
41. Huntley AC (1987) Electrophysiological and behavioral correlates of sleep in the desert iguana, *Dipsosaurus dorsalis* Hallowell. Comp. Biochem. Physiol. A 86, 325–330 [PubMed: 2881673]
42. Tauber ES et al. (1968) Electrophysiological and behavioral correlates of wakefulness and sleep in the lizard (*Ctenosaura pectinata*). Electroencephalogr. Clin. Neurophysiol 24, 424–443 [PubMed: 4172359]
43. Flanigan WF (1973) Sleep and wakefulness in iguanid lizards, *Ctenosaura pectinata* and *Iguana iguana*. Brain Behav. Evol 8, 401–436 [PubMed: 4802023]
44. Flanigan WF et al. (1974) Sleep and wakefulness in chelonian reptiles. 1. The box turtle, *Terrapene carolina*. Arch. Ital. Biol 112, 227–252 [PubMed: 4441206]
45. Eiland MM et al. (2001) State-related discharge of neurons in the brainstem of freely moving box turtles, *Terrapene carolina major*. Arch. Ital. Biol 139, 23–36 [PubMed: 11256184]
46. Amlaner CJ and Ball NJ (1994) Avian sleep. In Principles and Practice of Sleep Medicine (2nd edn) (Kryger MH et al., eds), pp. 81–94, W.B. Saunders
47. Rattenborg NC et al. (2004) Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). PLoS Biol 2, E212 [PubMed: 15252455]
48. Lesku JA et al. (2006) A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. Am. Nat 168, 441–453 [PubMed: 17004217]
49. Tobler I and Schwierin B (1996) Behavioural sleep in the giraffe (*Giraffa camelopardalis*) in a zoological garden. J. Sleep Res 5, 21–32 [PubMed: 8795798]
50. Tobler I (1992) Behavioral sleep in the Asian elephant in captivity. Sleep 15, 1–12 [PubMed: 1557589]
51. Jacobs BL and McGinty DJ (1971) Effects of food deprivation on sleep and wakefulness in the rat. Exp. Neurol 30, 212–222 [PubMed: 4323120]
52. Siegel JM et al. (1999) Sleep in the platypus. Neuroscience 91, 391–400 [PubMed: 10336087]
53. Lyamin OI et al. (1996) Paradoxical sleep in northern fur seals in water and on land. J. Sleep Res 5 (Suppl.), 130
54. Stafne GM and Manger PR (2004) Predominance of clockwise swimming during rest in Southern Hemisphere dolphins. Physiol. Behav 82, 919–926 [PubMed: 15451659]
55. Oleksenko AI et al. (1992) Unihemispheric sleep deprivation in bottlenose dolphins. J. Sleep Res 1, 40–44 [PubMed: 10607024]
56. Ridgway S et al. (2006) Dolphin continuous auditory vigilance for five days. J. Exp. Biol 209, 3621–3628 [PubMed: 16943502]
57. Mukhametov LM (2007) Sleep in marine mammals. Exp. Brain Res 8, 227–238
58. Mukhametov LM et al. (2002) Swimming styles and their relationship to rest and activity states in captive Commerson's dolphins. In Proceedings of the 14th Biennial Conference on the Biology of Marine Mammals, Vancouver, November 27–December 3. pp. 152
59. Lyamin O et al. (2005) Animal behaviour: continuous activity in cetaceans after birth. Nature 435, 1177 [PubMed: 15988513]

