c0012

Chapter 12

Sleep in Mammals

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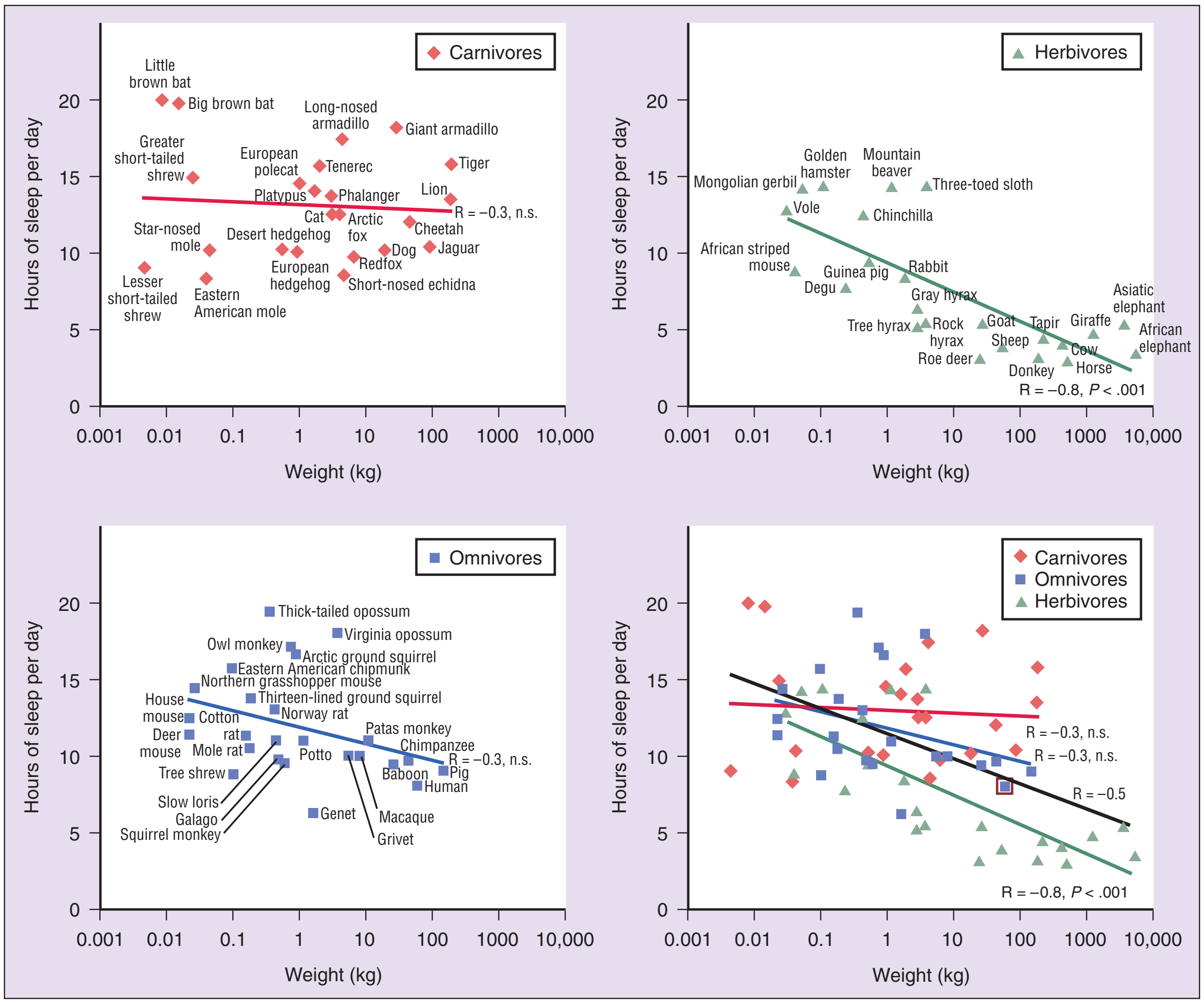
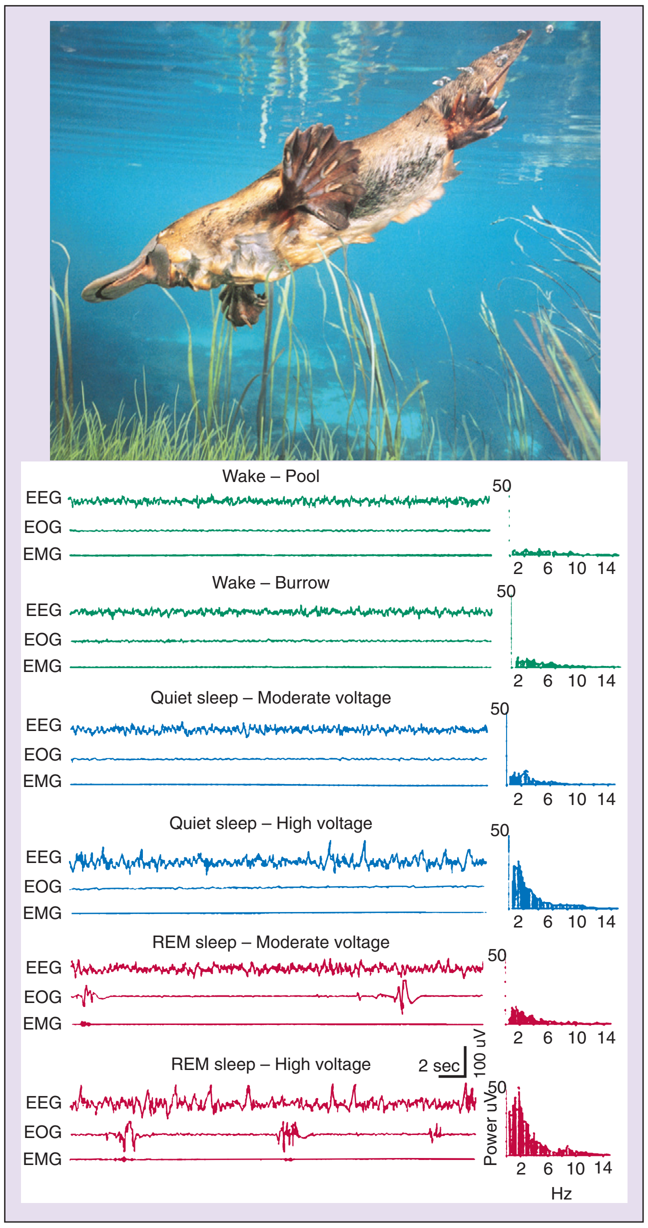
p0010 The amount of sleep required by animals varies greatly. The horse and elephant sleep about 2 to 4 hours a day, and the big brown bat sleeps 20 hours a day. Rapid eye movement (REM) sleep amounts have even greater variation across species (Fig. 12.1). The platypus has the most REM sleep of any animal, approximately 8 hours a day (Video 12.1, Fig. 12.2). Dolphins and other cetaceans do not appear to have any REM sleep, birds have very little, and conclusive evidence for the presence of REM sleep in reptiles is lacking. Fur seals (Fig. 12.3) average 80 minutes of REM sleep per 24 hours



