and responsiveness. Clearly, evolution rewards judicious activity, not continuous activity. Sleep often is viewed as a liability because of the associated reduced alertness in comparison with quiet waking. However, seen in the context of adaptive inactivity shown by most species, what is most notable about sleep in humans is its intermediate status, between the highly inactive unresponsive states seen in rotifers, insects, and hibernating mammals (which show little neuronal activity during hibernation) and the virtually continuous periods of activity and wakefulness that have been seen in migrating birds and cetaceans.

QUANTITATIVE ANALYSES OF THE CORRELATES OF SLEEP DURATION IN MAMMALS

Many studies have attempted to correlate the data that have been collected on sleep duration in mammals with physiologic and behavioral variables, to develop hypotheses regarding the function of sleep. The data on which these studies are based are not ideal. Only approximately 70 mammalian species have been studied with sufficient measurements to determine the amounts of REM and NREM sleep over the 24-hour period. These are by no means a random sample of the more than 5000 mammalian species. Rather, they are species that are viable and available for study in laboratories or, in some instances, for noninvasive (and less accurate) studies in zoos.

In laboratories, animal subjects for sleep studies typically are fed ad libitum and are housed at relatively invariant, thermoneutral temperatures and on artificial light cycles. These environments differ greatly from those in which they evolved. Digital recording and storage technologies now exist that will enable the collection of polygraphic data on animals in their natural environments,[24] but they have not yet been widely used. Such observations are necessary to determine the variation in sleep times caused by hunger, response to temperature changes, predation and the other variables that have driven evolution. Very few of these animals have been tested for arousal threshold, the nature and extent of sleep rebound, and other aspects of sleep whose variation across species may potentially contribute to an understanding of sleep evolution and function. An important issue in comparing sleep times in animals is determining sleep depth. In humans, sleep depth, as assessed by either arousal threshold or EEG amplitude, increases after sleep deprivation and often is greater during early stages of development when total sleep time is greatest. Can sleep time be profitably compared across animals without incorporating information on sleep depth? Can it be assumed that animals that sleep for longer periods also sleep more deeply, as is true across human development, or is the reverse more likely—that short-sleeping animals sleep more deeply as has been hypothesized[25]? It would be best not to make either assumption; any conclusions should be based on hard evidence about these dimensions of sleep.

One of the earliest studies comparing REM and NREM sleep durations with physiologic variables found that sleep duration was inversely correlated with body mass.[26,27] A subsequent analysis found that this relationship applied only to herbivores, not to carnivores or omnivores.[28] This study also showed that, as a group, carnivores slept more than omnivores, who in turn slept more than herbivores (Figure 10-1). In an early study, a significant negative correlation was found between brain weight and REM sleep time (but not total sleep time). A point worthy of emphasis is that this latter correlation was extremely small, accounting for only 4% of the variance in REM sleep time (Figure 10-2). The largest correlation emerging from these early studies was that between body or brain mass and the *duration* of the sleep cycle—that is, the time from the start of one REM sleep period to the start of the next, excluding interposed waking. This correlation accounted for as much as 80% of the variance in sleep cycle time between animals and has held up in subsequent studies in mammals. Sleep cycle duration is approximately 10 minutes in mice, 90 minutes in humans, and 120 minutes in elephants. Because sleep is linked to a reduction in body temperature[29] and reduces energy usage, it has been hypothesized that energy conservation may be a function of sleep.[30]

Several studies have reanalyzed the phylogenetic data set with the addition of data on the few more recently studied animals. These studies took a variety of strategies to extract relations from this data set. Lesku and colleagues[31] used a method of "independent contrasts" in an attempt to control for the relatedness of species being compared. Inclusion of many rodent species in earlier analyses would give the data for those animals a disproportionate effect on conclusions. These workers confirmed previous findings of a negative relationship between basal metabolic rate (which is correlated with body mass) and sleep time. In contrast with earlier and subsequent studies of the same data set, they reported a positive correlation between REM sleep and relative brain mass and a negative relationship between REM sleep time and predation risk.

