

## PERSPECTIVES

## SLEEP — OPINION

## Sleep viewed as a state of adaptive inactivity

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Darwin200

**Abstract** | Sleep is often viewed as a vulnerable state that is incompatible with behaviours that nourish and propagate species. This has led to the hypothesis that sleep has survived because it fulfills some universal, but as yet unknown, vital function. I propose that sleep is best understood as a variant of dormant states seen throughout the plant and animal kingdoms and that it is itself highly adaptive because it optimizes the timing and duration of behaviour. Current evidence indicates that ecological variables are the main determinants of sleep duration and intensity across species.

Sleep is a rapidly reversible state of reduced responsiveness, reduced motor activity and reduced metabolism. In mammals and birds, sleep can be divided into rapid eye movement (REM) and non-REM states, which can be differentiated through electroencephalographic (EEG) measurements of brain activity and electromyographic (EMG) measurements of muscle activity. In many other vertebrate and invertebrate species, sleep-like states of reduced activity and responsiveness have been documented. Although it has been proposed that sleep has a universal physiological function across all species, there is no consensus as to what that function might be.

In this Perspective I show that many behavioural, physiological and neurological aspects of sleep differ greatly between species and even within a species under different conditions. I propose that sleep should be viewed not as a vulnerable, maladaptive state that has persisted because it contains some unknown adaptive physiological function, but as a state that increases the efficiency of behaviour by regulating its timing and by reducing energy use<sup>1–5</sup> when activity is not beneficial. In this view, sleep can best be understood as one of the states of dormancy that are common throughout the plant and animal kingdoms.

Many species have evolved daily or seasonal dormancy patterns that allow them to anticipate periods that are not optimal for survival and propagation. In other species,

dormancy is triggered by environmental conditions. States of dormancy exist in living organisms with and without nervous systems (BOX 1).

**Sleep and dormant states**

In the mammalian class there is a continuum of dormant states that ranges from hibernation to continuous activity. Small animals that live in temperate zones or frigid environments and cannot migrate long distances often survive the winter by hibernating. This condition is entered from sleep. During hibernation, body temperature can be reduced to as low as  $-3^{\circ}\text{C}$ , cortical EEG activity largely ceases, neuronal activity throughout the brain is greatly reduced and responsiveness and energy consumption are greatly decreased<sup>6</sup>. Full arousal from hibernation can take an hour or more. Torpor<sup>6</sup> is another form of dormancy that, like sleep, can occur daily and is entered through sleep. Animals in shallow torpor are less difficult to arouse than hibernating animals, but are still unable to respond quickly when stimulated. Bears have extended periods of deep sleep in the winter during which their metabolic rate and body temperature are reduced (the latter by  $4\text{--}5^{\circ}\text{C}$ )<sup>7</sup>, but they remain much more responsive than animals in hibernation or torpor.

Sleep can be considered as a state of adaptive inactivity that lies on this continuum (FIG. 1). What is most remarkable about sleep

is not the unresponsiveness or vulnerability it creates, but rather its ability to reduce activity and body and brain metabolism while still allowing a high level of responsiveness relative to the states of dormancy described above. The often cited example of a parent arousing at a baby's whimper but sleeping through a thunderstorm dramatizes the ability of the sleeping human brain to continuously process sensory signals and trigger complete awakening to significant stimuli within a few hundred milliseconds. This capacity is retained despite the  $\sim 30\%$  reduction in cerebral energy consumption during non-REM sleep relative to quiet waking<sup>8–10</sup>. Neuronal recording studies suggest that subcortical energy savings during non-REM sleep are likely to be even greater<sup>11</sup>. In humans the brain constitutes on average 2% of the total body weight but consumes  $\sim 20\%$  of the energy used during quiet waking<sup>12</sup>, so these savings have considerable adaptive significance. These energy consumption benefits are in addition to the survival benefits of the reduction in activity that is enforced by sleep, for example reduced risk of injury, reduced resource consumption and, in many cases, reduced risk of detection by predators (which in part are also achieved simply by resting)<sup>13</sup>.