60. Bonnet MH (2000) Sleep deprivation. In Principles and Practice of Sleep Medicine (3rd edn) (Kryger MH et al., eds), pp. 53–71, W.B. Saunders
61. Sekiguchi Y et al. (2006) Sleep behaviour: sleep in continuously active dolphins. Nature 441, E9–E10 [PubMed: 16791150]
62. Gnone G et al. (2006) Sleep behaviour: activity and sleep in dolphins. Nature 441, E10–E11 [PubMed: 16791148]
63. Lyamin OI et al. (2006) Sleep behaviour: sleep in continuously active dolphins; activity and sleep in dolphins. Nature 441, E11
64. Siegel JM (2001) The REM sleep-memory consolidation hypothesis. Science 294, 1058–1063 [PubMed: 11691984]
65. Siegel JM (2005) Clues to the functions of mammalian sleep. Nature 437, 1264–1271 [PubMed: 16251951]
66. Takahashi Y et al. (1981) A model of human sleep-related growth hormone secretion in dogs: effects of 3, 6, and 12 hours of forced wakefulness on plasma growth hormone, cortisol, and sleep stages. Endocrinology 109, 262–272 [PubMed: 7238408]
67. Read PA et al. (1998) Dynamic changes in arousal threshold during sleep in the human infant. Pediatr. Res 43, 697–703 [PubMed: 9585018]
68. Piallat B and Gottesmann C (1995) The reticular arousal threshold during the transition from slow wave sleep to paradoxical sleep in the rat. Physiol. Behav 58, 199–202 [PubMed: 7667422]
69. Neckelmann D and Ursin R (1993) Sleep stages and EEG power spectrum in relation to acoustical stimulus arousal threshold in the rat. Sleep 16, 467–477 [PubMed: 8378687]
70. Hirshkowitz M and Schmidt MH (2005) Sleep-related erections: clinical perspectives and neural mechanisms. Sleep Med. Rev 9, 311–329 [PubMed: 15994100]
71. Affanni JM et al. (2001) Absence of penile erections during paradoxical sleep. Peculiar penile events during wakefulness and slow wave sleep in the armadillo. J. Sleep Res 10, 219–228 [PubMed: 11696075]
72. Braun AR et al. (1998) Dissociated pattern of activity in visual cortices and their projections during human rapid eye movement sleep. Science 279, 91–95 [PubMed: 9417032]
73. Maquet P et al. (1996) Functional neuroanatomy of human rapid-eye-movement sleep and dreaming. Nature 383, 163–166 [PubMed: 8774879]
74. Solms M (2000) Dreaming and REM sleep are controlled by different brain mechanisms. Behav. Brain Sci 23, 843–850 [PubMed: 11515144]
75. Foulkes D (1979) Home and laboratory dreams: four empirical studies and a conceptual reevaluation. Sleep 2, 233–251 [PubMed: 232567]
76. Siegel JM et al. (1996) The echidna *Tachyglossus aculeatus* combines REM and nonREM aspects in a single sleep state: implications for the evolution of sleep. J. Neurosci 16, 3500–3506 [PubMed: 8627382]
77. Van Dongen HP et al. (2005) Individual differences in adult human sleep and wakefulness: leitmotif for a research agenda. Sleep 28, 479–496 [PubMed: 16171293]

Box 1.

Sleep, but not as we know it

Despite relatively few detailed comparative studies of sleep physiology, many species differences have been identified even within the mammalian line. Human stage 4 non-REM sleep is linked to growth hormone secretion. Disruption of stage 4 sleep in children is thought to be linked to short stature. However, in dogs, growth hormone secretion normally occurs in waking, not sleep [66]. In humans, arousal threshold is lowest in REM sleep, but in rats it is highest in this state [67-69]. Erections have been shown to be present during REM sleep in humans and rats [70], however the armadillo has erections only in non-REM sleep [71]. Blood flow and metabolism differ dramatically between neocortical regions in adult human REM sleep [72,73], although most animal studies seem to assume that the neocortex behaves as a unit during sleep. Lesions of parietal cortex and certain other regions prevent dreaming in humans, even in individuals continuing to show normal REM sleep as judged by cortical EEG, suppression of muscle tone and rapid eye movements [74]. Humans before age 6 do not have dream mentation, perhaps because these cortical regions have not yet developed [75]. The physiological signs of REM sleep in both the platypus [52] and the related monotreme, the short-nosed echidna, [76] are largely restricted to the brainstem, in contrast to their propagation to the forebrain in adult placental and marsupial mammals. These findings make it questionable whether non-human mammals that have REM sleep, all of which have cortical regions whose structure differs from that of adult humans, have dream mentation. REM sleep is present in all terrestrial animals that have been studied, but so far, signs of this state have not been seen in cetaceans. A substantial variation in the response to sleep deprivation is seen between humans of similar age and health [77]. All of these findings illustrate the inadequacy of comparing sleep across and within species in isolation from ecologic variables by simply dichotomizing it into REM and non-REM sleep and measuring hours of sleep.

