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*Phil. Trans. R. Soc. B* 2010 **365**, 945-959

doi: 10.1098/rstb.2009.0209

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*Review*

# The ecological relevance of sleep: the trade-off between sleep, memory and energy conservation

Timothy C. Roth II<sup>1,\*</sup>, Niels C. Rattenborg<sup>2</sup>  
and Vladimir V. Pravosudov<sup>1</sup>

<sup>1</sup>*Department of Biology, University of Nevada, Reno, NV 89557, USA*

<sup>2</sup>*Sleep and Flight Group, Max Planck Institute for Ornithology, Seewiesen, Eberhard-Gwinner-Strasse, 82319 Starnberg, Germany*

All animals in which sleep has been studied express signs of sleep-like behaviour, suggesting that sleep must have some fundamental functions that are sustained by natural selection. Those functions, however, are still not clear. Here, we examine the ecological relevance of sleep from the perspective of behavioural trade-offs that might affect fitness. Specifically, we highlight the advantage of using food-caching animals as a system in which a conflict might occur between engaging in sleep for memory/learning and hypothermia/torpor to conserve energy. We briefly review the evidence for the importance of sleep for memory, the importance of memory for food-caching animals and the conflicts that might occur between sleep and energy conservation in these animals. We suggest that the food-caching paradigm represents a naturalistic and experimentally practical system that provides the opportunity for a new direction in sleep research that will expand our understanding of sleep, especially within the context of ecological and evolutionary processes.

**Keywords:** hypothermia; food caching; birds; mammals; synaptic plasticity; torpor

## 1. INTRODUCTION

Animals make numerous behavioural decisions, and one of the major goals of behavioural ecology is to understand the fitness consequences of such decisions. Behaviour may affect fitness in a variety of ways. To maximize fitness, animals must manage and balance competing selection pressures, which may result in a variety of trade-offs. For example, most prey species must balance the risk of starvation with the risk of predation while foraging (Lima & Dill 1990). In this case, an animal cannot maximize foraging rates to avoid starvation because it would lead to increased predation risk. However, the animal cannot maximize safety by avoiding all predators as this tactic will reduce its ability to forage and, thus, will result in certain starvation. Hence, a trade-off results.

One topic seldom considered by behavioural ecologists as an important factor of fitness is sleep. Although we do not fully understand sleep, we know that it is a critically important behaviour (Cirelli & Tononi 2008; Mignot 2008). Even moderate sleep deprivation can have an adverse impact on immune function (Majde & Krueger 2005; Imeri & Opp 2009; Preston *et al.* 2009), neurogenesis in the adult brain (Guzman-Marin *et al.* 2005; Mueller *et al.* 2008) and neural

physiology (McDermott *et al.* 2003). In some cases, extreme sleep deprivation can lead to death (Rechtschaffen & Bergmann 2002). Sleep loss also impairs alertness (Dinges *et al.* 1997), interferes with the consolidation of recently acquired information and may impair an animal's ability to acquire new information (Hairston *et al.* 2005). Therefore, sleep, like foraging, reproduction and predator avoidance, is very likely a necessary component of fitness. Furthermore, in general terms, sleep is a largely exclusive state that precludes an animal from performing other tasks. Sleep is, thus, a behaviour that might often be in conflict with other behaviours (Lima *et al.* 2005) and should be considered among possible fitness trade-offs.

Here, we emphasize the importance of including sleep when considering behavioural trade-offs. To illustrate the notion that trade-offs between sleep and other behaviours may exist, we highlight an ecologically relevant food-caching model in which a conflict might occur between memory and energy conservation. Briefly, many food-caching birds such as those in the family Paridae rely on spatial memory to store many thousands of food items during the winter (e.g. Shettleworth 1995; Roth *et al.* 2010; Smulders *et al.* 2010). Their survival appears dependent upon these caches, and thus there is likely strong selection pressure for accurate spatial memory. It has been hypothesized that such selection pressure should result in enhanced memory and in modifications in

\* Author for correspondence (tcroth@unr.edu).

One contribution of 10 to a Theme Issue 'Integrating ecology, psychology and neurobiology within a food-hoarding paradigm'.

neural mechanisms supporting spatial memory such as the hippocampus (Krebs *et al.* 1989; Sherry *et al.* 1989), a hypothesis that has been under intensive scrutiny (Roth *et al.* 2010; Smulders *et al.* 2010). However, many of these small birds also live in extremely harsh climates and may drop their body temperature at night (i.e. enter a state of hypothermia) in order to conserve energy (e.g. Reinertsen & Haftorn 1983). Energy management and conservation, such as nocturnal hypothermia, appear to be important adaptations to survival in harsh climates, but recent work suggests that sleep, which is important for memory (e.g. Mignot 2008), may not be compatible with torpor and thus energy conservation (e.g. Palchykova *et al.* 2002). Therefore, a trade-off may exist between sleeping for memory and entering torpor for energy conservation. We will explore this idea in detail below. Moreover, we will describe how this naturalistic avian food-caching paradigm, in which selection results in natural variation in memory and learning, may be a crucially important model for addressing questions about the evolution of sleep and its functions.

## 2. WHY WE SLEEP

All animals adequately studied to this point appear to engage in sleep (Cirelli & Tononi 2008). Sleep is broadly defined as a rapidly reversible period of immobility characterized by (i) a change in the neurophysiology of the brain, (ii) a characteristic posture, (iii) an increased response threshold to external stimulation, and (iv) homeostatic regulation (Tobler 1995). In arthropods, for example, sleep is simply characterized behaviourally by a quiescent period with an increased arousal threshold to external stimuli such as light and a characteristic dropped antenna posture (van Swinderen 2007). Although much work has been done in fruit flies (e.g. Shaw *et al.* 2000; Nitz *et al.* 2002; Hendricks & Sehgal 2004) and to a lesser extent in honey bees (Kaiser & Steiner-Kaiser 1983; Kaiser 1988; Sauer *et al.* 2003; Klein *et al.* 2008), work in other invertebrates is sparse. In poikilothermic vertebrates such as fish, reptiles and amphibians, sleep is again predominantly limited to behavioural definitions. Brain activity as measured with electroencephalograms (EEG) from these taxa characteristically shows high-voltage spikes, which are probably associated with sleep (reviewed in Hartse 1994). However, inconsistencies among studies have made the description of definitive sleep patterns in these groups challenging (Hartse 1994; Rattenborg 2007). Only in birds and mammals is sleep categorized by behavioural state as well as unequivocally distinct EEG patterns (see Rattenborg 2006 for review). In birds and mammals, sleep comprises two main states: slow-wave sleep (SWS) and rapid eye movement (REM) sleep. During SWS, the EEG shows high-amplitude, low-frequency activity. The amount of such slow-wave activity (SWA; spectral power density between 0.5 and 4.5 Hz) increases as a function of prior time spent awake and decreases as a function of time spent asleep. This relationship suggests that SWA reflects homeostatically regulated sleep-dependent processes potentially linked to the function

of SWS (Martinez-Gonzalez *et al.* 2008; Rattenborg *et al.* 2009). During REM sleep, the EEG resembles the low-amplitude, high-frequency pattern that occurs during wakefulness. In contrast to wakefulness, however, REM sleep is characterized by decreased responsiveness to the environment and a reduction in muscle tone. Interestingly, birds and mammals are the only taxonomic groups known to exhibit SWS and REM sleep.

The convergent evolution of similar sleep states in birds and mammals might be linked to the convergent evolution of complex brains and associated cognition in each group (Rattenborg 2006; Rattenborg *et al.* 2009). Indeed, it is quite interesting that both mammals and birds appear to have similar sleep patterns despite their independent evolution and differences in brain structures (e.g. birds have no true neocortex, but instead appear to have similarly functioning areas; Rattenborg 2006; Rattenborg *et al.* 2009). For example, instead of a neocortex, birds have a similarly functioning pallium that is organized into four main subdivisions: hyperpallium, mesopallium, nidopallium and arcopallium (Jarvis *et al.* 2005). The avian hyperpallium has a unique organization found only in birds (Medina & Reiner 2000), which functions like the primary visual and somatosensory cortex of mammals. The dorsal ventricular ridge contains the mesopallium, nidopallium and arcopallium and consists of stellate neurons arranged in a non-laminar manner. In birds, the adult pallium is approximately 75 per cent of the telencephalic volume, which is comparable to the pallial neocortex in mammals. It appears to process information in a similar manner to the mammalian sensory and motor cortices (Jarvis *et al.* 2005) and to serve as a linkage between sensory inputs and motor outputs, as does the mammalian cortex.

Although sleep must have some fundamental functions in order to be sustained by natural selection, those functions are still not clear. In fact, the function of sleep has been a topic of much debate over the past 40+ years (Rechtschaffen 1998). Sleep may have some functions associated with energy conservation (Berger & Phillips 1995), immune function (Majde & Krueger 2005; Imeri & Opp 2009; Preston *et al.* 2009), brain metabolism (Benington & Heller 1995), predation risk (Meddis 1975; Lima & Rattenborg 2007; Lesku *et al.* 2008), neural maintenance (Kavanau 1996; Krueger & Obal 2003; Cirelli *et al.* 2005; Tononi & Cirelli 2003, 2006) and/or memory consolidation (Stickgold & Walker 2005). Given the many possible benefits that sleep may provide, it would be short sighted to state that sleep has only one function. In fact, there may be a suite of benefits from the same process of sleep or variations in sub-processes that might produce different benefits (Siegel 2005; Lesku *et al.* 2006; Roth *et al.* 2006; Capellini *et al.* 2008; Mignot 2008). Once an animal becomes unresponsive and takes on the potential costs of sleep to fulfil a primary function, it should also benefit from secondary functions at this time as well.

## 3. THE IMPORTANCE OF SLEEP FOR MEMORY

Sleep seems to be particularly important for the brain and seems to have a function that is incompatible with

the significant sensory processing in wakefulness. The local regulation of SWS intensity indicates that sleep serves a function for the brain itself (Huber *et al.* 2004), an idea that has extensive support (Hobson 2005; Mignot 2008). Evidence for this is particularly striking in aquatic mammals and many (if not all) birds that exhibit interhemispheric asymmetries in SWS intensity, or outright unihemispheric SWS (e.g. Rattenborg *et al.* 2000; Lyamin *et al.* 2008) in which the hemispheres of the brain engage in SWS independently. Unihemispheric sleep may be a way to allow the entire brain to simultaneously engage in two otherwise mutually exclusive tasks, such as sleep and vigilance for predators (e.g. Rattenborg *et al.* 1999). The fact that these animals engage at least one hemisphere in sleep in spite of predation risk suggests that sleep must be important and necessary for overall survival; otherwise it may be expected that animals should abandon sleep entirely at times of heightened risk of predation. Further evidence for the relationship between sleep and the brain comes from numerous studies suggesting that sleep may benefit or facilitate neural maintenance (Kavanau 1996; Cirelli *et al.* 2005; Tononi & Cirelli 2003, 2006), neurogenesis (Guzman-Marín *et al.* 2005) and learning/memory (Ambrosini & Giuditta 2001; Ribeiro *et al.* 2002, 2004; Huber *et al.* 2004; Walker & Stickgold 2004; Derognaucourt *et al.* 2005; Stickgold & Walker 2005). This pattern may also be true over evolutionary time. In a large-scale comparative analysis, Lesku *et al.* (2006, 2009a,b) found a positive association between %REM sleep (the per cent total sleep time comprising REM sleep) and relative brain size in mammals (i.e. encephalization quotient, *sensu* Jerison 1985), suggesting that species with larger brains engage in more REM sleep. The importance of both REM sleep (e.g. Walker & Stickgold 2004) and SWS (e.g. Huber *et al.* 2004) for brain function has been well documented in humans as well.