f0010 **Figure 12.1** Sleep time in mammals. Carnivores are shown in *dark red*, herbivores in *green*, and omnivores in *blue*. Sleep times in each of these differ significantly, but carnivores sleep significantly more than herbivores. Sleep amount is an inverse function of body mass over all terrestrial mammals *(black line)*. This function accounts for approximately 25% of the interspecies variance *(bottom right)* in reported sleep amounts. Herbivores are responsible for this relation because body mass and sleep time were significantly and inversely correlated in herbivores but were not correlated in carnivores or omnivores. (From Siegel JM. Clues to the functions of mammalian sleep. *Nature.* 2005;437[7063]:1264–1271.)



f0020 **FIGURE 12.2** Brainstem rapid eye movement (REM) sleep state in the platypus. REM and twitches can occur while the forebrain is showing a slow-wave activity pattern. Electroencephalogram (EEG), electrooculogram (EOG), electromyogram (EMG), and EEG power spectra of samples show sleep-wake states in the platypus. (From Siegel JM, Manger PR, Nienhuis R, et al. Sleep and the platypus. *Neuroscience.* 1999;91[1]:391–400.)

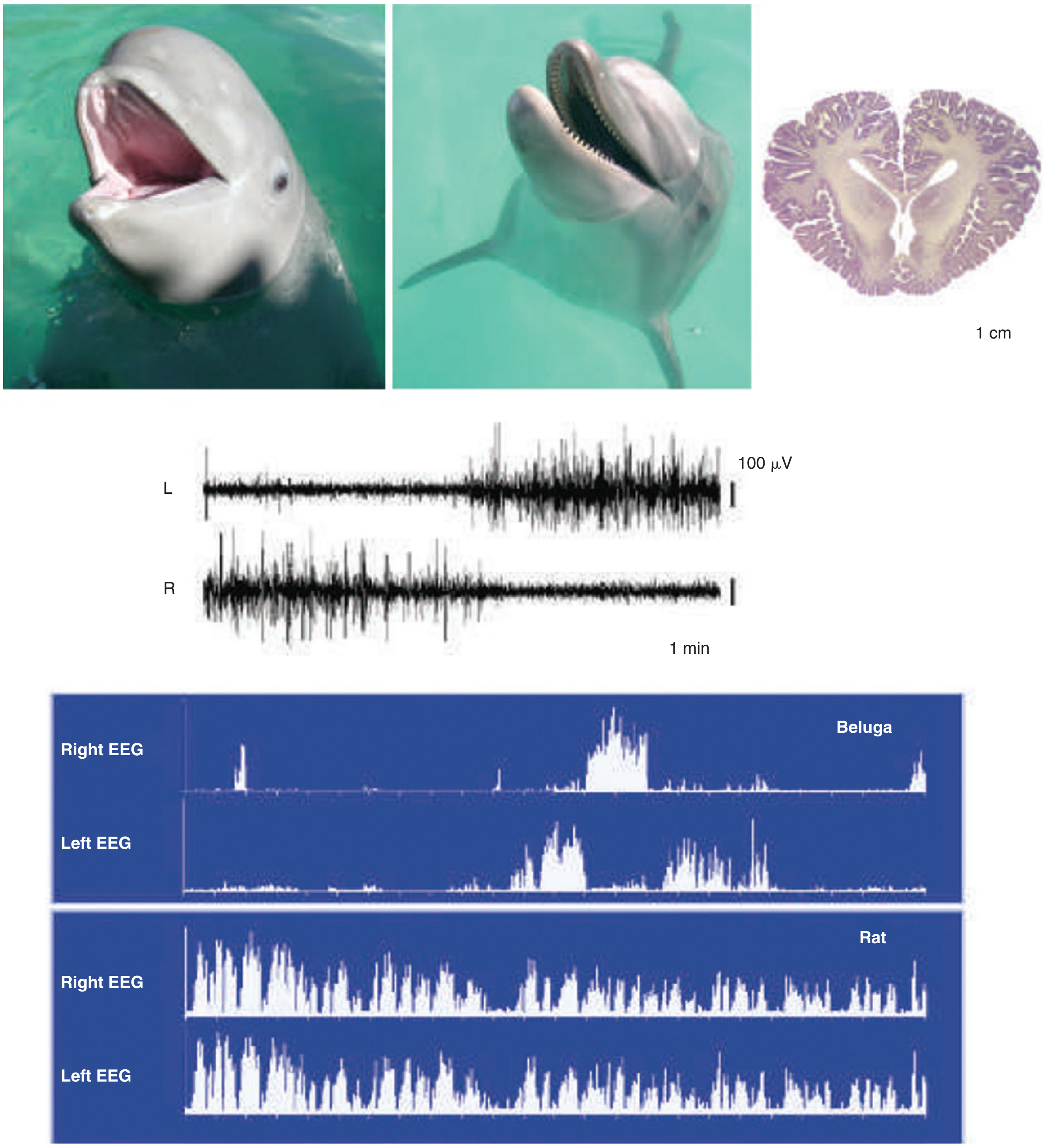
when they are on land, an amount of sleep similar to that in humans, but have little or no REM sleep when they are in water, where they spend about 7 months of the year. They have no “rebound” of REM sleep when they return to land.