**Sleep duration varies**

Total sleep time in mammals varies from fewer than 3 h to more than 20 h per day, and the portion of sleep devoted to the REM state varies from perhaps 0 h to 8h<sup>4,5</sup>. Current evidence suggests that short-sleeping animals do not make up for their short sleep duration by sleeping more 'deeply' as assessed by arousal threshold criteria, slow-wave amplitude or REM sleep percentage. Rather, it seems that the reverse is true, namely that long-sleeping animals sleep more deeply, just as humans and other species sleep more deeply during the developmental stages in which they sleep the most<sup>4,14–20</sup>. Lions sleep long and deeply, whereas one example of their prey, giraffes, have one of the lowest recorded sleep durations<sup>4</sup> and must not sleep deeply if they are to survive.

A common approach to testing hypotheses as to the function of sleep has been to correlate sleep duration in the relatively small number of mammals studied (60–70 of

the more than 4,000 mammalian species) with various physiological variables. However, these studies have produced conflicting results. Some have found that total sleep time is negatively correlated with body mass<sup>3,21,22</sup>, whereas others report a positive correlation with body mass<sup>23</sup>. It has been shown that a relation between mass and sleep duration holds only for herbivores and is weak even in these species<sup>4</sup>. This study also showed that carnivores sleep more than omnivores, which in turn sleep more than herbivores. Thus, the relation between sleep and body mass is unlike the inverse relationship between body mass and mass-specific metabolic rate and might be related to the calorific density of consumed foods<sup>24</sup>.

Some studies have found that REM sleep duration is negatively correlated with brain size<sup>21,22</sup>, others report a positive relation between the two<sup>25</sup> and still others see no relation<sup>26</sup>. Two studies found a positive relation between REM sleep duration in adulthood and the level of immaturity at birth (that is, species born in a less mature state had more REM sleep in adulthood<sup>21,22,25</sup>), but another study showed the opposite relation<sup>23</sup>. In general all of these correlational studies are derived from the same published data but use different mathematical techniques to weight each species' sleep times to 'correct' for over-represented species and extract relations between sleep and other factors.

The only study correlating body mass or various physiological variables with REM and non-REM sleep duration in birds found no significant correlations<sup>27</sup>, suggesting that any relation between physiological variables and total sleep time or REM or non-REM sleep duration in mammals does not generalize to all homeotherm (warm-blooded) animals. This conclusion is inconsistent with the hypothesis that any of these variables has a universal relation to sleep duration.

### Sleep physiology and neurochemistry

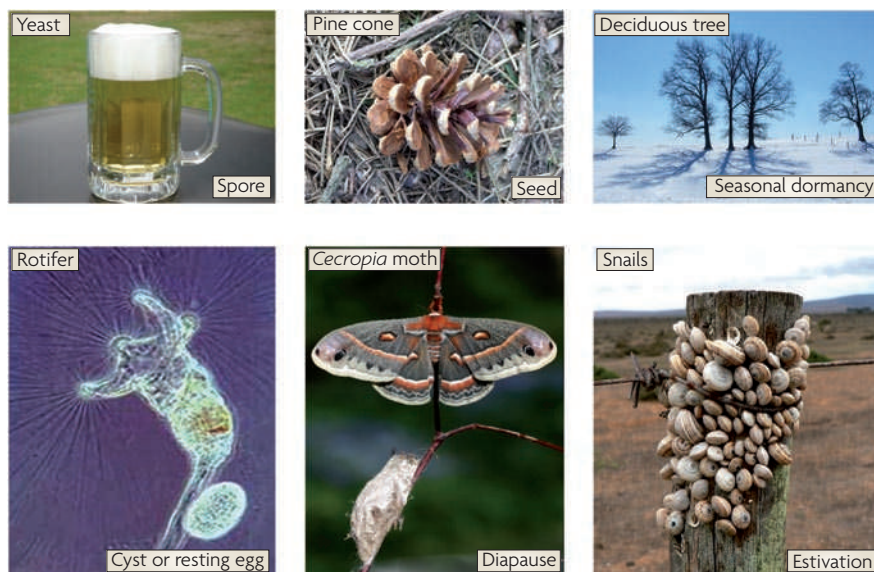
Many fundamental species differences in the physiology and neurochemistry of sleep have been identified even within the mammalian class, even though relatively few studies have examined this issue. Sleep deprivation by the 'disk-over-water' technique (which forces animals to walk, and thus to wake up, every time it has been detected that they have fallen asleep) is lethal to rats<sup>28</sup>, but depriving rats of sleep using other techniques has not been shown to be lethal and there are to date no reports that sleep deprivation is lethal in mice. Long-term deprivation of sleep in pigeons by the disk-over-water technique caused neither death nor any of the other thermoregulatory or health effects seen in rats deprived of sleep by the same technique<sup>29</sup>.