It appears that sleep may have some function related to brain plasticity (Maquet *et al.* 2003; Tononi & Cirelli 2006), i.e. the ability of the brain to change its structure in response to the environment such as when memories are reorganized and reactivated (Hennevin *et al.* 2007). Extensive research has examined the relationship between plasticity and sleep, especially in regard to learning and memory (see Maquet 2001; Maquet *et al.* 2003 and references therein; Hennevin *et al.* 2007). Much of this work has been directed towards humans and laboratory rats. In particular, such work has supported the idea that sleep might enhance one's ability to learn and remember (Kavanau 1997; Walker & Stickgold 2004; Stickgold 2006; Eichenbaum 2007). For example, sleep enhances the ability to recall spoken language (Fenn *et al.* 2003), spatial memories (Ferrara *et al.* 2003; Peigneux *et al.* 2004), auditory patterns (Gottselig *et al.* 2004), motor skills (Stickgold 2006; Peters *et al.* 2007; reviewed by Blischke & Erlacher 2007) and factual information (Ellenbogen *et al.* 2006a,b). Similarly, sleep in rats also enhances memory (e.g. Lee & Wilson 2002; McDermott *et al.* 2003; Colgin & Moser 2006).

This research further suggests that different types of memory may be enhanced by different types of sleep.

For example, memories involved in performing a task such as riding a bicycle (i.e. procedural memories), may be enhanced by REM sleep (reviewed by Born *et al.* 2006). In contrast, memories involved in remembering abstract ideas and facts (declarative memories) seem to benefit from SWS (reviewed by Born *et al.* 2006). However, there are exceptions to these patterns (e.g. Huber *et al.* 2004; Fogel & Smith 2006), and thus it is not entirely clear if specific sleep states are involved in different types of memory. Indeed, there is still discussion in the field about how to distinguish memory types, the neurological differences between them and how these issues might apply to non-human animals (Poldrack & Foerde 2008); nonetheless, there is overwhelming evidence that in some form sleep does enhance multiple qualities of memory and learning (Marshall & Born 2007).

Despite numerous studies supporting the relationship between sleep and memory, there is still some debate over the role of sleep in memory consolidation and learning. The effects of sleep on learning and memory are often tested by comparing the performance on memory tasks before and after a period of sleep deprivation and then again after sleep (Vertes 2004; Vertes & Siegel 2005). Critics claim that sleep deprivation may impose other physiological limitations, such as stress, that may impair memory performance (reviewed by Frank & Benington 2006), making the distinction between memory loss owing to sleep deprivation and memory loss owing to stress difficult. Whereas this was a valid criticism of many older studies, recent studies have taken steps to avoid this problem (Maquet *et al.* 2003). Huber *et al.* (2004), for example, resolved the possible confound of stress and sleep deprivation by testing subjects within their normal sleep/wake pattern, and their findings still supported the relationship between sleep and learning/memory. In addition, the link between local changes in SWA in specific regions of the brain as related to performance also excludes potential stress effects (e.g. Huber *et al.* 2004; Peigneux *et al.* 2004). Furthermore, recent evidence in birds suggests that moderate levels of chronic stress as measured by corticosterone levels actually increases learning and memory (Pravosudov 2003; see Pravosudov 2005 for full review). However, although the potential confound of stress has been ruled out, the link between sleep (particularly REM sleep) and memory is nonetheless still challenged. Notably, antidepressant drugs such as monoamine oxidase inhibitors reduce or in some cases completely abolish REM sleep (Wyatt *et al.* 1971). Despite the widespread therapeutic use of such drugs, there has been no evidence of mass disruptions to memory or learning (Siegel 2001). In fact, recent work by Rasch *et al.* (2009) found that drug-induced REM sleep suppression had no effect on memory consolidation for word pairs and enhanced memory for finger-tapping skills. In addition, recent work by Ruby *et al.* (2008) suggests that circadian rhythms may play an important role in memory that is independent of sleep itself. They found that eliminating circadian rhythms without reducing sleep significantly reduced memory of novel objects in Siberian hamsters (*Phodopus sungorus*). They suggest that

the circadian rhythm may play an important role in regulating plasticity in the hippocampus. Finally, cetaceans have little, if any, REM sleep (Lyamin *et al.* 2008), yet are thought to be animals highly capable of learning (Siegel 2000, but see discussions in Manger 2006; Marino *et al.* 2008). Thus, it seems that we still have much to learn about the effects of stress, sleep and memory.

#### 4. THE ECOLOGICAL RELEVANCE OF MEMORY

Memory is important for many animals in a variety of different contexts as it represents the method by which they obtain and retain information. For example, foraging animals may need to remember locations of food resources, locations that have already been used and, in the case of food-caching species, the locations of numerous caches (Shettleworth 1995, 1998; Sherry 2006). Memory in food-caching species in particular may be critically important for survival and thus may be highly influenced by natural selection. Memory also plays an important role in spatial use in general, not just in the context of foraging, but also in locating other resources, in knowing the location of refuges, the location of territory boundaries and simply remembering where one has been (Shettleworth 1998). Memory might also be important during social interactions in that animals may benefit from remembering with whom they have interacted (Mateo & Johnston 2000) both to identify potential rivals and kin. Memory is equally important in the development of species-specific calls and song (e.g. Margoliash 2005), even though avian song learning and memory may be fairly unique and rely on different mechanisms than all other types of memory both in birds and mammals (Clayton & Soha 1999). In many birds, for example, songs require intensive periods of practice before the appropriate song is sufficiently learned (Dave *et al.* 1998). Given the importance of memory in a variety of different ecological contexts, it is not surprising that there is strong selection pressure for accurate and flexible memory.

Memories are processed and stored in the brain. The process of memory storage appears to be a complex function of multiple brain regions (Desposito & Grossman 1996; Gilbert 2001) and may be better described as a multidimensional process rather than a direct path (Kenser & DiMattia 1987; Squire 2004). In mammals, memories seem to be initially processed in the hippocampus and later transferred to the neocortex (Wiltgen *et al.* 2004; Frankland & Bontempi 2005). The mechanisms for this memory transfer from one region of the brain to others are not well understood (Squire 2004), but may depend on SWS (Molle & Born 2009). The processing, transfer and storage of memories in birds are even less well known than in mammals. There is some evidence that caudomedial nidopallium plays an important role in the long-term storage of song memories produced elsewhere in the song-control system (Pinaud & Terleph 2008), but the evidence for a similar pattern involving the hippocampus is equivocal. Avian song learning paths are independent of the hippocampus and are uniquely avian (Clayton & Soha 1999), so

this pattern may or may not exist. We do know that spatial memories in particular seem to show strong association with the hippocampus (Sherry & Healy 1998). Lesions and oblations of the hippocampus destroy recent spatial memories and prevent further spatial memory acquisition (Sherry & Vaccarino 1989; Hampton & Shettleworth 1996). Further evidence for the importance of the hippocampus in spatial memory comes from comparative studies showing that animals with better memories have larger hippocampi, both within (Pravosudov & Clayton 2002; Pravosudov *et al.* 2005, 2006; Roth & Pravosudov 2009) and among species (Biegler *et al.* 2001), and have more hippocampal neurons (Pravosudov & Clayton 2002; Cristol *et al.* 2003; Pravosudov *et al.* 2005, 2006). In addition to managing memories, the hippocampus may also play important roles in arousal from and entrance into hibernation in mammals (Horowitz *et al.* 1987) as well as many other behavioural processes (reviewed by Bast 2007).

Adult hippocampal neurogenesis in particular might be important for memory maintenance (Nottebohm 2002). It has now been well established that both mammals and birds generate new neurons in adulthood, and adult neurogenesis is especially intense in the hippocampus (Ehninger & Kempermann 2008). Neurogenesis and apoptosis (cell death) appear to be key components in regulating neuron numbers in the hippocampus (Patel *et al.* 1997) and thus new neurons might be crucial for memory maintenance. However, it is still unclear how new neurons produced during adult neurogenesis are incorporated into old memories (see Bruel-Jungerman *et al.* 2007; Rasch & Born 2007). Many factors resulting in reduced neurogenesis rates also result in deteriorated memory performance, and sleep deprivation in particular has also been linked to lowered cell proliferation rates and neuronal maturation rates in the hippocampus (Guzman-Marin *et al.* 2003, 2005, 2007, 2008; Hairston *et al.* 2005). This result, however, does not appear to be mediated by stress, as adrenalectomized rats also show a reduction in neurogenesis rates following sleep deprivation (Mueller *et al.* 2008; see also Guzman-Marin *et al.* 2007; Meerlo *et al.* 2008). A reduction in REM sleep in particular may be responsible for the reduction in neurogenesis rates (Guzman-Marin *et al.* 2008; Mueller *et al.* 2008), although more research is required to completely separate the effects of SWS and REM sleep. Overall, these findings provide support to the idea that sleep is important for adaptive plasticity in the brain and, hence, may be crucial for memory function itself.

As one of sleep's functions then may be synaptic plasticity in the hippocampus and/or in the entire brain, sleep may be an important part of the ecology of memory. Possibly even small reductions in sleep, and thereby plasticity and neurogenesis rates, may have long-term effects on an animal's memory, which might have fitness consequences for an animal under strong selection pressures in natural settings. Such negative effects might become even more problematic when sleep amount or quality is chronically reduced. However, currently there is little information available about how much and how well animals actually sleep in the wild (but see Rattenborg *et al.* 2008).

## 5. A CONSIDERATION OF ENERGETIC DEMANDS

In harsh climates, energy management and conservation are important for survival. This is particularly true for small animals that have high relative surface areas and thus lose a great deal of heat to the environment (Schmidt-Nielsen 1983). To compensate, animals can increase their metabolic rates to produce more heat, but consequently require increased energy intake rates to fuel that increase in metabolism. For most animals, such an increase in metabolism means increasing foraging rates and thus increasing their exposure to predation, a trade-off that has been well studied, especially in birds (Lima & Dill 1990; Lima 1998). However, for many animals, the increased energy expenditure becomes particularly dangerous at night when they cannot forage and therefore cannot be active to replace lost energy. In such cases, animals must have adequate energy stores to survive the night before ending daily activity, but cannot maintain too much fat during the day as increased weight reduces take-off speeds, thereby increasing predation risk (Houston & McNamara 1993). Surviving the night is easier for larger animals that experience relatively less heat loss and may have relatively larger energy reserves in the form of proportionally more body fat, a larger crop, etc. Smaller animals, however, may not possess such characteristics and instead may use alternative strategies to increase their chances of surviving the night (Reinertsen 1996). For example, many hummingbirds (e.g. Hiebert 1990), mousebirds (*Colius* sp.; e.g. Bartholomew & Trost 1970) and Parid species (e.g. Chaplin 1974, 1976; Reinertsen & Haftorn 1983) reduce their body temperature, and thereby energy expenditure, at night.

Sleep itself appears to have some energy conserving properties. In fact, one of the early hypothesized functions of sleep was energy conservation (Horne 1977; Walker *et al.* 1979). During sleep, body temperature of many mammals naturally drops by up to 3°C as a result of a change in thermoregulatory patterns (McGinty & Szymusiak 1990). During REM sleep, thermoregulation is greatly or entirely reduced (Parmeggiani 2003). The reason for this effect is not entirely clear, but may be the result of conflicting demands between the function of the preoptic-hypothalamic thermostat and the function(s) of REM sleep (Parmeggiani 2003). However, this drop in temperature is generally not sufficient to save adequate amounts of energy in many species, especially those that live in particularly harsh environmental conditions. Thus, many animals, including many food-caching species, appear to actively use hypothermia, daily torpor or hibernation to drop their body temperatures and save energy.