Another study, confining its analysis to studies that met the investigators' more rigorous criteria, found that metabolic rate correlates negatively rather than positively with sleep quotas,[32] in contrast with earlier studies.[27] This result is not inconsistent with some earlier work.[28] They also reported that neither adult nor neonatal brain mass correlates positively with adult REM or NREM sleep times, differing from earlier studies.[27,32] In agreement with earlier analyses, animals with high predation risk were found to sleep less.[28,33] In keeping with the concept of some fixed need for an unknown function performed only during sleep, the researchers proposed that short-sleeping species sleep more intensely to achieve this function in less time, but they presented no experimental evidence for this hypothesis.

A notable feature of the studies by Lesku and Capellini and their coworkers is that both excluded animals that the investigators concluded had unusual sleep patterns. So the echidna, which combines REM and NREM features in its sleep,[34] was eliminated from the analysis. The platypus, with the largest amount of REM sleep of any animal yet studied,[35] also was excluded from this analysis, as it was from another study focusing on brain size relations.[36] The dolphin and three other cetacean species and two species of manatee were excluded from the Lesku et al. study because of their low levels of REM sleep and presence of unihemispheric slow waves. Including these species in such analyses would undoubtedly negate or reverse the positive relationship reported between brain size and REM sleep, because the platypus exhibits the largest amount of REM sleep time of any studied animal and one of the smallest brain sizes and the dolphin, which appears to have little or no REM sleep, has a larger brain size than humans.[37,38] As discussed further on, these "unusual" species that have been excluded from previous

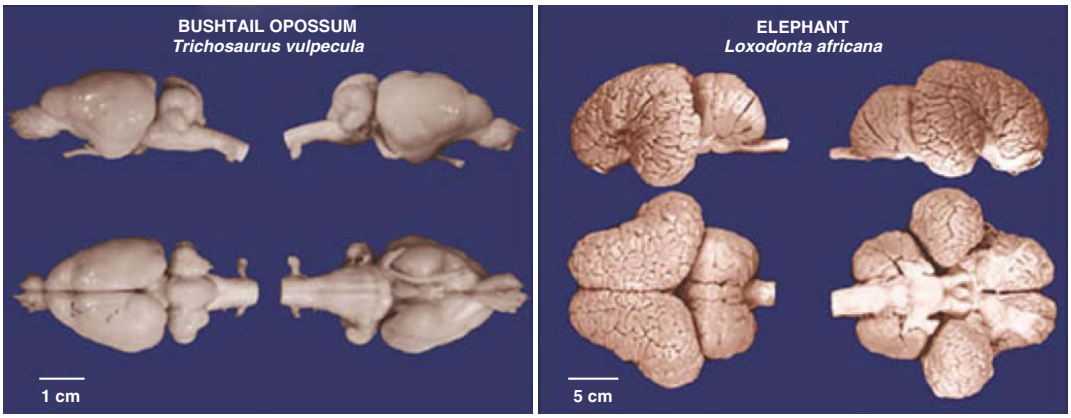

Figure 10-2 Sleep amount is not proportional to the relative size of the cerebral cortex or to the degree of encephalization, as illustrated by these two examples. (From Siegel JM. Clues to the functions of mammalian sleep. *Nature* 2005;437:1264–71.)