Human stage 4 slow-wave (non-REM) sleep is correlated with growth hormone secretion, although slow waves are not necessary for release of growth hormone<sup>30</sup>. However, in dogs and rats growth hormone secretion normally occurs during waking, not sleep<sup>31,32</sup>. Melatonin release is maximal during sleep in diurnal animals but is maximal during waking in nocturnal animals<sup>33</sup>. Erections are present during REM sleep in humans and rats<sup>34</sup> but only during non-REM sleep in the armadillo<sup>35</sup>. Arousal threshold is lowest during REM sleep in humans but is highest during REM sleep in rats<sup>5</sup>. There are major differences in the extent of sleep rebound after deprivation between different strains of mice<sup>36</sup>. These data illustrate the substantial differences between species and strains in the physiological and hormonal correlates of sleep, undermining the idea that sleep is physiologically similar across mammals.

### Sleep in monotremes

Most of the quantitative analyses of homeotherm sleep mentioned above excluded what were felt to be unusual species, including monotremes, marine mammals and birds. Such species could in fact hold the most important clues to the function of sleep across species, because they demonstrate that several of the features that are often

### Box 1 | Dormancy in plants and non-homeotherm animals



Many unicellular organisms have evolved to live in environments that can sustain them for only a small portion of the year, often remaining dormant for long periods of time. A colony of yeast trapped inside a Lebanese weevil covered in amber for 45 million years has been brought back to life and used to brew a modern beer (see [Food In The Fort](#) blog). In the plant kingdom, seeds such as those in pine cones (see the figure) are dormant until the correct season and until the correct heat, moisture and pH conditions are present. A lotus seed produced a healthy tree after a 1,300-year period of dormancy<sup>91</sup>, and seeds from an arctic tundra lupine produced healthy plants after a 10,000-year period of dormancy<sup>92</sup>. Most deciduous trees and plants have seasonal periods of dormancy during which they cease to photosynthesize (abscission).

Bdelloid rotifers form cysts and become dormant for days to months<sup>93</sup>. Parasites can remain dormant in an animal's tissues for years, emerging during periods when the immune system is compromised<sup>94</sup>. Some invertebrate parasites defend themselves during dormancy by forming a protective cyst<sup>95</sup>. Many insect species respond to unfavourable conditions by entering an analogous state called diapause, a state of reduced metabolism that may last for months or years<sup>96</sup>. Fish<sup>97</sup>, mollusks and reptiles<sup>98</sup> enter a hibernation-like state called estivation, which lasts for months, to avoid damage from high temperatures and desiccation.

Thus, animals that are not homeothermic (warm blooded) and even species that do not have neural tissue have extended periods of dormancy as a normal part of their life cycle and in many cases as the majority of their life cycle. These inactive periods are generally viewed as highly adaptive.

Image credits: beer courtesy of G. Barber; pine cone courtesy of B. Hanmer; deciduous trees courtesy of J. Barr; rotifer courtesy of W. van Egmond; *Cecropia* moth courtesy of S. Malcolm; estivating snails courtesy of G. Joubert.



**Figure 1 | A continuum of states, from adaptive inactivity to high activity, in homeotherms.** States of adaptive inactivity include hibernation, torpor and sleep. Hibernation is the deepest form of dormancy in mammals, taking many minutes to reverse. Some bats, many species of rodents, marsupials and insectivores hibernate. The term torpor has been used to include not only extended periods of inactivity termed hibernation but also shorter periods of greatly reduced metabolism that may last as little as one night and that are frequently seen in birds and small mammals, such as certain species of bats and rodents. The walrus has recently been observed to spontaneously stop sleeping for periods of several days. Birds exhibit greatly increased duration of waking during migratory periods. Cetacean mothers and calves are continuously active for several weeks after birth. Image credits: ground squirrel courtesy of H. Carey; hummingbird courtesy of E. Sullivan; dog courtesy of P. K. Friedman, walrus courtesy of Y. Komine; white-crowned sparrow courtesy of W. Kitundu; killer whale courtesy of M. Aguilera/SeaWorld San Diego.

considered to be integral to sleep are not always present in homeotherm animals.