There is some inconsistency and debate about the distinction between hypothermia, torpor and hibernation (see Geiser & Ruf 1995). These three categories appear to run along a continuum of the decline in temperature, time in the state, and time (and energy) required to return to the normothermic state. Hypothermia is generally considered to be a relatively small drop in body temperature (1–10°C below normothermia) that can be quickly reversed. Torpor generally involves maintaining lower temperatures

(minimum body temperatures between 10°C and 25°C), requires more effort to regain function and generally occurs for no more than 24 h (Geiser & Ruf 1995). Hibernation is generally much longer (several days to weeks) with a severe drop in body temperature (minimum body temperature generally less than 10°C) that requires considerable energy to regain function (Snapp & Heller 1981). Although body temperature has traditionally been used as a way to distinguish these states, Geiser & Ruf (1995) argue that the distinction between torpor and hibernation in both birds and mammals should be based on metabolic rate and the duration of the state rather than temperature alone, as the latter shows considerable overlap between categories.

Historically, torpor, hibernation and sleep (SWS in particular) were considered to be homologous processes (Walker *et al.* 1977, 1983; Krilowicz *et al.* 1988; Trachsel *et al.* 1991). While they all involve general 'sleep-like' behaviour and all have energy-saving properties, the relationship between them and their origins are difficult to determine. Given that animals usually enter hibernation/torpor through SWS, Walker *et al.* (1979) hypothesized that SWS and hibernation reflect different degrees of a homologous process. However, other lines of evidence suggest that SWS and hibernation are quite different states. For example, Djungarian hamsters show an increase in SWA after arousal from torpor that is consistent with waking sleep deprivation (Palchykova *et al.* 2002). So, SWS may be a logical/conductive stage through which animals enter hibernation, but may have nothing to do with sleep *per se*. Indeed, the fact that animals periodically arouse from hibernation and enter sleep suggests that they accrue a sleep deficit during hibernation that must be repaid, despite the high associated metabolic costs of arousal. This idea is still controversial, however, as Larkin & Heller (1999) found no evidence of the homeostatic regulation of sleep after arousal. They suggest that the need for SWA after arousal may not be the result of a sleep debt, but instead may be necessary to repair neural structures lost during hypothermia (Larkin & Heller 1999; see also Larkin *et al.* 2002). For our discussion here, the origins of hibernation and torpor are not necessarily important, nor are the exact mechanisms involved in the need for sleep after arousing from a hypothermic state. What is important is that there is clearly a cost to hypometabolic states that impact brain function, which may have adverse impacts on memory. This is discussed in more detail below.

One of the main differences between torpor and sleep is that severe drops in body temperature may actually be detrimental to brain chemistry and physiology. Extreme reductions in body temperature may limit neurochemistry, thus limiting brain functions. For example, synaptic transmission in the brain is reduced at lower temperatures owing to an elevation in concentrations of potassium, calcium and magnesium in the brain (Igelmund 1995). In addition, hibernating mammals experience a significant loss of synapses throughout the brain (von der Ohe *et al.* 2006, 2007), a change in synaptic morphology (Popov *et al.* 1992) and an overall loss of synaptic

efficacy, especially in the hippocampus (Strijkstra *et al.* 2003). Interestingly, synaptic proteins are not lost, but rather accumulate in a reservoir that can be used upon reaching euthermia (von der Ohe *et al.* 2007). This loss of synaptic structure may explain in part the loss of memory observed in some hibernating mammals. For instance, upon re-entering euthermia ground squirrels (*Spermophilus* sp.) fail to recognize previously familiar conspecifics (e.g. Mateo & Johnston 2000; Palchykova & Tobler 2006; but see Milesi *et al.* 2001) and have reduced spatial and operant memory function (Milesi *et al.* 2001; Strijkstra *et al.* 2003). Thus, there appear to be severe neurological (and thus potentially ecological) costs to lowering body temperature and entering a hypothermic state that may have a direct impact on memory. Likewise, daily torpor has a negative effect on memory retention, especially in complex spatial tasks in hamsters (Palchykova *et al.* 2006). Thus, the effect of reduced body temperature on sleep and memory may occur along the continuum of thermal reductions. To our knowledge, though, there have been no studies of this sort in birds.

Consistent with the physiological evidence for a cost of torpor and hibernation are behavioural observations of birds entering hypothermia only under particularly harsh conditions. For example, an animal can choose to go hypothermic on a daily basis and does not always drop body temperature to same level. For example, willow tits in poor condition drop their body temperatures lower and decrease their oxygen consumption further compared with tits in better condition (Reinertsen & Haftorn 1984), suggesting that there is a cost to dropping body temperature. Similarly, torpor in Inca doves (*Scardafella inca*; MacMillen & Trost 1967), parids (e.g. Sharbaugh 2001), nightjars (Dawson & Fisher 1969) and sunbirds (*Nectarinia* sp.; Cheke 1971) was the result of low ambient temperatures and/or starvation (but see Chaplin 1976). However, if food supplies are adequate, even some very small birds living in very harsh climates (e.g. goldcrest, *Regulus regulus*) may not necessarily engage in hypothermia (Reinertsen *et al.* 1988) or may reduce its depth (e.g. willow tits, *Parus montanus*; Reinertsen & Haftorn 1984). It is likely then that the level to which a bird drops its body temperature is a function of energy levels and required energy expenditure to survive the night (Pravosudov & Lucas 2000). Birds might drop their body temperatures when the ambient temperature is particularly low, when they begin the night with low energy reserves, or when they are chronically starved (see Walker *et al.* 1983). The dynamics of these systems and the reluctance of birds in good condition to enter a state of hypothermia then seem to support the idea of a cost of hypothermia (Pravosudov & Lucas 2000).

Given the thermal consequences to neurophysiology that occur during torpor and hibernation, one of the primary costs of hypothermia may be a reduction in the beneficial qualities of sleep (Trachsel *et al.* 1991). If neurophysiological pathways are limited during low temperatures, then sleep itself might be limited as well. In fact, this seems to be the case, not only in extreme situations of long-term hibernation and torpor (see below), but also in short term and

relatively low levels of hypothermia. Sleep architecture itself is sensitive to changes in ambient temperature even if the animal does not enter torpor (see Deboer 1998 for a full review). For example, in a study on rats, the duration of REM sleep drastically decreased at low ambient temperatures relative to control animals. The amount of time spent in SWS and the level of EEG SWA (a measure of SWS intensity) also decreased at low ambient temperatures (Cerri *et al.* 2005). Therefore, if REM sleep and the SWA that defines SWS are directly involved in maintaining brain function (Tononi & Cirelli 2006) and there are reductions in REM and SWA that occur during torpor and hibernation, these states of hypothermia may consequently impair memory.

The most persuasive evidence that sleep and torpor are not compatible comes from small mammals. In many cases, both REM sleep and SWS-related SWA are reduced while these animals are in torpor (e.g. Trachsel *et al.* 1991; Deboer & Tobler 1996, 2000, 2003; Milesi *et al.* 2001; Palchykova & Tobler 2006). In some cases, REM sleep is entirely absent during deep torpor (e.g. Krilowicz *et al.* 1988). So, in these cases, it seems that the benefits of sleep are very much reduced or not realized at all during hibernation. As a result, it has been proposed that hibernating animals become thermogenic and arouse in order to sleep (e.g. Daan *et al.* 1991). This idea is based on the observation that immediately after arousal, ground squirrels increase SWA proportionally to the time spent in hibernation (Trachsel *et al.* 1991; but see Larkin & Heller 1996) and inversely proportional to the body temperature during hibernation (Larkin & Heller 1996; Strijkstra *et al.* 2003). Similarly, SWA in Djungarian hamsters increases after arousal from torpor regardless of the mode of arousal and only after returning to euthermia (Deboer & Tobler 1996, 2000). Still, there is some debate as to whether the increase in SWA after arousal is indeed a compensatory response to sleep deprivation or simply a consequence of thermoregulatory processes (such as synaptic degradation) unrelated to sleep homeostasis (Berger 1998; Daan & Strijkstra 1998; Larkin & Heller 1999). Regardless, the evidence suggests that the restorative functions of sleep are suppressed at low temperatures, as in the case of impaired memory during hibernation (e.g. Mateo & Johnston 2000). Thus, hypothermia along the gradient of torpor and hibernation are likely in effect forms of sleep deprivation (Deboer & Tobler 1996, 2000; Palchykova & Tobler 2006). When animals are not allowed to sleep after arousal, they show reductions in spatial and operant memory (Milesi *et al.* 2000) similar to the loss of memory during traditional forms of sleep deprivation (Deboer & Tobler 2000, 2003; Palchykova & Tobler 2006). Thus, there are physiological and potentially ecological costs to hypothermic states yielding a reduction in memory.

In addition, the level of SWA required after hibernation may be a function of the level of neurodegradation caused by temperature and duration. This could occur in the absence of sleep deprivation *per se*. If hibernation temperatures are extremely low and synapses are degraded, it is possible

that an increase in SWA would be needed after arousal in order to either repair the damage directly or to maintain synaptic homeostasis after the large-scale synaptogenesis that would be required during the return to euthermia. European ground squirrels (*Spermophilus citellus*), for example, required SWS recovery after arousal only at body temperatures below 15°C (Strijkstra & Daan 1997*a,b*). At these very low temperatures, animals may not experience a sleep debt in the traditional sense owing to the thermally induced reduction in brain activity, but instead might need to arouse in order to restore the neural connections that break down in the hippocampus and other parts of the brain, which are lost at such low temperatures (Strijkstra *et al.* 2003; von der Ohe *et al.* 2006, 2007). At very low temperatures, then, the brain function may not be maintained. Thus, the effects of hibernation or deep torpor on sleep may be somewhat dissimilar to normal sleep regulation or deprivation in such species (Strijkstra & Daan 1998), even if sleep debt accrued during daily torpor in others is more similar to that incurred during euthermia. Overall, hibernating animals are expending considerable amounts of energy in the arousal state in order to sleep and seem to do so in order to gain the restorative benefits of the sleep process, whatever those may be.

Despite the work in mammals on the relationship between energy conservation, reduction in body temperature, memory and sleep, very little work has been done in birds. To our knowledge, only two studies have considered sleep and torpor/hypothermia in birds (Walker *et al.* 1983; Graf *et al.* 1987). Walker *et al.* (1983) found that starved ringed turtle doves (*Streptopelia risoria*) progressively reduced REM sleep (as well as SWA during SWS; although not total sleep time) and dropped their body temperatures as ambient temperatures dropped over a series of nights. Once the birds' body temperatures reached approximately 30°C, REM sleep stopped almost entirely. Likewise in pigeons (*Columba livia*), REM sleep as a proportion of total sleep time was reduced as body temperatures were experimentally reduced (Graf *et al.* 1987). These results are consistent with those of mammals (e.g. Krilowicz *et al.* 1988) and suggest that the domination of SWS typical of many mammalian hibernators may be the result of a reduction in REM sleep during torpor, although the level or reduction may depend upon temperature. This extreme reduction in REM sleep during periods of hypothermia may in some way be related to the thermoregulatory inhibition of that sleep state. In addition, the amplitude of the EEG decreased in both states during the experiment (Graf *et al.* 1987; see also Walker *et al.* 1983), which may have led to a reduction in sleep quality. However, it is not known whether cold-induced suppression of SWA results in a compensatory increase in SWA once euthermia is restored in birds as has been shown in mammals. Furthermore, it is not clear how frequently large birds such as pigeons and doves even use torpor on a regular basis in the wild, although hypothermia is clearly reported elsewhere in this group during extreme experimental conditions (e.g. Graf *et al.* 1989). In contrast, we know that a large number of small birds regularly

enter torpor or hypothermia on a daily basis (Brodin 2007); thus, the relationship between torpor and sleep in birds might be better investigated in these species.