p0015 Recent findings undermine the idea that sleep has a vital universal neural or physiologic function across species. Dolphins and other cetaceans never have high-voltage slow waves in both sides of the brain, in contrast to all terrestrial mammals (Fig. 12.4). Instead, they have unihemispheric slow waves with closure of the eye contralateral to the hemisphere with slow waves. Furthermore, orca and dolphin mothers and their calves are continuously active, and calves keep both eyes open for 2 months or longer after birth. No rebound of inactive behavior

FIGURE 12.3 Fur seals have bilateral sleep on land, but unihemispheric sleep in water. (From Lyamin OI, Kosenko PO, Korneva SM, et al. Fur seals suppress REM sleep for very long periods without subsequent rebound. *Curr Biol.* 2018;28[12]:2000–2005.) f0030

follows. During this period, the calf’s brain and body grow to their prodigious size and capacity without any apparent need for sleep. An equally remarkable observation is that adult dolphins working for reward can discriminate between visual stimuli presented at 30-second intervals on their left or right sides, 24 hours a day, for as long as 15 days. During this time their performance shows no progressive decline, and no rebound of inactivity follows the continuous vigilance task. In contrast, humans whose sleep is interrupted on a similar schedule are dramatically impaired, demonstrating the variability of sleep need across species.

Migrating birds experience greatly reduced sleep time with p0020 intact learning abilities, high rates of performance, and no subsequent sleep rebound. The polygynous pectoral sandpiper was shown to greatly reduce its sleep time during a 3-week mating period without signs of performance decrement or sleep rebound. Such variation in sleep time may well be typical under natural conditions. In contrast, animal (or human) studies done under safe laboratory conditions of controlled temperature and ad libitum food availability may lead to the incorrect conclusion that sleep durations are fixed.



f0040 **FIGURE 12.4** Cetacean sleep: unihemispheric slow waves in cetaceans. *Top,* Immature beluga, adult dolphin, and section of adult dolphin brain. Electroencephalographic (EEG) readings of adult cetaceans, represented here by the beluga, are shown during sleep. All species of cetacean so far recorded have unihemispheric slow-wave activity. Top traces show left and right EEG activity. The spectral plots show 1 to 3 Hz power in the two hemispheres over a 12-hour period. The pattern in the cetaceans contrasts with the bilateral pattern of slow waves seen under normal conditions in all terrestrial mammals, represented here by the rat *(bottom traces).* (From Siegel JM. Clues to the functions of mammalian sleep. *Nature.* 2005;437[7063]:1264–1271.)

p0025 People of similar intelligence, age, sex, and body build can have very different sleep times. They also vary in their response to sleep loss; some are highly impaired and some are unable to resist sleep, whereas others show high levels of functioning despite sleep loss. The effect of sleep deprivation on performance is not strongly related to baseline sleep duration. Furthermore, human sleep duration is not linearly related to health; both high and low values are linked to shortened life span. Some evidence suggests that individuals (without preexisting conditions such as sleep apnea) with longer than normal spontaneous sleep durations are at greater risk for a shortened lifespan than are those with less than average sleep time compared to individuals sleeping 7 hours, the optimal duration. A report that sleep deprivation by the "disk over water" technique leads to death in rats may be related to the stress of frequent awakenings rather than sleep loss. Sleep deprivation has not been reported to cause death in mice or rats deprived by other techniques. Fatal familial insomnia and sleeping sickness can cause death in humans, but sleep loss or excess sleep does not appear to be responsible; these diseases affect many body organs.

p0030 Numerous attempts have been made to correlate the variation in sleep time across species with physiologic variables such as body mass, life span, brain size, brain/body weight ratio, and litter size. However, such studies have not identified correlations that account for a significant amount of the cross-species variance (Figs. 12.5 and 12.6). The few weak and inconsistent correlations that have been reported appear to be largely a function of the way the data are handled and which animals are excluded from the dataset. The definitive study of the phylogeny of REM and non-REM (NREM) sleep times in birds concluded that none of the physiologic parameters typically studied in mammals showed even a weak relationship with sleep time. However, one relation does appear to be consistent across both birds and mammals: species such as herbivores, which eat food with low caloric density, sleep significantly less than those that eat more nutritionally dense foods (carnivores; see Fig. 12.6). In other words, if a species needs to eat more than 12 hours a day, it cannot sleep more than 12 hours; animals have evolved to adjust sleep time appropriately to such waking needs. Most species, including humans, can reduce sleep to acquire food, avoid predation, mate, be available to their young during critical periods, and deal with other needs.