The mammalian class can be divided into three subclasses: placentals, marsupials and monotremes. There are just three extant monotreme species: the short-beaked and the long-beaked echidna and the platypus. Although they have fur and nurse their young, monotremes lay eggs and have certain genetic<sup>37</sup> and physiological similarities to birds and reptiles.

We found that sleep in the echidna is characterized by a REM sleep-like activity pattern in the brainstem, which occurred while the forebrain showed non-REM sleep-like brain wave patterns<sup>38</sup>. Other investigators also concluded that the echidna had a REM sleep-like state<sup>39</sup>. Similarly, we found that the platypus forebrain EEG exhibited non-REM sleep-like, high-voltage activity while REM sleep occurred in brainstem systems (see [Sleep in the Monotremes Platypus and Echidna video](#))<sup>40</sup>. Not only was the twitching and eye movement activity during platypus sleep equal to or greater in intensity than that seen during REM sleep in other animals, but the daily amount of the brainstem REM sleep-like state was greater than in any other animal.

Thus, it seems that brainstem REM-like sleep was probably present in early mammals, perhaps in large amounts. It is possible that the brainstem quiescence during non-REM sleep (and the resulting reduction in brain energy consumption) and the cortical activation during REM sleep — perhaps facilitating alertness on awakening — are the most recently evolved aspects of mammalian sleep.

There were scattered early reports that claimed to show REM sleep in reptiles; however, these have not been replicated<sup>41–47</sup>. When we applied the recording techniques

we had used in the echidna to the turtle we saw no evidence of forebrain slow waves resembling those in mammalian non-REM sleep and no phasic brainstem neuronal activity resembling that of REM sleep during quiescent states<sup>48</sup>.

#### Marine mammal ‘sleep’ is different

**Walrus.** A recent study of the walrus (FIG. 1) revealed that these bottom-feeding animals frequently remain continuously active for periods of several days, even when they are fully fed and under no apparent stress<sup>49</sup>. Such behaviour has not been reported in any land mammals. Animals living in marine environments might not be as strongly affected by circadian variables because their evolution has been shaped by marine tidal and weather features.

**Cetaceans (dolphins and whales).** REM sleep and periods of bilateral slow-wave (non-REM) sleep are present in all land mammals studied to date, but clear signs of these states have not been detected in cetaceans. Cetaceans do produce unihemispheric slow waves (USWs), which can be confined to one hemisphere for as long as 2 h<sup>50</sup>. When USWs are present the animals sometimes float at the surface, which might represent sleep, but often they continue swimming.

Large cetaceans may float or sink and remain motionless for several minutes when USWs are present, but in smaller cetaceans, such as the harbour porpoise<sup>51</sup> and Commerson’s dolphin<sup>52</sup>, motor activity is essentially continuous from birth to death. Continuous motion could help to maintain body temperature — which is lost more rapidly in animals with a greater surface area to volume ratio — and also is needed

to maintain the position in the water. When cetaceans of any size swim while USWs are being produced, their motor activity is not asymmetric and they continue to avoid obstacles, including conspecifics. Therefore, brain sensory and motor processing and neuronal activity rates must differ radically during this USW state from those seen in land mammals during non-REM sleep, in which such systems have minimal activity and sensory response thresholds are substantially elevated<sup>11,53</sup>. It is difficult to accept the behaviour of swimming with USWs as sleep without discarding all aspects of the behavioural definition of sleep that we apply to other animals<sup>5</sup>. During USWs cetaceans achieve a reduction of energy use in one brain hemisphere<sup>8–10</sup> while exhibiting behaviour, brain activity (in the other hemisphere and subcortically) and sensory–motor responsiveness that, together, are best described as waking. Slow waves and related EEG activity are an adaptation that allows animals to continue to monitor the environment while minimizing brain energy consumption. In land mammals this EEG pattern is bilateral and is confined to periods of behavioural sleep. Only in pathological states is gross motor activity seen in land mammals during states with high-voltage EEG, and when it occurs it frequently causes serious injury<sup>54</sup>.