## 6. THE COMPLICATION OF RISK

An additional factor that we must also consider in this discussion is the effect of predation risk. Traditionally, nocturnal predation risk is thought to be the primary limiting factor in the drop in body temperature (Grubb & Pravosudov 1994; Reinertsen 1996). At low body temperatures, animals cannot react as quickly to a potential threat (Reinertsen 1996). As a result, animals under high predation risk tend not to drop their body temperatures as low in order to maintain the possibility of escape (Pravosudov & Lucas 2000; Laurila & Hohtola 2005). However, sleep may interact with this risk/body temperature trade-off as sleep itself is risky (Lima *et al.* 2005). Especially in REM sleep and deep SWS, animals may be vulnerable to predation since response thresholds may be higher and reaction times longer than in other states of sleep (Tobler 1995). Consequently, taxa that sleep in risky areas appear to sleep less and engage in less REM sleep (Lesku *et al.* 2006). In addition, following a threatening encounter, rats sleep less in general and spend less time in REM sleep (Lesku *et al.* 2009*a,b*). Furthermore, not sleeping may make foraging more dangerous if memory is indeed reduced as a consequence of sleep deprivation and additional time spent foraging. Not only does the risk of starvation increase when it is difficult to find food, but predation increases as well, as more time is spent exposed to predation while foraging. In other words, if animals cannot remember where their food is located, they put themselves at risk while searching for it.

## 7. THE TRADE-OFF BETWEEN SLEEP, MEMORY AND ENERGY CONSERVATION

The conflict between sleep and energy conservation might well present a trade-off between saving energy in torpor or hypothermia and sleeping for memory. Reducing energy expenditure during the night by dropping body temperature seems to make sleep less efficient. This creates an interesting conflict between sleeping to form memories about where food is located and reducing sleep to save energy when food is in short supply. Especially for food-caching animals, memory and torpor both can enhance fitness by increasing available energy.

If the trade-off is true, then we can make some predictions. First, animals from more harsh climates, in which selection should favour memory, should sleep more and/or have more efficient sleep. This increase in sleep or sleep efficiency should be the result of increased selection for memory and maintaining a larger hippocampus (e.g. Roth & Pravosudov 2009). Second, all else equal, animals with a reduced need for memory should be more willing to drop their body temperature. If an animal does not need to engage in sleep to consolidate its memories, then it should be more willing to forgo sleep and save

energy by becoming torpid. Third, when an animal's energy levels are low, it should favour sleep if caches are readily available, but favour a body temperature drop if they are not. Again, if remembering caching sites is crucial, then the animal should be more willing to pay the energy costs of maintaining its memories for future benefit. If, however, an animal has few caches available to it, memory should be less valuable, sleep should be reduced and body temperatures reduced to provide the largest possible energy savings. There may also be gradations of trade-off through reducing one phase of sleep preferentially (e.g. reducing REM but not SWS when memories are not as critical). In addition, some animals may solve the trade-off by always entering hypothermia during the winter, but do so to differing degrees based on food availability (e.g. willow tits (Reinertsen & Haftorn 1984), compare with goldcrests that use hypothermia only when food is limited (Reinertsen *et al.* 1988)). Alternatively, it may be possible that food-caching animals have evolved mechanisms allowing them to sleep while in hypothermia, yielding both the benefits of sleep and energy conservation. Conversely, they may be able to perform 'sleep-dependent' memory consolidation in short bouts during wakefulness. If this were the case, elucidating such mechanisms (e.g. 'microsleeps') would be especially important as it would provide an ecological and evolutionary basis for the diversification of sleep behaviours.

## 8. A MODEL SYSTEM FOR THE STUDY OF SLEEP

Few studies have focused on the relevance of memory and sleep in an ecological setting, even under semi-natural conditions. To our knowledge, only one study in humans has considered spatial memory in a realistic environment. Ferrara *et al.* (2003) tested the influence of sleep on spatial memory by giving subjects a specific route to follow in an unfamiliar neighbourhood and then later testing their ability to remember the route by identifying the correct sequence of landmarks. Subjects performed better in the identification of the correct sequence after sleep than those that were sleep deprived overnight or those that were tested later the same day (passage of time without sleep deprivation). Many studies in rodents test spatial memory using mazes or tracks (see Clark & Martin 2005). While these systems can tell us much about some of the mechanisms involved in spatial memory such as the recent work on place cells and the spatial sequence of neuronal firing during sleep (e.g. Lee & Wilson 2002; Foster & Wilson 2006), they may not fully represent the demands placed on memory in the natural environment. In addition, these studies are based mostly on the laboratory rat and as such may not reveal the ecological and evolutionary trade-offs that might have produced large variation across other taxa that have evolved under different selection pressures.

Likewise, the memories of birds in relation to sleep have not been well studied. Aside from the recent work in bird song (e.g. Deregnacourt *et al.* 2005; Margoliash 2005; Shank & Margoliash 2009), only two other studies have addressed the effect of sleep

on memory. Rattenborg *et al.* (2004) found that experimentally induced sleep restriction in white-crowned sparrows (*Zonotrichia leucophrys*) reduced the performance of a cognitive task during non-migratory periods. However, it is unclear whether stress and/or sleepiness impaired performance. In addition, Jackson *et al.* (2008) found that domestic chicks required sleep shortly after imprinting in order to maximize the responsiveness of neurons involved in learning. Furthermore, this sleep was required to stabilize long-term memories of imprinting both at behavioural and neurological levels. To our knowledge, though, no study has addressed the effects of sleep on spatial memory in birds.

To facilitate new advances, the field could benefit greatly from additional systems in which to investigate the relationship between sleep and memory (Benington & Frank 2003; Frank & Benington 2006). While work on humans tells us about sleep in ourselves, such studies are necessarily limited by ethical guidelines while being taxonomically limited. Using laboratory rats and mice, we can investigate the basis of the physiological and neurological foundation of sleep and memory, but these studies are inevitably limited because they do not consider the diversity of patterns that may exist across species and are therefore unsuited for establishing ecological and evolutionary trade-offs that most probably shaped the evolution of sleep and memory. Recent work on fruit flies (e.g. Shaw *et al.* 2002; Koh *et al.* 2008) has been enhanced by groundbreaking discoveries in genetics (Allada & Siegel 2008), but again, it is still limited in its ability to provide comprehensive understanding of trade-offs that have likely produced the diversity of sleep patterns in various species, and may not be suitable for revealing the functions of SWS and REM sleep which are only present in mammals and birds. Thus, a more naturalistic animal system would help us to understand better why animals exhibit specific sleep patterns and how these patterns might be influenced by different selection pressures.

We suggest that scatter-hoarding animals (e.g. corvids, sittids, parids in birds, and rodents in mammals) may be good models to study the relationship and potential trade-offs associated with sleep and memory. As mentioned above, spatial memory is critically important to these animals as they routinely make and retrieve thousands of caches scattered throughout their home ranges (Vander Wall 1990). As the retrieval of these caches appears critical specifically to their overwinter survival (Pravosudov & Grubb 1997), particularly in harsh climates, there is likely strong selection pressure for accurate memory (Pravosudov & Lucas 2000, 2001). Furthermore, there is large natural variation in memory and in the hippocampal size in many of these systems (e.g. Pravosudov & Clayton 2002; Roth & Pravosudov 2009) that has also probably resulted from differential selection pressures. In more harsh climates, where selection pressures for memory might be strongest, caching animals appear to have better memories than animals from less harsh climates (Pravosudov & Clayton 2002; Roth & Pravosudov 2009). For example, black-capped chickadees from northern climates (e.g.

Alaska), where the winters are long and cold, have larger hippocampi with more neurons than individuals from more southern climates (e.g. Kansas), where winters are relatively less demanding (Roth & Pravosudov 2009).

We suggest that a model of birds in particular would be an excellent complement to the research in the sleep field that has traditionally focused on mammals. Indeed, birds are a particularly useful animal model with which to determine the specific neurophysiological functions of SWS and REM sleep as they could reveal overriding principles not specific to the mammalian lineage (Rattenborg *et al.* 2009). While some work has been done on seed-caching rodents (e.g. Jacobs & Spencer 1994), tests of memory in this group are rather limited. We suspect that future research on the memory of caching rodents (e.g. pocket mice; Heteromyidae) may be fruitful, especially as it relates to sleep. Here, however, we will focus our effort on benefits of studying memory in food-caching birds.

Food-caching birds as a group constitute an excellent system in which to study memory. An entire paradigm exists focusing on the spatial memory of food-caching birds (e.g. Krebs *et al.* 1996; Clayton 1998; Smulders 2006; Brodin & Bolhuis 2008). In particular, parids and corvids have figured prominently in this type of research, having been studied both in laboratory (e.g. Brodin & Kunz 1997; Pravosudov 2003; Dally *et al.* 2006; Male & Smulders 2007) and field experiments (e.g. Ekman *et al.* 1996; Lahti *et al.* 1998; Hoshoooley *et al.* 2007). In addition, much of the neuronal groundwork is already in place to study birds. For example, the link between memory and the hippocampus has been well demonstrated in caching birds (e.g. Sherry & Vaccarino 1989; Hampton & Shettleworth 1996) as well as homing pigeons (e.g. Cnotka *et al.* 2008).

Overall, food-caching birds such as small parids might provide a perfect model system for investigating the potential trade-offs of sleep, memory and energy. These birds make thousands of food caches every year while relying, at least in part, on hippocampus-dependent spatial memory to recover them. At the same time, these birds often live in extremely severe environmental conditions in which they have only a few hours to forage and many hours of inactivity in the dark at extremely low temperatures. In such conditions, both memory for cache locations and hypothermia to save energy at night may be crucial for survival.

## 9. FUTURE DIRECTIONS FOR SLEEP RESEARCH IN ECOLOGY

The future of sleep research in ecology is filled with possibilities. Sleep is one of the great unknowns in biology and, thus, represents a fruitful direction for research, especially in the fields of ecology and behaviour. It will be particularly important for future studies to emphasize the functional roles of sleep and how selection may act upon it (Frank & Benington 2006). Not until we understand the selection pressures that might affect sleep and the consequences and interactions of these pressures for the mechanisms of

sleep can we fully understand the mystery of sleep itself. In order to address sleep on an evolutionary and ecological scale, we need to consider more naturalistic animal models of sleep. One excellent example of such a naturalistic model is that of song learning in birds (e.g. Margoliash 2005). A system for spatial learning in food-caching animals presents an equally excellent model possibility. A great deal of work exists on the neurological and behavioural components of spatial memory in food-caching animals. Thus, the system is developed enough for the incorporation of questions about sleep. Finally, we will need to focus on the mechanisms of why sleep may be needed for the brain. A system that can integrate behavioural and mechanistic tests (Frank & Benington 2006) through the combination of neurobiology, physiology and behaviour in an ecologically relevant context (Deregnacourt *et al.* 2005) should allow for a novel examination of sleep and the progression of the field.

In short, in order to better understand sleep, it is crucial that we complement the standard human/rat systems with a system that might be better suited to asking evolutionary questions. The study of humans, rats and flies has provided us with the mechanistic background for our current understanding of sleep. We should take the tremendous amount that we have learned from these groups and apply it to other systems to get a better understanding of the full nature of sleep, especially within the context of selection and naturalistic situations.

We have presented the argument for using food-caching animals as a model system to study sleep, especially as it relates to memory and energy conservation. In these systems, we find natural variation in memory owing to different selection pressures as well as interesting trade-offs that might make the system particularly tenable for experimental sleep research. Food-caching birds in particular might be a good model to consider because they sleep like mammals despite independent evolutionary lines and provide us with a new direction in sleep research that might expand our understanding of sleep in general.

Although all animals experience sleep, some aspects of sleep may be fundamentally different throughout Animalia. We have only begun to consider how selection might act differently on various systems and produce the range of variation that we see in sleep patterns. Not until we look at sleep on a broader scale and consider how sleep has been modified under different environmental conditions will we fully understand sleep, its evolution and its many possible functions. In the end, we hope that such examinations beyond the standard research paradigms might help us to unravel some of the mysteries of sleep and better understand why we all need sleep.

We thank J. Lesku for helpful ideas and discussions. J. Lesku and L. LaDage provided comments on drafts of this manuscript. T.C.R. was supported by a National Science Foundation grant (IOB-0615021) to V.V.P., who was in addition also supported by National Institutes of Health grants (MH079892 and MH076797). N.C.R. was supported by the Max Planck Society.