p0035 It does not appear that sleep intensity—as measured by electroencephalogram (EEG) synchrony, REM sleep time, or lack of responsiveness—is negatively correlated with sleep time. In other words, the horse and giraffe, which sleep 2 to 4 hours a day, do not sleep *more deeply* than the lion, which sleeps 12 to 14 hours a day. In the same way, elderly humans, who sleep 6 to 7 hours a day, do not sleep more deeply than teenagers, who sleep more than 10 hours a day. To the contrary, both developmentally and phylogenetically, the general tendency is for short sleepers to sleep less deeply than long sleepers.

So why do most of us feel so poorly when we reduce sleep? p0040
Natural selection has imposed a certain amount of sleep on us to restrict activity to appropriate times of day and to reduce long-term nonvital energy expenditure. The pressure to sleep operates by reducing brain activity. Although individuals with naturally short sleep are not at elevated risk of death compared with those who have naturally long sleep times, repeated sleep deprivation below the body's programmed level is stressful and is likely to have significant health consequences. Certain hormonal processes are linked to sleep; but these are species specific, not universal.

It has been argued that quiet waking could serve the p0045
energy conservation functions attributed to sleep without the risks associated with the sleep state. However, the brain consumes as much as 25% of the body's energy at rest. This amount does not greatly differ between active and quiet waking, but it is greatly reduced in sleep. Animals with safe sleeping sites will achieve a selective advantage in reducing brain energy consumption by sleep. Animals with unsafe sleep sites do not sleep deeply.

Species whose environment has a severe seasonal variation p0050
in food availability have evolved to increase sleep during periods of food shortage and decrease sleep when food is available. Others who have safe sites hibernate during periods of greatly reduced availability, achieving even more reduction in energy expenditure.

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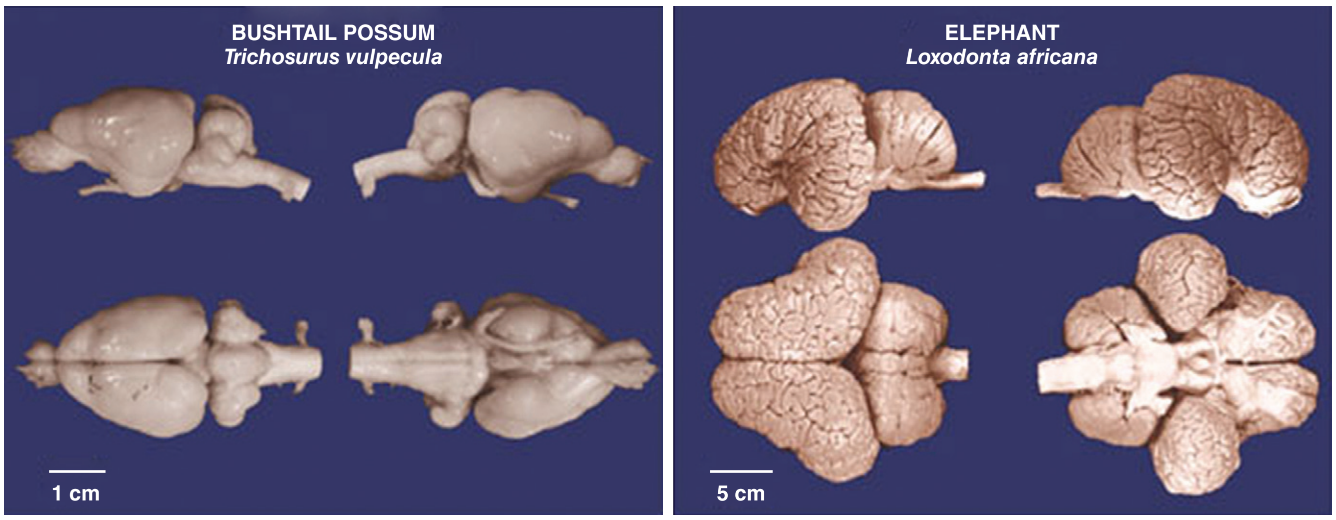


18 hours of sleep, 6.6 hours of REM

3.6 hours of sleep, 1.8 hours of REM

f0050 **Figure 12.5** Sleep amount is not proportional to the relative size of the cerebral cortex or to the degree of encephalization, as illustrated by a comparison between the bushtail possum and the elephant. *REM,* Rapid eye movement [sleep]. (From Siegel JM. Clues to the functions of mammalian sleep. *Nature.* 2005;437[7063]:1264–1271.)