**Otariids (eared seals).** On land, sleep in the fur seal generally resembles that in most land mammals. The EEG is bilaterally synchronized and the animal closes both eyes, seems 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 behaviour, with one of the flippers being active in maintaining body



position while the other flipper is inactive. This differs from the symmetrical, bilateral movements of the dolphin during USWs. During this behaviour, the fur seal produces USWs and there is a reduction in acetylcholine release<sup>55</sup> in the hemisphere contralateral to the immobile flipper. Therefore, it seems that half of the brain and body may be ‘asleep’ and the other half ‘awake’. The diversity of sleep characteristics in tetrapods is illustrated in FIG. 2.

**Sleep rebound is variable**

Sleep rebound is an increase in sleep after a period of sleep loss. It is thought to be homeostatically regulated, like many physiologically vital functions, and has been considered to be a defining feature of sleep. It

has been most extensively studied in rodents and humans. Typically 30% or less of the duration of lost sleep is recovered after deprivation. During rebound, slow-wave amplitude and duration are sometimes but not always increased<sup>56,57</sup>. In fact, the effects of long-term sleep deprivation on alertness, thermoregulation, skin condition and immune function in rats deprived by the disk-over-water method are completely reversed by a rebound consisting mainly of REM sleep<sup>5,28</sup>. Sleep rebound in humans can also be primarily comprised of REM sleep, with an actual reduction of non-REM sleep<sup>58</sup>. Short-term deprivation tends to be followed by a non-REM sleep rebound and long-term deprivation by a REM sleep rebound. A similar, ~30%, ‘sleep’ rebound

is seen in other species, including some invertebrates<sup>59</sup>.

One might wonder why animals that have the ability to regain lost sleep in ~30% of the time that it would normally have taken have not evolved shorter sleep durations to take advantage of the presumed benefits of being awake. However, if sleep is viewed as a form of ‘adaptive inactivity’ this question is answered. A small sleep rebound may be necessary to compensate for processes that can only occur, or only occur optimally, in sleep, but in each species the major determinant of sleep duration is the trade-off between the evolutionary benefits of being active and awake and those of adaptive inactivity.

Sleep rebound does not always occur in some species or under some conditions. This