## REFERENCES

- Allada, R. & Siegel, J. M. 2008 Unearthing the phylogenetic roots of sleep. *Curr. Biol.* **18**, R670–R679. (doi:10.1016/j.cub.2008.06.033)
- Ambrosini, M. V. & Giuditta, A. 2001 Learning and sleep: the sequential hypothesis. *Sleep Med. Rev.* **5**, 477–490. (doi:10.1053/smr.2001.0180)
- Bartholomew, G. A. & Trost, C. H. 1970 Temperature regulation in speckled mousebird, *Colius striatus*. *Condor* **72**, 141–146. (doi:10.2307/1366623)
- Bast, T. 2007 Toward an integrative perspective on hippocampal function: from the rapid encoding of experience to adaptive behavior. *Rev. Neurosci.* **18**, 253–281.
- Benington, J. H. & Frank, M. G. 2003 Cellular and molecular connections between sleep and synaptic plasticity. *Prog. Neurobiol.* **69**, 71–101. (doi:10.1016/S0301-0082(03)00018-2)
- Benington, J. H. & Heller, H. C. 1995 Restoration of brain energy = metabolism as the function of sleep. *Prog. Neurobiol.* **45**, 347–360. (doi:10.1016/0301-0082(94)00057-O)
- Berger, R. J. 1998 Does post-torpor EEG slow wave activity in ground squirrels reflect a 'sleep debt' or a thermoregulatory process? *J. Sleep Res.* **7**, 69–70. (doi:10.1046/j.1365-2869.1998.00097.x)
- Berger, R. J. & Phillips, N. H. 1995 Energy conservation and sleep. *Behav. Brain Res.* **69**, 65–73. (doi:10.1016/0166-4328(95)00002-B)
- Biegler, R., McGregor, A., Krebs, J. R. & Healy, S. D. 2001 A larger hippocampus is associated with longer-lasting spatial memory. *Proc. Natl Acad. Sci. USA* **98**, 6941–6944. (doi:10.1073/pnas.121034798)
- Blischke, K. & Erlacher, D. 2007 How sleep enhances motor learning—a review. *J. Hum. Kinet.* **17**, 3–14.
- Born, J., Rasch, B. & Gais, S. 2006 Sleep to remember. *Neuroscientist* **12**, 410–424. (doi:10.1177/1073858406292647)
- Brodin, A. 2007 Theoretical models of adaptive energy management in small wintering birds. *Phil. Trans. R. Soc. B* **362**, 1857–1871. (doi:10.1098/rstb.2006.1812)
- Brodin, A. & Bolhuis, J. J. 2008 Memory and brain in food-storing birds: space oddities or adaptive specializations? *Ethology* **114**, 633–645. (doi:10.1111/j.1439-0310.2008.01508.x)
- Brodin, A. & Kunz, C. 1997 An experimental study of cache recovery by hoarding willow tits after different retention intervals. *Behaviour* **134**, 881–890. (doi:10.1163/156853997X00205)
- Bruel-Jungerman, E., Rampon, C. & Laroche, S. 2007 Adult hippocampal neurogenesis, synaptic plasticity and memory: facts and hypotheses. *Rev. Neurosci.* **18**, 93–114.
- Capellini, I., Barton, R. A., McNamara, P., Preston, B. T. & Nunn, C. L. 2008 Phylogenetic analysis of the ecology and evolution of mammalian sleep. *Evolution* **62**, 1764–1775. (doi:10.1111/j.1558-5646.2008.00392.x)
- Cerri, M. *et al.* 2005 Cold exposure and sleep in the rat: effects on sleep architecture and the electroencephalogram. *Sleep* **28**, 694–705.
- Chaplin, S. B. 1974 Daily energetics of the black-capped chickadee, *Parus atricapillus*, in winter. *J. Comp. Physiol.* **89**, 321–330. (doi:10.1007/BF00695350)
- Chaplin, S. B. 1976 The physiology of hypothermia in the black-capped chickadee, *Parus atricapillus*. *J. Comp. Physiol.* **112**, 335–344.
- Cheke, R. A. 1971 Temperature rhythms in African montane sunbirds. *IBIS* **113**, 500–506. (doi:10.1111/j.1474-919X.1971.tb05184.x)
- Cirelli, C. & Tononi, G. 2008 Is sleep essential? *PLOS Biol.* **6**, 1605–1611. (doi:10.1371/journal.pbio.0060216)
- Cirelli, C., Bushey, D., Hill, S., Huber, R., Kreber, R., Ganetzky, B. & Tononi, G. 2005 Reduced sleep in *Drosophila* shaker mutants. *Nature* **434**, 1087–1092. (doi:10.1038/nature03486)
- Clark, R. E. & Martin, S. J. 2005 Interrogating rodents regarding their object and spatial memory. *Curr. Opin. Neurobiol.* **15**, 593–598. (doi:10.1016/j.conb.2005.08.014)
- Clayton, N. S. 1998 Memory and the hippocampus in food-storing birds: a comparative approach. *Neuropharmacology* **37**, 441–452. (doi:10.1016/S0028-3908(98)00037-9)
- Clayton, N. S. & Soha, J. A. 1999 Memory in avian food caching and song learning: a general mechanism or different processes? *Adv. Study Anim. Behav.* **28**, 115–171. (doi:10.1016/S0065-3454(08)60217-X)
- Cnotka, J., Mohle, M. & Rehkemper, G. 2008 Navigational experience affects hippocampus size in homing pigeons. *Brain Behav. Evol.* **72**, 233–238. (doi:10.1159/000165102)
- Colgin, L. L. & Moser, E. I. 2006 Neuroscience—rewinding the memory record. *Nature* **440**, 615–617. (doi:10.1038/440615a)
- Cristol, D. A., Reynolds, E. B., LeClerc, J. E., Donner, A. H., Farabaugh, C. F. & Ziegenfus, C. W. S. 2003 Migratory dark-eyed juncos have better spatial memory and denser hippocampal neurons than non-migratory conspecifics. *Anim. Behav.* **66**, 317–328. (doi:10.1006/anbe.2003.2194)
- Daan, S. & Strijkstra, A. M. 1998 Does post-torpor EEG slow-wave activity in ground squirrels reflect a 'sleep debt' or a thermoregulatory process? Reply. *J. Sleep Res.* **7**, 71–72.
- Daan, S., Barnes, B. M. & Strijkstra, A. M. 1991 Warming up for sleep—ground-squirrels sleep during arousals from hibernation. *Neurosci. Lett.* **128**, 265–268. (doi:10.1016/0304-3940(91)90276-Y)
- Dally, J. M., Emery, N. J. & Clayton, N. S. 2006 Food-caching western scrub-jays keep track of who was watching when. *Science* **312**, 1662–1665. (doi:10.1126/science.1126539)
- Dave, A. S., Yu, A. C. & Margoliash, D. 1998 Behavioural state modulation of auditory activity in a vocal motor system. *Science* **282**, 2250–2254. (doi:10.1126/science.282.5397.2250)
- Dawson, W. R. & Fisher, C. D. 1969 Response to temperature by spotted nightjar (*Eurostopodus guttatus*). *Condor* **71**, 49–53. (doi:10.2307/1366047)
- Deboer, T. 1998 Brain temperature dependent changes in the electroencephalogram power spectrum of humans and animals. *J. Sleep Res.* **7**, 254–262. (doi:10.1046/j.1365-2869.1998.00125.x)
- Deboer, T. & Tobler, I. 1996 Natural hypothermia and sleep deprivation: common effects on recovery sleep in the Djungarian hamster. *Am. J. Physiol.* **271**, R1364–R1371.
- Deboer, T. & Tobler, I. 2000 Slow waves in the sleep electroencephalogram after daily torpor are homeostatically regulated. *Neuroreport* **11**, 881–885.
- Deboer, T. & Tobler, I. 2003 Sleep regulation in the Djungarian hamster: comparison of the dynamics leading to the slow-wave activity increase after sleep deprivation and daily torpor. *Sleep* **26**, 567–572.
- Deregnacourt, S., Mitra, P. P., Feher, O., Pytte, C. & Tchernichovski, O. 2005 How sleep affects the developmental learning of bird song. *Nature* **433**, 710–716. (doi:10.1038/nature03275)
- Desposito, M. & Grossman, M. 1996 The physiological basis of executive function and working memory. *Neuroscientist* **2**, 345–352.
- Dinges, D. F., Pack, F., Williams, K., Gillen, K. A., Powel, J. W., Ott, G. E., Aptowicz, C. & Pack, A. I. 1997