THE DIVERSITY OF SLEEP

Overview

On the assumption that sleep satisfies an unknown yet universal function in all animals, some work has been carried out in animals whose genetics and neuroanatomy are better understood and more easily manipulated than in mammals. Much of this work has focused on the fruit fly, *Drosophila melanogaster.* These animals appear to meet the behavioral definition of sleep. Their response threshold is elevated during periods of immobility, but they will rapidly "awaken" when sufficiently intense stimuli are applied. They make up for "sleep" deprivation with a partial rebound of inactivity when left undisturbed. However, major differences between the physiology and anatomy of these organisms and those of mammals make it difficult to transfer insights gleaned from studies of *Drosophila* sleep to human sleep. The *Drosophila* brain does not resemble the vertebrate brain. Octopamine, a major sleep-regulating transmitter in *Drosophila,* does not exist in mammals. Hypocretin, a major sleep-regulating transmitter in mammals, is not produced by *Drosophila.*[40] *Drosophila* flies are not homeotherms, whereas thermoregulation has been closely linked to fundamental aspects of mammalian sleep.[28,29,41] There is no evidence for the occurrence of a state resembling REM sleep in *Drosophila.* Thus the neurochemistry, neuroanatomy, and neurophysiology of sleep must necessarily differ between *Drosophila* and humans and other mammals. Any commonality of sleep phenomena would have to be restricted to cellular level processes. Two studies have shown that *Drosophila* sleep and sleep rebound are markedly impaired by genetic alteration of a potassium current that regulates neuronal membrane excitability.[42,43] Regulation of potassium currents may be a core function of sleep, or it may instead affect the excitability of circuits regulating activity and quiescence, much as such currents affect seizure susceptibility.[44,45]

Caenorhabditis elegans, a roundworm with a nervous system much simpler than that of *Drosophila,* has also been investigated for sleep like behavior.[46] *C. elegans* reaches adulthood in 60 hours and has periods of inactivity during this maturation, called "lethargus," occurring before each of the four molts it undergoes before reaching maturity. Stimulation of *C. elegans* during the lethargus period produced a small but significant decrease in activity during the remainder of the lethargus period but did not delay the subsequent period of activity or increase quiescence overall, phenomena that differ from the effects of sleep deprivation in mammals. It is not clear if adult *C. elegans* shows any aspect of sleep behavior.[47]

Fundamental species differences in the physiology and neurochemistry of sleep have been identified even within the mammalian line. Although many similarities have been recognized, the EEG aspects of sleep also differ considerably between humans, rats, and cats, the most-studied species.[48-50] Human stage 4 NREM sleep is linked to growth hormone secretion. Disruption of stage 4 sleep in children is thought to be a factor in the pathogenesis of short stature. In dogs, however, growth hormone secretion normally occurs in waking, not sleep.[51] Melatonin release is maximal during sleep in diurnal animals, but is maximal in waking in nocturnal animals.[52] Erections have been shown to be present during REM sleep in humans and rats[53]; the armadillo, however, has erections only in NREM sleep.[54] Blood flow and metabolism differ dramatically between neocortical regions in adult human REM sleep,[55] although most animal sleep deprivation and sleep metabolism studies treat the neocortex as a unit. Lesions of parietal cortex and certain other regions prevent dreaming in humans, even in subjects who continue to show normal REM sleep as judged by cortical EEG activity, rapid eye movements, and suppression of muscle tone.[56] Children younger than 6 years of age do not generally report dream mentation, perhaps because these cortical regions have not yet developed.[57] These findings make it questionable whether nonhuman mammals that exhibit REM sleep, all of which have cortical regions whose structure differs from that in adult humans, have dream mentation.