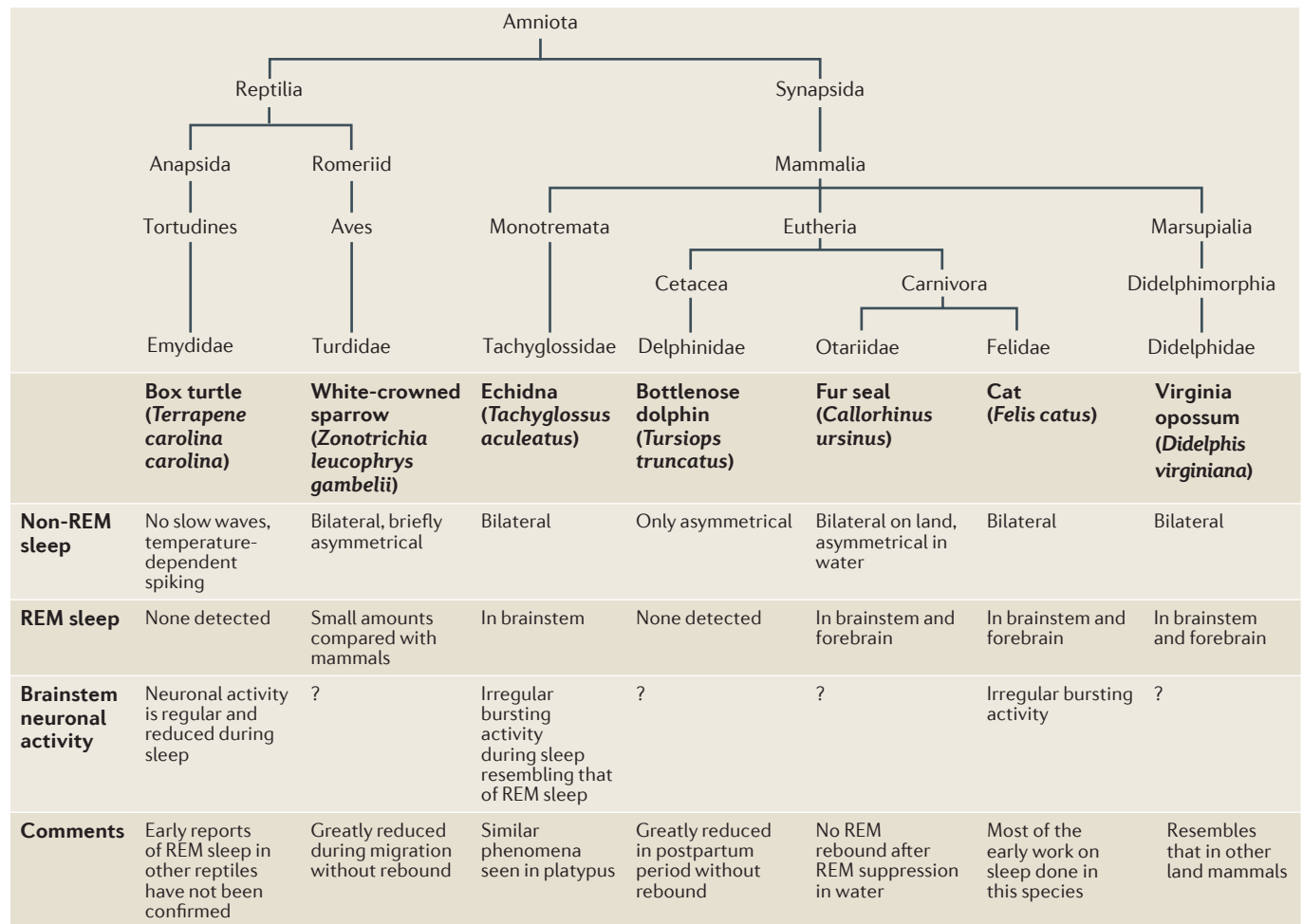


Figure 2 | **Diversity of sleep in tetrapods.** A phylogenetic tree, with representative animals, which shows that aspects of sleep such as rapid eye movement (REM)-like and non-REM-like cortical activity and brainstem activity differ greatly between species. Slow waves and spindles are electroencephalographic (EEG) patterns that are typical of non-REM sleep in mammals, but they are not seen in turtles. Indeed, turtles show little change in forebrain EEG between waking and sleep states, although EEG spikes may occur at certain temperatures. No REM sleep-like activation of brainstem neuronal activity has been observed during sleep states

in the turtle<sup>48</sup>. Slow waves are briefly asymmetrical in sleeping birds, always asymmetrical in cetaceans and mostly asymmetrical in fur seals when they are in water but not when they are on land. Sleep duration is greatly reduced during migration in the white-crowned sparrow and no long-duration periods of sleep-like behaviour occur in the postpartum period in examined cetacean species. Recordings of neuronal activity have not been performed during sleep in birds, cetaceans or seals. Sleep in studied marsupial mammals seems to resemble that in placental mammals<sup>121</sup>.

challenges the idea that sleep is always homeostatically regulated. When fur seals stay in the water for extended periods, as they do for periods of months in winter, REM sleep duration is greatly reduced, by up to 90% of its level on land. There is no rebound of lost REM sleep when the fur seals return to land, even after several weeks in the water<sup>60</sup>. The only study of USW rebound after USW deprivation in dolphins produced variable results, with little or no relation between the amount of slow-wave activity lost in each hemisphere and the amount of slow-wave activity recovered when the animals were subsequently left undisturbed<sup>61</sup>. Another study showed that dolphins can maintain continuous vigilance for 5 days with no progressive decline in response accuracy. At the end of this period there was no detectable decrease of activity from normal levels and no evidence of inattention or sleep rebound such as would be expected of a rat or human after sleep deprivation<sup>4,5,62,63</sup>.

Newborn dolphins and killer whales and their mothers show an almost total lack of extended periods of sleep-like immobility for several weeks during the postpartum period, when these animals normally migrate (FIG. 1). This is followed by a slow increase to baseline levels with no evidence of rebound or longer than normal periods of immobility<sup>64</sup>. Both eyes are open when the animals surface at average intervals of less than 1 minute, indicating that any slow-wave pattern could not last longer than this period<sup>64</sup>; human 'sleep' is not restorative if interrupted on such a schedule<sup>65</sup>. Similar extended periods of alertness with a lack of sleep rebound occur in white-crowned sparrows during their normal migratory periods<sup>66</sup>. Manic humans also have greatly reduced sleep duration for extended periods and there is no persuasive evidence for progressive loss of physiological function during manic phases or for subsequent sleep rebound. Zebrafish deprived of 'sleep' for 3 days by placement in continuous light show no rebound when they are returned to a 12 h–12 h light–dark cycle. On the other hand, when they are sleep-deprived through repetitive electrical stimulation they do show rebound<sup>67</sup>; the cause of this difference has not been identified.