- Cumulative sleepiness, mood disturbance, and psychomotor vigilance performance decrements during a week of sleep restricted to 4–5 hours per night. *Sleep* **20**, 267–277.
- Ehninger, D. & Kempermann, G. 2008 Neurogenesis in the adult hippocampus. *Cell Tissue Res.* **331**, 243–250. (doi:10.1007/s00441-007-0478-3)
- Eichenbaum, H. 2007 To sleep, perchance to integrate. *Proc. Natl Acad. Sci. USA* **104**, 7317–7318. (doi:10.1073/pnas.0702503104)
- Ekman, J., Brodin, A., Bylin, A. & Sklepkovych, B. 1996 Selfish long-term benefits of hoarding in the Siberian jay. *Behav. Ecol.* **7**, 140–144. (doi:10.1093/beheco/7.2.140)
- Ellenbogen, J. M., Payne, J. D. & Stickgold, R. 2006a The role of sleep in declarative memory consolidation: passive, permissive, active or none? *Curr. Opin. Neurobiol.* **16**, 716–722. (doi:10.1016/j.conb.2006.10.006)
- Ellenbogen, J. M., Hulbert, J. C., Stickgold, R., Dinges, D. F. & Thompson-Schill, S. L. 2006b Interfering with theories of sleep and memory: sleep, declarative memory, and associative interference. *Curr. Biol.* **16**, 1290–1294. (doi:10.1016/j.cub.2006.05.024)
- Fenn, K. M., Nusbaum, H. C. & Margoliash, D. 2003 Consolidation during sleep of perceptual learning of spoken language. *Nature* **425**, 614–616. (doi:10.1038/nature01951)
- Ferrara, M., Iaria, G., De Gennaro, L., Guariglia, C., Curcio, G., Tempesta, D. & Bertini, M. 2003 The role of sleep in the consolidation of route learning in humans: a behavioural study. *Brain Res. Bull.* **71**, 4–9. (doi:10.1016/j.brainresbull.2006.07.015)
- Fogel, S. M. & Smith, C. T. 2006 Declarative learning-dependent changes in theta power during REM sleep. *Sleep* **29**, A375–A375.
- Foster, D. J. & Wilson, M. A. 2006 Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature* **440**, 680–683. (doi:10.1038/nature04587)
- Frank, M. G. & Benington, J. H. 2006 The role of sleep in memory consolidation and brain plasticity: dream or reality? *Neuroscientist* **12**, 477–488. (doi:10.1177/1073858406293552)
- Frankland, P. W. & Bontempi, B. 2005 The organization of recent and remote memories. *Nat. Rev. Neurosci.* **6**, 119–130. (doi:10.1038/nrn1607)
- Geiser, F. & Ruf, T. 1995 Hibernation versus daily torpor in mammals and birds—physiological variables and classification of torpor patterns. *Physiol. Zool.* **68**, 935–966.
- Gilbert, P. F. C. 2001 An outline of brain function. *Cogn. Brain Res.* **12**, 61–74. (doi:10.1016/S0926-6410(01)00035-0)
- Gottselig, J. M., Hofer-Tinguely, G., Borbely, A. A., Regel, S. J., Landolt, H. P., Retey, J. V. & Achermann, P. 2004 Sleep and rest facilitate auditory learning. *Neuroscience* **127**, 557–561. (doi:10.1016/j.neuroscience.2004.05.053)
- Graf, R., Heller, H. C., Sakaguchi, S. & Krishna, S. 1987 Influence of spinal and hypothalamic warming on metabolism and sleep in pigeons. *Am. J. Physiol.* **252**, 661–667.
- Graf, R., Krishna, S. & Heller, H. C. 1989 Regulated nocturnal hypothermia induced in pigeons by food deprivation. *Am. J. Physiol.* **256**, R733–R738.
- Grubb, T. C. & Pravosudov, V. V. 1994 Toward a general theory of energy management in wintering birds. *J. Avian Biol.* **26**, 255–260. (doi:10.2307/3677271)
- Guzman-Marin, R., Suntsova, N., Stewart, D. R., Gong, H., Szymusiak, R. & McGinty, D. 2003 Sleep deprivation reduces proliferation of cells in the dentate gyrus of the hippocampus in rats. *J. Physiol.* **549**, 563–571. (doi:10.1113/jphysiol.2003.041665)
- Guzman-Marin, R., Suntsova, N., Methippara, M., Greiffenstein, R., Szymusiak, R. & McGinty, D. 2005 Sleep deprivation suppresses neurogenesis in the adult hippocampus of rats. *Eur. J. Neurosci.* **22**, 2111–2116. (doi:10.1111/j.1460-9568.2005.04376.x)
- Guzman-Marin, R., Bashir, T., Suntsova, N., Szymusiak, R. & McGinty, D. 2007 Hippocampal neurogenesis is reduced by sleep fragmentation in the adult rat. *Neuroscience* **148**, 325–333. (doi:10.1016/j.neuroscience.2007.05.030)
- Guzman-Marin, R., Suntsova, N., Bashir, T., Nienhuis, R., Szymusiak, R. & McGinty, D. 2008 Rapid eye movement sleep deprivation contributes to reduction of neurogenesis in the hippocampal dentate gyrus of the adult rat. *Sleep* **31**, 167–175.
- Hairston, I. S., Little, M. T. M., Scanlon, M. D., Barakat, M. T., Palmer, T. D., Sapolsky, R. M. & Heller, H. C. 2005 Sleep restriction suppresses neurogenesis induced by hippocampus-dependent learning. *J. Neurophysiol.* **94**, 4224–4233. (doi:10.1152/jn.00218.2005)
- Hampton, R. R. & Shettleworth, S. J. 1996 Hippocampal lesions impair memory for location but not color in passerine birds. *Behav. Neurosci.* **110**, 831–835. (doi:10.1037/0735-7044.110.4.831)
- Hartse, K. M. 1994 Sleep in insects and nonmammalian vertebrates. In *Principles and practice of sleep medicine* (eds M. H. Kryger, T. Roth & W. C. Dement), pp. 95–104, 1st edn. Philadelphia, PA: Elsevier Saunders.
- Hendricks, J. C. & Sehgal, A. 2004 Why a fly? Using *Drosophila* to understand the genetics of circadian rhythms and sleep. *Sleep* **27**, 334–342.
- Hennevin, E., Huetz, C. & Edeline, J. M. 2007 Neural representations during sleep: from sensory processing to memory traces. *Neurobiol. Learn. Mem.* **87**, 416–440. (doi:10.1016/j.nlm.2006.10.006)
- Hiebert, S. M. 1990 Energy costs and temporal organization of torpor in the rufous hummingbird (*Selasphorus rufus*). *Physiol. Zool.* **63**, 1082–1097.
- Hobson, J. A. 2005 Sleep is of the brain, by the brain and for the brain. *Nature* **437**, 1254–1256. (doi:10.1038/nature04283)
- Horne, J. A. 1977 Factors relating to energy conservation during sleep in mammals. *Physiol. Psychol.* **5**, 403–408.
- Horowitz, J. M., Thomas, M. P. & Eckerman, P. 1987 Thermal-dependence of neural activity in the hamster hippocampal slice preparation. *J. Therm. Biol.* **12**, 97–101. (doi:10.1016/0306-4565(87)90045-3)
- Hoshooley, J. S., Phillmore, L. S., Sherry, D. F. & MacDougall-Shackleton, S. A. 2007 Annual cycle of the black-capped chickadee: seasonality of food-storing and the hippocampus. *Brain Behav. Evol.* **69**, 161–168. (doi:10.1159/000096984)
- Houston, A. I. & McNamara, J. M. 1993 A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scand.* **24**, 205–219. (doi:10.2307/3676736)
- Huber, R., Ghilardi, M. F., Massimini, M. & Tononi, G. 2004 Local sleep and learning. *Nature* **430**, 78–81. (doi:10.1038/nature02663)
- Igelmund, P. 1995 Modulation of synaptic transmission at low-temperatures by hibernation-related changes in ionic microenvironment in hippocampal slices of golden-hamsters. *Cryobiology* **32**, 334–343. (doi:10.1006/cryo.1995.1034)
- Imeri, L. & Opp, M. R. 2009 How (and why) the immune system makes us sleep. *Nat. Rev. Neurosci.* **10**, 199–210. (doi:10.1038/nrn2576)
- Jackson, C., McCabe, B. J., Nicol, A. U., Grout, A. S., Brown, M. W. & Horn, G. 2008 Dynamic effects of a memory trace: sleep on consolidation. *Curr. Biol.* **18**, 393–400. (doi:10.1016/j.cub.2008.01.062)

- Jacobs, L. F. & Spencer, W. D. 1994 Natural space-use patterns and hippocampal site in kangaroo rats. *Brain Behav. Evol.* **44**, 125–132. (doi:10.1159/000113584)
- Jarvis, E. D. *et al.* 2005 Avian Brain Nomenclature Consortium. Avian brains and a new understanding of vertebrate brain evolution. *Nat. Rev. Neurosci.* **6**, 151–159. (doi:10.1038/nrn1606)
- Jerison, H. J. 1985 Animal intelligence as encephalization. *Phil. Trans. R. Soc. B* **308**, 21–35. (doi:10.1098/rstb.1985.0007)
- Kaiser, W. 1988 Busy bees need rest too—behavioural and electromyographical sleep signs in honeybees. *J. Comp. Physiol. A* **163**, 565–584. (doi:10.1007/BF00603841)
- Kaiser, W. & Steiner-Kaiser, J. 1983 Neuronal correlates of sleep, wakefulness and arousal in a diurnal insect. *Nature* **301**, 707–709. (doi:10.1038/301707a0)
- Kavanau, J. L. 1996 Memory, sleep, and dynamic stabilization of neural circuitry: evolutionary perspectives. *Neurosci. Biobehav. Rev.* **20**, 289–311. (doi:10.1016/0149-7634(95)00019-4)
- Kavanau, J. L. 1997 Memory, sleep and the evolution of mechanisms of synaptic efficacy maintenance. *Neuroscience* **79**, 7–44. (doi:10.1016/S0306-4522(96)00610-0)
- Kenser, R. P. & DiMattia, B. V. 1987 Neurobiology of an attribute model of memory. In *Progress in psychobiology and physiological psychology*, vol. 12 (eds A. N. Epstein & A. Morrison), pp. 207–277. New York, NY: Academic Press.
- Klein, B. A., Olzowy, K. M., Klein, A., Saunders, K. M. & Seeley, T. D. 2008 Caste-dependent sleep of worker honey bees. *J. Exp. Biol.* **211**, 3028–3040. (doi:10.1242/jeb.017426)
- Koh, K., Joiner, W. J., Wu, M. N., Yue, Z. F., Smith, C. J. & Sehgal, A. 2008 Identification of SLEEPLESS, a sleep-promoting factor. *Science* **321**, 372–376. (doi:10.1126/science.1155942)
- Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H. & Vaccarino, A. L. 1989 Hippocampal specialization of food-storing birds. *Proc. Natl Acad. Sci. USA* **86**, 1388–1392.
- Krebs, J. R., Clayton, N. S., Healy, S. D., Cristol, D. A., Patel, S. N. & Jolliffe, A. R. 1996 The ecology of the avian brain: food-storing memory and the hippocampus. *IBIS* **138**, 34–46.
- Krillowicz, B. L., Glotzbach, S. F. & Heller, H. C. 1988 Neuronal activity during sleep and complete bouts of hibernation. *Am. J. Physiol.* **255**, R1008–R1019.
- Krueger, J. M. & Obal, F. 2003 Sleep function. *Front. Biosci.* **8**, 511–519. (doi:10.2741/1031)
- Lahti, K., Koivula, K., Rytönen, S., Mustonen, T., Welling, P., Pravosudov, V. V. & Orell, M. 1998 Social influences on food caching in willow tits: a field experiment. *Behav. Ecol.* **9**, 122–129. (doi:10.1093/beheco/9.2.122)
- Larkin, J. E. & Heller, H. C. 1996 Temperature sensitivity of sleep homeostasis during hibernation in the golden-mantled ground squirrel. *Am. J. Physiol.* **270**, 777–784.
- Larkin, J. E. & Heller, H. C. 1999 Sleep after arousal from hibernation is not homeostatically regulated. *Am. J. Physiol.* **276**, R522–R529.
- Larkin, J. E., Franken, P. & Heller, H. C. 2002 Loss of circadian organization of sleep and wakefulness during hibernation. *Am. J. Physiol.* **282**, R1086–R1095.
- Laurila, M. & Hohtola, E. 2005 The effect of ambient temperature and simulated predation risk on fasting-induced nocturnal hypothermia of pigeons in outdoor conditions. *J. Therm. Biol.* **30**, 392–399. (doi:10.1016/j.jtherbio.2005.04.001)
- Lee, A. K. & Wilson, M. A. 2002 Memory of sequential experience in the hippocampus during slow wave sleep. *Neuron* **36**, 1183–1194. (doi:10.1016/S0896-6273(02)01096-6)
- Lesku, J. A., Roth, T. C., Amlaner, C. J. & Lima, S. L. 2006 A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *Am. Nat.* **168**, 441–453. (doi:10.1086/506973)
- Lesku, J. A., Bark, R. J., Martinez-Gonzalez, D., Rattenborg, N. C., Amlaner, C. J. & Lima, S. L. 2008 Predator-induced plasticity in sleep architecture in wild-caught Norway rats (*Rattus norvegicus*). *Behav. Brain Res.* **189**, 298–305. (doi:10.1016/j.bbr.2008.01.006)
- Lesku, J. A., Martinez-Gonzalez, D. & Rattenborg, N. C. 2009a Sleep and sleep states: phylogeny and ontogeny. In *The new encyclopedia of neuroscience* (ed. L. R. Squire), pp. 963–971. Oxford, UK: Elsevier.
- Lesku, J. A., Roth, T. C., Rattenborg, N. C., Amlaner, C. J. & Lima, S. L. 2009b History and future of comparative analyses in sleep research. *Neurosci. Biobehav. Rev.* **33**, 1024–1036.
- Lima, S. L. 1998 Stress and decision making under the risk of predation: recent developments from behavioural, reproductive, and ecological perspectives. *Adv. Study Behav.* **27**, 215–290. (doi:10.1016/S0065-3454(08)60366-6)
- Lima, S. L. & Dill, L. M. 1990 Behavioural decisions made under the risk of predation—a review and prospectus. *Can. J. Zool.* **68**, 619–640. (doi:10.1139/z90-092)
- Lima, S. L. & Rattenborg, N. C. 2007 A behavioural shut-down can make sleeping safer: a strategic perspective on the function of sleep. *Anim. Behav.* **74**, 189–197. (doi:10.1016/j.anbehav.2006.12.007)
- Lima, S. L., Rattenborg, N. C., Lesku, J. A. & Amlaner, C. J. 2005 Sleeping under the risk of predation. *Anim. Behav.* **70**, 723–736. (doi:10.1016/j.anbehav.2005.01.008)
- Lyamin, O. I., Manger, P. R., Ridgway, S. H., Mukhametov, L. M. & Siegel, J. M. 2008 Cetacean sleep: an unusual form of mammalian sleep. *Neurosci. Biobehav. Rev.* **32**, 1451–1484. (doi:10.1016/j.neubiorev.2008.05.023)
- MacMillen, R. E. & Trost, C. H. 1967 Thermoregulation and water loss in Inca dove. *Comp. Biochem. Physiol.* **20**, 263–273. (doi:10.1016/0010-406X(67)90739-6)
- Majde, J. A. & Krueger, J. M. 2005 Links between the innate immune system and sleep. *J. Allergy Clin. Immunol.* **116**, 1188–1198. (doi:10.1016/j.jaci.2005.08.005)
- Male, L. H. & Smulders, T. V. 2007 Memory decay and cache site preferences in hoarding coal tits—a laboratory study. *Behaviour* **144**, 693–710. (doi:10.1163/156853907781347808)
- Manger, P. R. 2006 An examination of cetacean brain structure with a novel hypothesis correlating thermogenesis to the evolution of a big brain. *Biol. Rev. Camb. Phil. Soc.* **81**, 293–338. (doi:10.1017/S1464793106007019)
- Maquet, P. 2001 The role of sleep in learning and memory. *Science* **294**, 1048–1052. (doi:10.1126/science.1062856)
- Maquet, P., Schwartz, S., Passingham, R. & Froth, C. 2003 Sleep-related consolidation of a visuomotor skill: brain mechanisms as assessed by functional magnetic resonance imaging. *J. Neurosci.* **23**, 1432–1440.
- Margoliash, D. 2005 Song learning and sleep. *Nat. Neurosci.* **8**, 546–548. (doi:10.1038/nn0505-546)
- Marino, L. *et al.* 2008 A claim in search of evidence: reply to Manger's thermogenesis hypothesis of cetaceans' brain structure. *Biol. Rev. Camb. Phil. Soc.* **83**, 417–440.
- Marshall, U. & Born, J. 2007 The contribution of sleep to hippocampus-dependent memory consolidation. *Trends Cogn. Sci.* **11**, 442–450. (doi:10.1016/j.tics.2007.09.001)
- Martinez-Gonzalez, D., Lesku, J. A. & Rattenborg, N. C. 2008 Increased EEG spectral power density during sleep following short-term sleep deprivation in pigeons (*Columba livia*): evidence for avian sleep homeostasis.