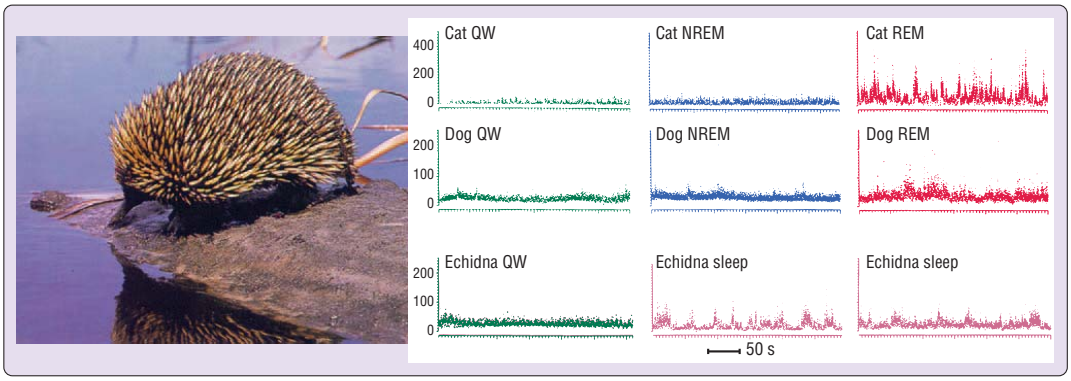

Figure 10-6 **Brainstem Activation during Sleep in the Echidna.** Instantaneous compressed rate plots of representative units recorded in nucleus reticularis pontis oralis of the cat, dog, and echidna. Each point represents the discharge rate for the previous interspike interval. In cat quiet waking (QW) and NREM sleep, the discharge rate is low and relatively regular. The rate increases and becomes highly variable during REM sleep. A similar pattern can be seen in a unit recorded in the dog. In the echidna, sleep is characterized by variable unit discharge rates, as is seen in REM sleep, but this occurs while the cortex is showing high-voltage activity. (From Siegel JM, Manger P, Nienhuis R, et al. The echidna Tachyglossus aculeatus combines REM and nonREM aspects in a single sleep state: implications for the evolution of sleep. *J Neurosci* 1996;16:3500–6.)

found that many polygynous pectoral sandpipers, which breed during a period of continuous summer light, cease sleeping or greatly reduce sleep during breeding. Furthermore, the males with the greatest reduction in sleep sired the most offspring—a unique and dramatic example of adaptive sleep loss increasing genetic propagation.[90] What was most surprising, in view of the strength of this selective benefit, was that *any* males remained sleeping during the breeding period. It was speculated that the continuously active males would be at a competitive disadvantage if their food was scarce after the breeding season relative to those that saved energy by sleeping. In periods of reduced food availability, it is the second group of birds that would survive to mate the next year, leading to a dynamic balance between birds with these two behaviors.[91]

Studies in the ostrich, considered to be in many respects a "primitive" bird, provided novel support for the link between bird and mammalian sleep. It was found that sleep in the ostrich resembles that in the platypus and echidna, with rapid eye movements and muscle tone suppression, brainstem aspects of REM sleep occurring with high-voltage EEG activity, resembling the weak or nonexistent EEG voltage reduction seen in monotremes, whereas their brainstem shows the neuronal activity activation and rapid eye movements that characterize REM sleep.[92]

The observations in monotremes and birds suggest that the reptilian common ancestor of both mammals and birds exhibited REM sleep or a closely related precursor state, rather than the previously advanced speculation that REM sleep must have evolved twice, based on the conclusion that monotremes did not have REM sleep. Although scattered early reports claimed to have identified REM sleep in reptiles, these findings have not been replicated.[28] In the experience of my own research group, when the same recording techniques used in the echidna were appplied in the turtle in a search for evidence of REM sleep, no evidence of phasic brainstem neuronal activity during quiescent states in this reptile was found.[93]

SLEEP REBOUND

The phenomenon of sleep rebound[94] is not always seen. When fur seals go in the water for extended periods, as they do in winter, REM sleep time is greatly reduced. Little or no rebound of lost REM sleep occurs when the animals return to land, even after several weeks in the water.[95] In the cases of the dolphins and killer whales mentioned previously, a near-total abolition of "sleep-like behavior" for periods of several weeks during migration is followed by a slow increase back to baseline levels, with no rebound. The same phenomenon is seen in migrating white sparrows, a migratory species that has been carefully studied under laboratory conditions.[88] In human studies, persons with bipolar disorder in a "manic" phase greatly reduce sleep time for extended periods, and persuasive evidence for progressive degradation of performance, physiologic function, or sleep rebound during this period is lacking. Zebra fish can be completely deprived of sleep for more than three days by placing them in continuous light but show no rebound when returned to a "12-12" light-dark cycle.[96] By contrast, when they are deprived by repetitive tactile stimulation, they do show rebound, suggesting that the deprivation procedure rather than the sleep loss underlies the rebound.