Some aspects of rebound can be due to the deprivation procedure rather than the sleep loss. For example, in rats restraint can produce increased REM sleep even when no sleep has been lost. This is mediated by the stress-induced release of pituitary hormones<sup>68–70</sup>. It is possible that aspects of sleep rebound are driven by a loss of sleep-linked hormone release or by changes induced by

the sleep deprivation procedure that may be species-specific and rapidly reversible, rather than by some intrinsic universal property of sleep.

### Conclusions and future directions

Sleep can be seen as an adaptive state that benefits animals by increasing the efficiency of their activity. It does this by suppressing activity at times that have maximal predator risk and minimal opportunity for efficiently meeting vital needs, and by permitting activity at times of maximal food and prey availability and minimal predator risk. It also increases efficiency by decreasing muscle tone and brain and body metabolism during periods of inactivity, analogous to turning out the lights when you leave a room. Thus, the inactivity associated with sleep not only saves energy but also is useful *per se* as it reduces the risk of injury and predation. However, unlike the dormant states that occur in some plants, simple multicellular organisms and ectothermic organisms, and the hibernation and torpor that occur 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 might be to promote this rapid response through periodic brainstem activation and brainstem warming in homeotherms<sup>4,5,71,72</sup>. For animals that are vulnerable because of their size or ecological niche if they reduce responsiveness and for animals that require time-consuming consumption of large amounts of low-calorific-density foods, constant care of offspring or other activities, the risks of deep sleep may outweigh its energetic savings, making it favourable for them to have sleep of reduced depth and duration, or even no sleep at all<sup>5</sup>. Animals that need to seek food or mates when they are likely to be available or that need to migrate to avoid famine, cold or heat benefit from reduced sleep and increased activity at these times. Conversely, one can expect evolution to have selected animals that increase their sleep duration — and so avoid the risk and energy expenditure associated with foraging — when food is not available or environmental conditions are not propitious: such inactivity reduces risk of injury, reduces thermoregulatory requirements in species that do not sleep in the open, keeps mothers close to their infants and in many species greatly reduces predation risk.

Many aspects of sleep can be better understood from this evolutionary perspective: the long sleep duration of young humans could be an energy conservation measure at an age with a relatively high metabolic rate

and at which vital needs are attended to by older members of the family. Conversely, the decrease in sleep duration with aging could be a correlate of reduced metabolic rate and a consequent change in the adaptive trade-off between waking tasks and sleep benefits.

The big brown bat specializes in eating mosquitoes and moths. It sleeps for 20 h a day<sup>22</sup>, making it perhaps the longest-sleeping mammal. The long sleep period of this animal could be explained by the need for some time-consuming, unknown process that occurs only during sleep and requires 20 h to complete. However, it seems more easily explained by the ecological specializations of this bat, which include echolocation and selective predation on flying insects that are active only between dusk and the initial hours of darkness. Increased waking time would seem to be highly maladaptive for this animal, since it would expend energy and be exposed to predatory birds with better vision and better flight abilities if it became active earlier in the circadian cycle. If it stayed out later, it would expend energy but not be as successful in hunting. Similarly, it is adaptive for bears<sup>7</sup>, elephants<sup>73</sup> and reindeer<sup>74</sup> to increase sleep in the winter because their food is not available during that season. It is adaptive for large adult herbivores to maximize waking time in order to eat and remain alert to deal with predators, explaining their short sleep durations. Similarly, 'sleep' time in ectothermic animals is probably primarily determined by the effects of temperature, light and other environmental variables on survival in the wild, rather than by any information processing or physiological maintenance requirement. An approach that takes the environmental conditions in which each species evolved into account may better explain the variance in sleep duration between mammals.