- J. Sleep Res.* **17**, 140–153. (doi:10.1111/j.1365-2869.2008.00636.x)
- Mateo, J. M. & Johnston, R. E. 2000 Retention of social recognition after hibernation in Belding's ground squirrels. *Anim. Behav.* **59**, 491–499. (doi:10.1006/anbe.1999.1363)
- McDermott, C. M., LaHoste, G. J., Chen, C., Musto, A., Bazan, N. G. & Magee, J. C. 2003 Sleep deprivation causes behavioural, synaptic, and membrane excitability alterations in hippocampal neurons. *J. Neurosci.* **23**, 9687–9695.
- McGinty, D. & Szymusiak, R. 1990 Keeping cool: a hypothesis about the mechanisms and functions of slow-wave sleep. *Trends Neurosci.* **13**, 480–487. (doi:10.1016/0166-2236(90)90081-K)
- Meddis, R. 1975 Function of sleep. *Anim. Behav.* **23**, 676–691. (doi:10.1016/0003-3472(75)90144-X)
- Medina, L. & Reiner, A. 2000 Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends Neurosci.* **23**, 1–12. (doi:10.1016/S0166-2236(99)01486-1)
- Meerlo, P., Sgoifo, A. & Suchecki, D. 2008 Restricted and disrupted sleep: effects on autonomic function, neuroendocrine stress systems and stress responsivity. *Sleep Med. Rev.* **12**, 197–210. (doi:10.1016/j.smrv.2007.07.007)
- Mignot, E. 2008 Why we sleep: the temporal organization of recovery. *PLoS Biol.* **6**, 661–669. (doi:10.1371/journal.pbio.0060106)
- Millesi, E., Prossinger, H., Dittami, J. P. & Fieder, M. 2001 Hibernation effects on memory in European ground squirrels (*Spermophilus citellus*). *J. Biol. Rhythm* **16**, 264–271.
- Molle, M. & Born, J. 2009 Hippocampus whispering in deep sleep to prefrontal cortex—for good memories? *Neuron* **61**, 496–498. (doi:10.1016/j.neuron.2009.02.002)
- Mueller, A. D., Pollock, M. S., Lieblisch, S. E., Epp, J. R., Galea, L. A. M. & Mistlberger, R. E. 2008 Sleep deprivation can inhibit adult hippocampal neurogenesis independent of adrenal stress hormones. *Am. J. Physiol.* **294**, R1693–R1703.
- Nitz, D. A., van Swinderen, B., Tononi, G. & Greenspan, R. J. 2002 Electrophysiological correlates of rest and activity in *Drosophila melanogaster*. *Curr. Biol.* **12**, 1934–1940. (doi:10.1016/S0960-9822(02)01300-3)
- Nottebohm, F. 2002 Neuronal replacement in adult brain. *Brain Res. Bull.* **57**, 737–749. (doi:10.1016/S0361-9230(02)00750-5)
- Palchykova, S. & Tobler, I. 2006 Sleep, torpor and memory impairment. *J. Br. Interplanet. Soc.* **59**, 134–138.
- Palchykova, S., Deboer, T. & Tobler, I. 2002 Selective sleep deprivation after daily torpor in the Djungarian hamster. *J. Sleep Res.* **11**, 313–319. (doi:10.1046/j.1365-2869.2002.00310.x)
- Palchykova, S., Crestani, F., Meerlo, P. & Tobler, I. 2006 Sleep deprivation and daily torpor impair object recognition in Djungarian hamsters. *Physiol. Behav.* **87**, 144–153. (doi:10.1016/j.physbeh.2005.09.005)
- Parmegiani, P. L. 2003 Thermoregulation and sleep. *Front. Biosci.* **8**, S557–S567. (doi:10.2741/1054)
- Patel, S. N., Clayton, N. S. & Krebs, J. R. 1997 Spatial learning induces neurogenesis in the avian brain. *Behav. Brain Res.* **89**, 115–128. (doi:10.1016/S0166-4328(97)00051-X)
- Peigneux, P. et al. 2004 Are spatial memories strengthened in the human hippocampus during slow wave sleep? *Neuron* **44**, 535–545. (doi:10.1016/j.neuron.2004.10.007)
- Peters, K. R., Smith, V. & Smith, C. T. 2007 Changes in sleep architecture following motor learning depend on initial skill level. *J. Cogn. Neurosci.* **19**, 817–829. (doi:10.1162/jocn.2007.19.5.817)
- Pinaud, R. & Terleph, T. A. 2008 A songbird forebrain area potentially involved in auditory discrimination and memory formation. *J. Biosci.* **33**, 145–155. (doi:10.1007/s12038-008-0030-y)
- Poldrack, R. A. & Foerde, K. 2008 Category learning and the memory systems debate. *Neurosci. Biobehav. Rev.* **32**, 197–205. (doi:10.1016/j.neubiorev.2007.07.007)
- Popov, V. I., Bocharova, L. S. & Bragin, A. G. 1992 Repeated changes of dendritic morphology in the hippocampus of ground-squirrels in the course of hibernation. *Neuroscience* **48**, 45–51. (doi:10.1016/0306-4522(92)90336-Z)
- Pravosudov, V. V. 2003 Long-term moderate elevation of corticosterone facilitates avian food-caching behaviour and enhances spatial memory. *Proc. R. Soc. Lond. B* **270**, 2599–2604. (doi:10.1098/rspb.2003.2551)
- Pravosudov, V. V. 2005 Corticosterone and memory in birds. In *Functional avian endocrinology* (eds A. Dawson & P. Sharp), pp. 257–268. New Delhi, India: Narosa.
- Pravosudov, V. V. & Clayton, N. S. 2002 A test of the adaptive specialization hypothesis: population differences in caching, memory and the hippocampus in black-capped chickadees (*Poecile atricapilla*). *Behav. Neurosci.* **116**, 515–522. (doi:10.1037/0735-7044.116.4.515)
- Pravosudov, V. V. & Grubb, T. C. 1997 Management of fat reserves and food caches in tufted titmice (*Parus bicolor*) in relation to unpredictable food. *Behav. Ecol.* **8**, 332–339. (doi:10.1093/beheco/8.3.332)
- Pravosudov, V. V. & Lucas, J. R. 2000 The cost of being cool: a dynamic model of nocturnal hypothermia by small food-caching birds in winter. *J. Avian Biol.* **31**, 463–472. (doi:10.1034/j.1600-048X.2000.310405.x)
- Pravosudov, V. V. & Lucas, J. R. 2001 A dynamic model of short-term energy management in small food-caching and non-caching birds. *Behav. Ecol.* **12**, 207–218. (doi:10.1093/beheco/12.2.207)
- Pravosudov, V. V., Lavenex, P. & Omanska, A. 2005 Nutritional deficits during early development affect hippocampal structure and spatial memory later in life. *Behav. Neurosci.* **119**, 1368–1374. (doi:10.1037/0735-7044.119.5.1368)
- Pravosudov, V. V., Kitaysky, A. S. & Omanska, A. 2006 The relationship between migratory behavior, memory and the hippocampus: an intraspecific comparison. *Proc. R. Soc. B* **273**, 2641–2649. (doi:10.1098/rspb.2006.3624)
- Preston, B. T., Capellini, I., McNamara, P., Barton, R. A. & Nunn, C. L. 2009 Parasite resistance and the adaptive significance of sleep. *BMC Evol. Biol.* **9**, 7. (doi:10.1186/1471-2148-9-7)
- Rasch, B. & Born, J. 2007 Maintaining memories by reactivation. *Curr. Opin. Neurobiol.* **17**, 698–703. (doi:10.1016/j.conb.2007.11.007)
- Rasch, B., Pommer, J., Diekelmann, S. & Born, J. 2009 Pharmacological REM sleep suppression paradoxically improves rather than impairs skill memory. *Nat. Neurosci.* **12**, 396–397. (doi:10.1038/nn.2206)
- Rattenborg, N. C. 2006 Evolution of slow-wave sleep and palliopallial connectivity in mammals and birds: a hypothesis. *Brain Res. Bull.* **69**, 20–29. (doi:10.1016/j.brainresbull.2005.11.002)
- Rattenborg, N. C. 2007 Response to commentary on evolution of slow-wave sleep and palliopallial connectivity in mammals and birds: a hypothesis. *Brain Res. Bull.* **72**, 187–193. (doi:10.1016/j.brainresbull.2007.02.010)
- Rattenborg, N. C., Lima, S. L. & Amlaner, C. J. 1999 Facultative control of avian unihemispheric sleep under the risk of predation. *Behav. Brain Res.* **105**, 163–172. (doi:10.1016/S0166-4328(99)00070-4)
- Rattenborg, N. C., Amlaner, C. J. & Lima, S. L. 2000 Behavioural, neurophysiological and evolutionary