Typically, 30% or less of sleep time lost during deprivation is recovered in the human and rodent, in which the phenomenon has been most extensively studied. A similar percentage of rebound is seen in other species including some invertebrates.[97] One may ask why, if sleep is essentially a maladaptive state, animals that have the ability to regain lost sleep in 30% of the time it would normally have taken have not evolved shorter sleep times to take advantage of the adaptive benefits of increased waking. If sleep is viewed as a form of adaptive inactivity, however, this paradox vanishes. A small sleep rebound may be necessary to compensate for processes that can occur only, or optimally, in sleep, but for the most part,

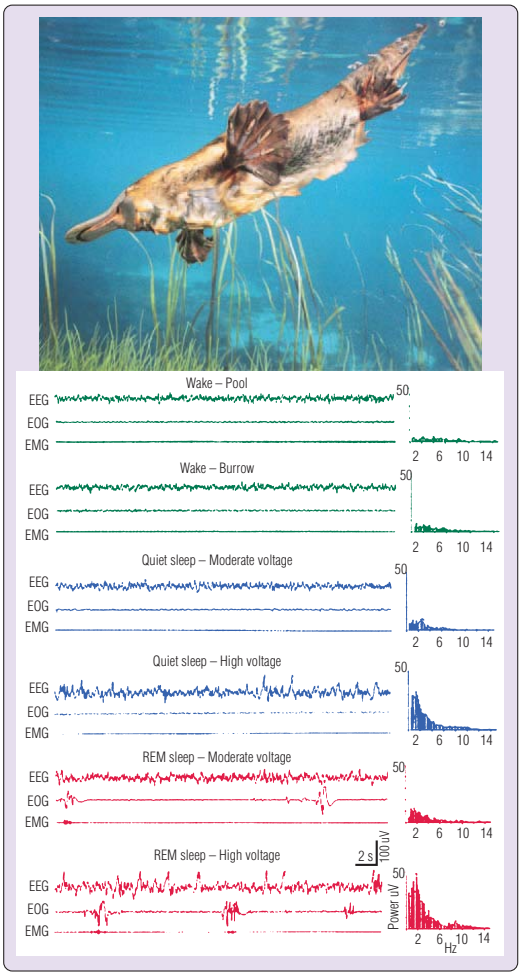

Figure 10-7 **Brainstem REM Sleep State in the Platypus.** Rapid eye movements and twitches can occur while the forebrain is showing a slow wave activity pattern. EEG, EOG, EMG, and EEG power spectra of samples shown of sleep-wake states in the platypus. EEG, Electroencephalogram; EMG, electromyogram; EOG, electrooculogram. (From Siegel JM, Manger PR, Nienhuis R, et al. Sleep in the platypus. *Neuroscience* 1999;91(1):391–400.)

sleep time is determined in each species by the evolved tradeoffs between active waking and adaptive inactivity.

The variation in rebound within and across species needs to be more carefully studied. Some aspects of rebound have been shown to be due to the deprivation procedure, rather than to the sleep loss itself. For example, stressing rats by restraint can produce increased REM sleep even when no sleep has been lost. This effect is mediated by the release of pituitary hormones.[98,99] It is possible that in some species, other aspects of rebound are driven by changes in hormonal release linked to sleep deprivation,[1] rather than by some intrinsic property of sleep.

CLINICAL PEARL

Although sleep and sleep stages differ in amount between species, human sleep does not appear to be qualitatively unique. This factor makes animal models suitable for the investigation of many aspects of pharmacology and pathology in sleep science.

SUMMARY

Sleep can be seen as an adaptive state, benefiting animals by increasing the efficiency of their activity. Sleep does this by suppressing activity at times associated with maximal predator risk and permitting activity at times of maximal food and prey availability and minimal predator risk. It also increases efficiency by decreasing brain and body metabolism. However, unlike the dormant states employed in plants, simple multicellular organisms, and ectothermic organisms, and the hibernation and torpor employed in some mammals and birds, sleep allows rapid arousal for tending to infants, dealing with predators, and responding to environmental changes. A major function of REM sleep may be to allow rapid awakening with alertness, by means of periodic brainstem activation. Many organisms can reduce sleep for long periods of time without rebound during periods of migration or other periods in which a selective advantage can be obtained by continuous waking.