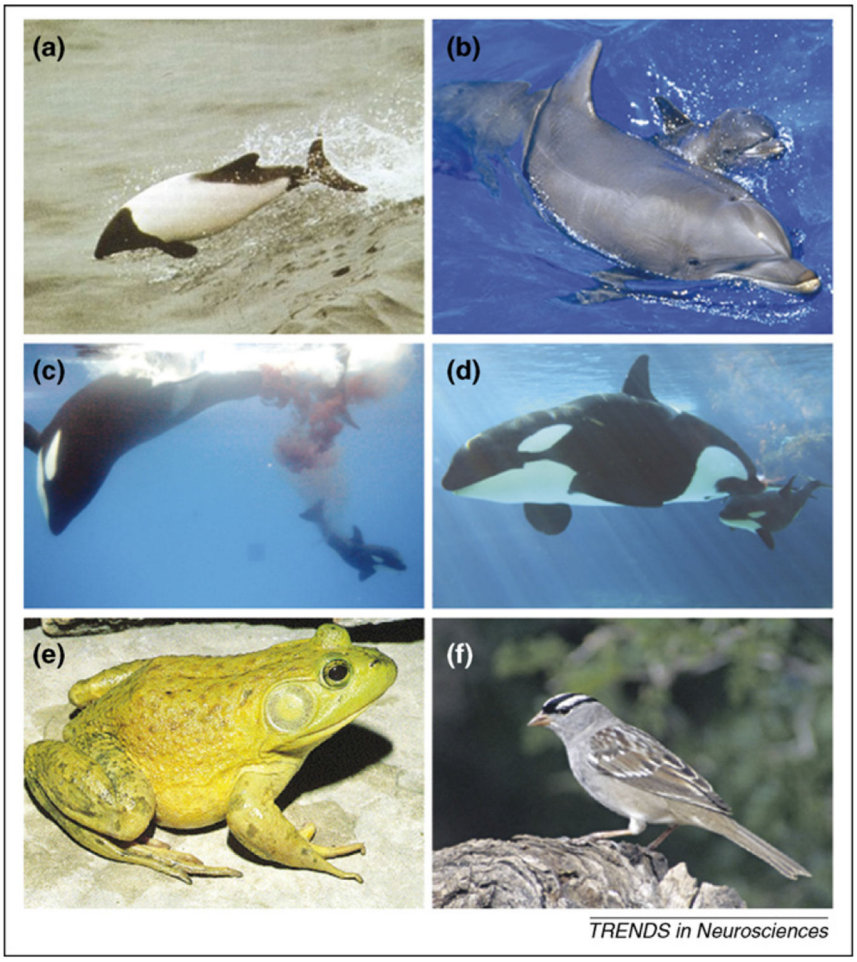

Figure 1.

Light sleepers: animals that show little or no sleep during migrations, in the postpartum period or throughout their lives. (a) Commerson's dolphin; (b) bottlenose dolphin *Tursiops truncatus*; (c) and (d) killer whale *Orcinus orca* being born; (e) bullfrog *Rana catesbeiana*; (f) white-crowned sparrow *Zonotrichia leucophrys*. *Rana catesbeiana* photo courtesy of James Harding; killer whale photos courtesy of SeaWorld, San Diego.