It has been claimed that sleep has an essential role in learning, but recent evidence has disputed these claims<sup>75–81</sup>. It has also been suggested that sleep is associated with neurogenesis<sup>82</sup>, 'synaptic downscaling'<sup>83</sup>, immune system regulation<sup>84–87</sup> or reversal of oxidative stress<sup>88,89</sup> in mammals, and persuasive evidence has been presented for some of these claims. It remains to be seen whether these or any other vital functions can be performed only in sleep<sup>90</sup> or whether they are performed in sleep in a wide variety of species (BOX 2). However, this Perspective suggests that, although many such processes undoubtedly occur in sleep, such functions cannot explain the variation of sleep amounts and the evident flexibility of sleep physiology and neurochemistry within and between animals. Why would some species

## Box 2 | Some theories of sleep function

A large number of theories of sleep function have been proposed, but none is well established. Many theories seem to be mutually exclusive, whereas others might not be incompatible.

'Information processing theories' include claims that either non-rapid eye movement (non-REM)<sup>99</sup> sleep, REM sleep<sup>100</sup> or both<sup>101</sup> are required or important for forming new neural connections for memory consolidation. By contrast, other theories propose that the main function of either REM sleep<sup>102</sup> or non-REM sleep<sup>103</sup> is to remove unimportant connections from the brain, thereby making room for more information.

One theory holds that REM sleep is important for development, because it is maximal at birth in land mammals<sup>104</sup>. Other work emphasizes instead the role of non-REM sleep in brain development<sup>105</sup>.

It has been proposed that REM sleep is important in stimulating the cortex<sup>106</sup> or awakening the animal so that it can check the environment<sup>72</sup>. By contrast, Freud held that dreams are a disguised attempt at wish fulfilment that have the important function of preserving sleep<sup>107</sup>.

Another theory holds that sleep is necessary to reverse damage that occurs in waking, including oxidative stress<sup>88,89,108</sup>, depletion of energy stores<sup>109</sup>, death of neurons in the hippocampus and olfactory bulb<sup>82</sup> and downregulation of receptors<sup>110</sup>. It has been proposed that brain and body cooling are a principal homeostatic function of sleep<sup>111</sup>. The regulation of K<sup>+</sup> channels has been proposed to be an essential homeostatic controller of sleep<sup>112,113</sup>. It has been proposed that sleep time is linked to parasitic load<sup>87</sup>. A related idea holds that sleep promotes longevity, but the phylogenetic evidence does not support this hypothesis<sup>114</sup>. Lifespan in the best-studied species, humans, does not correlate positively with sleep duration<sup>115–117</sup> (this, of course, should not be taken to suggest that sleep deprivation does not affect health)<sup>118,119</sup>.

The observation that some electroencephalographic aspects of sleep occur in sleep-deprived individuals has led to the proposition that short periods of electroencephalographic change or change in local processes in small groups of neurons may have recuperative function in a state that might best be described as waking<sup>90</sup>.

It has long been thought that ecological factors were correlated with the duration of sleep<sup>120</sup>. This idea has generally been presented as an adaptation of sleep's functional role to the environment rather than as indicating that sleep itself has an adaptive benefit. The history and development of these views is discussed in greater detail in the main portion of this article.

need so much more of the mysterious restorative process that has been proposed to determine sleep duration than other species?

Viewing sleep as a period of species-specific, well-timed adaptive inactivity can better explain this variation. Studies in simpler organisms are vital because they can reveal common genetic mechanisms that regulate periods of activity and inactivity. However, the diversity of sleep and sleep-like states across mammals and tetrapods demonstrates that sleep phenomena are highly variable across species.

Studies that monitor waking and sleep under natural conditions and in the context of ecological variables are becoming possible with advances in telemetry and digital storage technology. Investigations using such techniques may help us to better understand the dynamic and adaptive functions of sleep. Such studies should evaluate not only sleep parameters, but also the 24 h time budget of waking behaviour in each species, including time spent hunting, eating, grooming, in sexual activity, in taking care of newborns and in engaging in other behaviours, and should evaluate how they vary with environmental conditions in order to better understand the adaptive role of sleep.

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**FURTHER INFORMATION**

Jerome M. Siegel's homepage:  
<http://www.semel.ucla.edu/sleepresearch>  
**Food In The Fort blog:**  
<http://www.foodinthefort.com/tag/raul-cano/>  
**Sleep in the Monotremes Platypus and Echidna video:**  
<http://www.npi.ucla.edu/sleepresearch/media.php>

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