The big brown bat specializes in eating mosquitoes and moths that are active from dusk to early evening. The big brown bat typically is awake only approximately 4 hours a day.[27] Not surprisingly, this waking is synchronized to the period when its insect prey species are active. It is not likely that this short waking period, one of the shortest yet observed, can be explained by the need for some time-consuming unknown process that occurs only during sleep and requires 20 hours to complete. This extremely brief period of wakefulness can be more easily explained by the ecologicl specializations of this bat. Similarly, "sleep" in ectothermic animals is most likely to be determined by temperature and other environmental variables, rather than any information processing or physiologic maintenance requirement. An approach that takes the environmental conditions in which each species evolved into account can better explain the variance in sleep time among mammals.

Many vital processes occur in both waking and sleep, including recovery of muscles from exertion, control of blood flow, respiration, growth of various organs, and digestion. Some processes may occur more efficiently in sleep but can also occur in waking. It has been claimed that sleep has an essential role in learning, but further investigations have disputed such claims.[101-105] It is highly probable that some functions have migrated into or out of sleep in various animals. Neurogenesis,[106] synaptic downscaling,[107] immune system activation,[108] and reversal of oxidative stress[109,110] may be accomplished in sleep in mammals. It remains to be seen if these or any other vital functions can be performed only in sleep. As suggested by the available evidence, however, such functions cannot explain the variation of sleep amounts and the apparent flexibility of sleep physiology within and between

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REVIEW QUESTIONS

1. Dormant states include:
   A. Sleep
   B. Abscission
   C. Hibernation
   D. Diapause
   E. All of the above
2. Hibernation is entered from a state of:
   A. REM sleep
   B. NREM sleep
   C. Cataplexy
   D. Waking
3. With respect to sleep amounts, three phylogenetic groups of animals arranged in *descending* order, from those that sleep the most to those that sleep the least, are:
   A. Carnivores, omnivores, herbivores
   B. Herbivores, omnivores, carnivores
   C. Marsupials, placentals, monotremes
   D. Marsupials, monotremes, placentals
4. Which animal experiences the *most* REM sleep?
   A. Platypus
   B. Dolphin
   C. Human
   D. Big brown bat
5. Which statement regarding sleep time is *true*?
   A. Fur seals greatly reduce REM sleep when in water.
   B. Dolphins experience REM sleep only in the first week of life.
   C. Primates, as a group, devote a higher percentage of their sleep time to REM sleep than any other mammalian order.
   D. Smaller cetacean (dolphin and whale) species sleep more than larger cetaceans.
6. Animals that can go without sleep for long periods of time without sleep rebound include:
   A. Dolphin
   B. Polygynous pectoral sandpipers
   c. Manic humans
   D. Killer whales
   E. All of the above
7. Which animal experiences the *least* amount of REM sleep?
   A. Platypus
   B. Dolphin
   C. Human
   D. Big brown bat
8. Which of the following statements regarding phylogenetic sleep differences is *true*?
   A. Human REM and NREM sleep amounts are neither higher nor lower than REM or NREM sleep amounts in other animals.
   B. Dolphins experience REM sleep only in the first week of life.
   C. Primates, as a group, devote a higher percentage of their sleep time to REM sleep than any other mammalian order.
   D. Smaller cetacean (dolphin and whale) species sleep more than larger cetaceans.
9. Humans with insomnia:
   A. Frequently fall asleep during the day
   B. Make up for lost sleep with substantial sleep rebounds
   C. Are not sleepy during the day
   D. Have a reduced lifespan

ANSWERS

1. **E.**
2. **B.**
3. **A.**
4. **A.**
5. **A.**
6. **E.**
7. **B.**
8. **A.**
9. **C.**