High Sleep | **Low Sleep**

Rodentia

Golden mantled ground squirrel
Spermophilus lateralis

Degu
Octodon degu

	Golden mantled ground squirrel	Degu
Total sleep	15.9	7.7
REM sleep	3.0	0.9
Body weight	0.193	0.240
Brain weight	0.003	0.0025
Brain/body weight ratio	0.016	0.010
Life span	7	11
Caloric density of food	++	+

Carnivora

Cat
Felis catus

Genet
Genetta genetta

	Cat	Genet
Total sleep	12.5	6.3
REM sleep	3.2	1.3
Body weight (kg)	3.3	1.3
Brain weight (kg)	0.030	0.016
Brain/body weight ratio	0.009	0.012
Life span	13	13
Caloric density of food	+++	++

Chiroptera

Big brown bat
Eptesicus fuscus

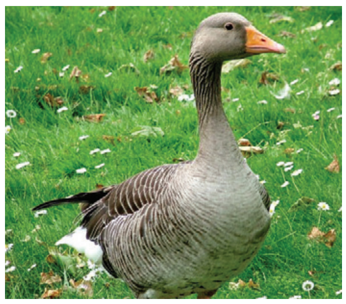
Greater short-nosed fruit bat
Cynopterus sphinx

	Big brown bat	Greater short-nosed fruit bat
Total sleep	20	15.0
REM sleep	3.9	1.15
Body weight (kg)	0.0136	0.0424
Brain weight (mg)	0.238	1.061
Brain/body weight ratio	0.0175	0.025
Life span	20	10
Caloric density of food	+++	+

Aves

Burrowing owl
Athene cunicularia

Greylag goose
Anser anser



	Burrowing owl	Greylag goose
Total sleep	14.3	6.4
REM sleep	0.7	0.7
Body weight (kg)	0.120	3.3
Brain weight (kg)	0.003	0.011
Brain/body weight ratio	0.025	0.003
Life span	8	8
Caloric density of food	+++	+

f0060 **FIGURE 12.6** Sleep, brain, and life span parameters across mammalian orders and the avian class. The strongest correlate of sleep time across species is diet. Animals that eat food with high caloric density do not need to spend as much time ingesting food as animals that eat food with low caloric density. In zoos and laboratories, where most sleep studies have been done and animals are well fed, carnivores sleep more than omnivores, who sleep more than herbivores. However, food deprivation increases waking and decreases sleep in carnivores and omnivores. Flexibility in sleep time increases the likelihood that energy input and output will be equalized and that there will be time for other essential tasks, such as mating and care of young. +++, Carnivores; ++, omnivores; +, herbivores. Sleep durations in hours/24-hour period; life span in years. (Owl data from http://Birdsflight.com; photos of other animals courtesy of Wikipedia Commons site.)

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Abstract: The most popular approach to understanding the function of sleep is to perform sleep deprivation in humans or in animals and note the resulting deficits. It can then be concluded that the function of sleep is to prevent these deficits. An obvious problem with this approach is that the deficits may result from the stress and disruption produced by the deprivation rather than the sleep loss itself. Although this problem has been recognized, it is very difficult to deal with. Awakening that the clinician sees as benign can be perceived as stressful by the subject. This is clear in humans and even more obvious in uncooperative or uncomprehending animals. An alternate approach, based on the assumption that sleep has universal function(s), is to determine the amount of sleep across species under natural, zoo, or laboratory conditions in which the environment can be controlled. Species vary greatly in body and brain size, cognitive abilities, metabolic rate, body temperature, predator-prey status, diet, and a host of other aspects. They also vary considerably in total sleep amounts and amounts of REM and non-REM sleep. Correlation of these species-specific aspects with sleep quality amount leads to important insights into the evolution and function of sleep.

Key Words: Mammals, cetaceans, unihemispheric, platypus, migration, predator, prey, carnivore, herbivore, omnivore