- perspectives on unihemispheric sleep. *Neurosci. Biobehav. Rev.* **24**, 817–842. (doi:10.1016/S0149-7634(00)00039-7)
- Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M. & Benca, R. M. 2004 Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLoS Biol.* **2**, 924–936. (doi:10.1371/journal.pbio.0020212)
- Rattenborg, N. C., Voirin, B., Vyssotski, A. L., Kays, R. W., Spoelstra, K., Kuemmeth, F., Heidrich, W. & Wikelski, M. 2008 Sleeping outside the box: electroencephalographic measures of sleep in sloths inhabiting a rainforest. *Biol. Lett.* **4**, 402–405. (doi:10.1098/rsbl.2008.0203)
- Rattenborg, N. C., Martinez-Gonzalez, D. & Lesku, J. A. 2009 Avian sleep homeostasis: convergent evolution of complex brains, cognition and sleep functions in mammals and birds. *Neurosci. Biobehav. Rev.* **33**, 253–270.
- Rechtschaffen, A. 1998 Current perspectives on the function of sleep. *Perspect. Biol. Med.* **41**, 359–390.
- Rechtschaffen, A. & Bergmann, B. M. 2002 Sleep deprivation in the rat: an update of the 1989 paper. *Sleep* **25**, 18–24.
- Reinertsen, R. E. 1996 Physiological and ecological aspects of hypothermia. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 125–157. New York, NY: Chapman and Hall.
- Reinertsen, R. E. & Haftorn, S. 1983 Nocturnal hypothermia and metabolism in the willow tit (*Parus montanus*) at 63 degrees north. *J. Comp. Physiol.* **151**, 109–118.
- Reinertsen, R. E. & Haftorn, S. 1984 The effect of short time fasting on metabolism and nocturnal hypothermia in the willow tit (*Parus montanus*). *J. Comp. Physiol.* **154**, 23–28.
- Reinertsen, R. E., Haftorn, S. & Thaler, E. 1988 Is hypothermia necessary for the winter survival of the goldcrest (*Regulus regulus*). *J. Ornithol.* **129**, 433–437. (doi:10.1007/BF01644486)
- Ribeiro, S., Mello, C. V., Velho, T., Gardner, T. J., Jarvis, E. D. & Pavlides, C. 2002 Induction of hippocampal long-term potentiation during waking leads to increased extrahippocampal zif-268 expression during ensuing rapid-eye-movement sleep. *J. Neurosci.* **22**, 10914–10923.
- Ribeiro, S., Gervasoni, D., Soares, E. S., Zhou, Y., Lin, S. C., Pantoja, J., Lavine, M. & Nicolelis, M. A. L. 2004 Long-lasting novelty-induced neuronal reverberation during slow-wave sleep in multiple forebrain areas. *PLoS Biol.* **2**, 126–137. (doi:10.1371/journal.pbio.0020024)
- Roth, T. C. & Pravosudov, V. V. 2009 Hippocampal volume and neuron numbers increase along a gradient of environmental harshness: a large-scale comparison. *Proc. R. Soc. B* **276**, 401–405. (doi:10.1098/rspb.2008.1184)
- Roth, T. C., Lesku, J. A., Amlaner, C. J. & Lima, S. L. 2006 A phylogenetic analysis of the correlates of sleep in birds. *J. Sleep Res.* **15**, 395–402. (doi:10.1111/j.1365-2869.2006.00559.x)
- Roth, T. C., Brodin, A., Smulders, T. V., LaDage, L. D. & Pravosudov, V. V. 2010 Is bigger always better? A critical appraisal of the use of volumetric analysis in the study of the hippocampus. *Phil. Trans. R. Soc. B* **365**, 915–931. (doi:10.1098/rstb.2009.0208)
- Ruby, N. F., Hwang, C. E., Wessells, C., Fernandez, F., Zhang, P., Sapolsky, R. & Heller, H. C. 2008 Hippocampal-dependent learning requires a functional circadian system. *Proc. Natl Acad. Sci. USA* **105**, 15 593–15 598. (doi:10.1073/pnas.0808259105)
- Sauer, S., Kinkelin, M., Herrmann, E. & Kaiser, W. 2003 The dynamics of sleep-like behaviour in honey bees. *J. Comp. Physiol. A* **189**, 599–607. (doi:10.1007/s00359-003-0436-9)
- Schmidt-Nielsen, K. 1983 *Animal physiology: adaptation and environment*, 3rd edn. New York, NY: Cambridge University Press.
- Shank, S. S. & Margoliash, D. 2009 Sleep and sensorimotor integration during early vocal learning in a songbird. *Nature* **458**, 73–77. (doi:10.1038/nature07615)
- Sharbaugh, S. M. 2001 Seasonal acclimatization to extreme climatic conditions by black-capped chickadees (*Poecile atricapilla*) in interior Alaska (64° N). *Physiol. Biochem. Zool.* **74**, 568–575. (doi:10.1086/322170)
- Shaw, P. J., Cirelli, C., Greenspan, R. J. & Tononi, G. 2000 Correlates of sleep and waking in *Drosophila melanogaster*. *Science* **287**, 1834–1837. (doi:10.1126/science.287.5459.1834)
- Shaw, P. J., Tononi, G., Greenspan, R. J. & Robinson, D. F. 2002 Stress response genes protect against lethal effects of sleep deprivation in *Drosophila*. *Nature* **417**, 287–291. (doi:10.1038/417287a)
- Sherry, D. F. 2006 Neuroecology. *Annu. Rev. Psychol.* **57**, 167–197. (doi:10.1146/annurev.psych.56.091103.070324)
- Sherry, D. F. & Healy, S. 1998 Neural mechanisms of spatial representation. In *Spatial representation in animals* (ed. S. Healy), pp. 133–157. London, UK: Oxford University Press.
- Sherry, D. F. & Vaccarino, A. L. 1989 Hippocampus and memory for food caches in black-capped chickadees. *Behav. Neurosci.* **103**, 308–318. (doi:10.1037/0735-7044.103.2.308)
- Sherry, D. F., Vaccarino, A. L., Buckenham, K. & Herz, R. S. 1989 The hippocampal complex of food-storing birds. *Brain Behav. Evol.* **34**, 308–317.
- Shettleworth, S. J. 1995 Comparative studies of memory in food storing birds: from the field to the Skinner box. In *Behavioural brain research in naturalistic and semi-naturalistic settings* (eds E. Alleva, A. Fasolo, H. P. Lipp, L. Nadel & L. Ricceri), pp. 159–192. Dordrecht, The Netherlands: Kluwer Academic.
- Shettleworth, S. J. 1998 *Cognition, evolution and behavior*. New York, NY: Oxford University Press.
- Siegel, J. M. 2000 Phylogenetic data bearing on the REM sleep learning connection. *Behav. Brain Sci.* **23**, 1007. (doi:10.1017/S0140525X00214039)
- Siegel, J. M. 2001 The REM sleep—memory consolidation hypothesis. *Science* **294**, 1058–1063. (doi:10.1126/science.1063049)
- Siegel, J. M. 2005 Clues to the functions of mammalian sleep. *Nature* **437**, 1264–1271. (doi:10.1038/nature04285)
- Smulders, T. V. 2006 A multi-disciplinary approach to understanding hippocampal function in food-hoarding birds. *Rev. Neurosci.* **17**, 53–69.
- Smulders, T. V., Gould, K. L. & Leaver, L. A. 2010 Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals. *Phil. Trans. R. Soc. B* **365**, 883–900. (doi:10.1098/rstb.2009.0211)
- Snapp, B. D. & Heller, H. C. 1981 Suppression of metabolism during hibernation in ground squirrels (*Citellus lateralis*). *Physiol. Zool.* **54**, 297–307.
- Squire, L. R. 2004 Memory systems of the brain: a brief history and current perspective. *Neurobiol. Learn. Mem.* **82**, 171–177. (doi:10.1016/j.nlm.2004.06.005)
- Stickgold, R. 2006 Neuroscience—a memory boost while you sleep. *Nature* **444**, 559–560. (doi:10.1038/nature05309)
- Stickgold, R. & Walker, M. P. 2005 Memory consolidation and reconsolidation: what is the role of sleep? *Trends Neurosci.* **28**, 408–415. (doi:10.1016/j.tins.2005.06.004)

- Strijkstra, A. M. & Daan, S. 1997a Ambient temperature during torpor affects NREM sleep EEG during arousal episodes in hibernating European ground squirrels. *Neurosci. Lett.* **221**, 177–180. (doi:10.1016/S0304-3940(96)13321-8)
- Strijkstra, A. M. & Daan, S. 1997b Sleep during arousal episodes as a function of prior torpor duration in hibernating European ground squirrels. *J. Sleep Res.* **6**, 36–43. (doi:10.1046/j.1365-2869.1997.00024.x)
- Strijkstra, A. M. & Daan, S. 1998 Dissimilarity of slow-wave activity enhancement by torpor and sleep deprivation in a hibernator. *Am. J. Physiol.* **275**, R1110–R1117.
- Strijkstra, A. M., Beersma, D. G. M., Drayer, B., Halbesma, N. & Daan, S. 2003 Subjective sleepiness correlates negatively with global alpha (8–12 Hz) and positively with central frontal theta (4–8 Hz) frequencies in the human resting awake electroencephalogram. *Neurosci. Lett.* **340**, 17–20. (doi:10.1016/S0304-3940(03)00033-8)
- Tobler, I. 1995 Is sleep fundamentally different between mammalian species? *Behav. Brain Res.* **69**, 35–41. (doi:10.1016/0166-4328(95)00025-O)
- Tononi, G. & Cirelli, C. 2003 Sleep and synaptic homeostasis: a hypothesis. *Brain Res. Bull.* **62**, 143–150. (doi:10.1016/j.brainresbull.2003.09.004)
- Tononi, G. & Cirelli, C. 2006 Sleep function and synaptic homeostasis. *Sleep Med. Rev.* **10**, 49–62. (doi:10.1016/j.smr.2005.05.002)
- Trachsel, L., Edgar, D. M. & Heller, H. C. 1991 Are ground squirrels sleep-deprived during hibernation. *Am. J. Physiol.* **260**, 1123–1129.
- van Swinderen, B. 2007 Sleep in invertebrates. In *Evolution of nervous systems: a comprehensive reference*, vol. 1 (eds J. H. Kass, G. F. Striedter & J. L. R. Rubenstein), pp. 451–456. New York, NY: Elsevier Academic Press.
- Vander Wall, S. B. 1990 *Food hoarding in animals*. Chicago, IL: University of Chicago Press.
- Vertes, R. P. 2004 Memory consolidation in sleep: dream or reality. *Neuron* **44**, 135–148. (doi:10.1016/j.neuron.2004.08.034)
- Vertes, R. P. & Siegel, J. M. 2005 Time for the sleep community to take a critical look at the purported role of sleep in memory processing. *Sleep* **28**, 1228–1229.
- von der Ohe, C. G., Darian-Smith, C., Garner, C. C. & Heller, H. C. 2006 Ubiquitous and temperature-dependent neural plasticity in hibernators. *J. Neurosci.* **26**, 10590–10598. (doi:10.1523/JNEUROSCI.2874-06.2006)
- von der Ohe, C. G., Garner, C. C., Darian-Smith, C. & Heller, H. C. 2007 Synaptic protein dynamics in hibernation. *J. Neurosci.* **27**, 84–92. (doi:10.1523/JNEUROSCI.4385-06.2007)
- Walker, M. P. & Stickgold, R. 2004 Sleep-dependent learning and memory consolidation. *Neuron* **44**, 121–133. (doi:10.1016/j.neuron.2004.08.031)
- Walker, J. M., Glotzbach, S. F., Berger, R. J. & Heller, H. C. 1977 Sleep and hibernation in ground squirrels (*Citellus* spp.)—electrophysiological observations. *Am. J. Physiol.* **233**, 213–221.
- Walker, J. M., Garber, A., Berger, R. J. & Heller, H. C. 1979 Sleep and estivation (shallow torpor)—continuous processes of energy conservation. *Science* **204**, 1098–1100. (doi:10.1126/science.221974)
- Walker, L. E., Walker, J. M., Palca, J. W. & Berger, R. J. 1983 A continuum of sleep and shallow torpor in fasting doves. *Science* **221**, 194–195. (doi:10.1126/science.221.4606.194)
- Wiltgen, B. J., Brown, R. A. M., Talton, L. E. & Silva, A. J. 2004 New circuits for old memories: the role of the neocortex in consolidation. *Neuron* **44**, 101–108. (doi:10.1016/j.neuron.2004.09.015)
- Wyatt, R. J., Fram, D. H., Kupfer, D. J. & Snyder, F. 1971 Total prolonged drug-induced REN sleep suppression in anxious-depressed patients. *Arch. Gen. Psychiat.* **24**, 145–155.