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REVIEW

Sleeping under the risk of predation

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Every studied animal engages in sleep, and many animals spend much of their lives in this vulnerable behavioural state. We believe that an explicit description of this vulnerability will provide many insights into both the function and architecture (or organization) of sleep. Early studies of sleep recognized this idea, but it has been largely overlooked during the last 20 years. We critically evaluate early models that suggested that the function of sleep is antipredator in nature, and outline a new model in which we argue that whole-brain or 'blackout' sleep may be the safest way to sleep given a functionally interconnected brain. Early comparative work also suggested that the predatory environment is an important determinant of sleep architecture. For example, species that sleep in risky environments spend less time in the relatively vulnerable states of sleep. Recent experimental work suggests that mammals and birds shift to relatively vigilant (lighter) states of sleep in response to an increase in perceived risk; these results mirror the influence of stress on sleep in humans and rats. We also outline a conceptual model of sleep architecture in which dynamic changes in sleep states reflect a trade-off between the benefits of reducing a sleep debt and the cost of predation. Overall, many aspects of plasticity in sleep related to predation risk require further study, as do the ways in which sleeping animals monitor predatory threats. More work outside of the dominant mammalian paradigm in sleep is also needed. An ecologically based view of sleeping under the risk of predation will provide an important complement to the traditional physiological and neurological approaches to studying sleep and its functions.

Every animal studied to date engages in some form of sleep or sleep-like behaviour (Hartse 1994; Tobler 2000; Rattenborg & Amlaner 2002; Lesku et al., in press). Recent studies on *Drosophila* (Shaw et al. 2000), bees, *Apis mellifera* (Sauer et al. 2003, 2004) and crayfish, *Procambarus clarkii* (Ramón et al. 2004), suggest an ancient evolutionary homology in sleep across the animal kingdom. The actual functions of sleep are, however, still ill defined (Rechtschaffen 1998), but new theories are arising as advances are made in the molecular biology and biochemistry of sleep (see Siegel 2003; Cirelli et al. 2004). Most evidence suggests that sleep has some important restorative function (Siegel 2003, see below). Evidence from long-term sleep-deprivation studies even suggests that death may occur with a severe lack of sleep (Rechtschaffen & Bergmann 2002; Shaw et al. 2002). The nature of the restorative effects of sleep is, however, still a matter of much study and speculation.

Regardless of its functions, sleep is clearly among the most prominent of animal behaviours. Humans spend about one-third of their lives in this behavioural state, and many mammal species spend even more time asleep (Zepelin 2000). However, despite its prominence in the lives of animals, sleep has received little attention from animal behaviourists. If sleep is considered at all, it is treated as something that happens when there is nothing else to do or as some sort of unavoidable constraint. However, just as with other, better-characterized behaviours, sleep is likely to be a behaviour that responds dynamically and adaptively to a host of environmental variables.

Here, we take such an 'adaptationist' perspective (Mitchell & Valone 1990) on the functions and dynamics of sleep. We focus on the one clear aspect of sleep that is apparent across the animal kingdom: when compared to alert and awake animals, sleeping animals are relatively

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unresponsive and unaware of their environment. The dangers of sleep are thus readily apparent. However, certain ways of sleeping are probably safer than others, and an explicit consideration of this fact should provide insight into many aspects of sleep in general. Considerations of predation risk were, in fact, prominent in some early comparative work on sleep (Hediger 1969; Zepelin 1970; Allison & Cicchetti 1976; Meddis 1977, 1983; Amlaner & Ball 1983; but see Zepelin & Rechtschaffen 1974). Indeed, the antipredator implications of sleep also figured prominently in early considerations of the function of sleep itself (e.g. Snyder 1966; Meddis 1977; see also Horne 1988; Zepelin 1989). Since this early comparative work, however, this focus has largely disappeared from studies on sleep. This situation undoubtedly reflects the clinical, human-oriented nature of the vast majority of research on sleep, and perhaps the relative difficulty in studying aspects of the risk of predation (e.g. Elgar et al. 1988). Nevertheless, predation-risk perspectives have yielded several insights into behaviour in a variety of contexts (Sih 1987, 1994; Lima & Dill 1990; Lima 1998), and we believe they will yield similar insights in the study of sleep.

Our goal here is thus to provide the first wide-ranging treatment of sleep under the risk of predation. We review past work on this topic and the historical role of antipredator thinking in the evolution of our view of sleep and its function. We devote much attention to several aspects of sleep architecture, including the distribution and function of various states of sleep. Our focus is mainly on the fitness or strategic consequences of various patterns of sleep rather than its physiological or biochemical functions. We highlight the things that we understand reasonably well, the many areas in need of much more attention, and the sorts of things that we might expect to see in future work.

The taxonomic coverage of our review is focused almost entirely on endothermic vertebrates (especially mammals). This bias is unavoidable because the vast majority of work on sleep has focused on humans and rats. The majority of comparative data on sleep also comes from mammals (Zepelin & Rechtschaffen 1974; Campbell & Tobler 1984; Zepelin 2000; Rattenborg & Amlaner 2002; Lesku et al., in press). A fair amount of information is available for birds as well (Amlaner & Ball 1983, 1994). Work on sleep in reptiles has been sparse, and work on amphibians, fish and invertebrates has been even rarer (Hartse 1994; Tobler 2000; Rattenborg & Amlaner 2002; Lesku et al., in press). Nevertheless, we expect that the strategic considerations outlined below apply to a wide variety of animals.

Some Sleep Basics

Sleep can be defined using behavioural criteria and electroencephalographic recordings. Behaviourally, sleep is a state characterized by (1) typical sleep posture, (2) behavioural quiescence, (3) increased stimulus threshold for arousal to an alert state, and (4) rapid reversibility to wakefulness once aroused (Piéron 1913; Flanigan 1972). Tobler (1985) added a fifth characteristic of behavioural sleep: compensatory increase following sleep deprivation. The criterion of increased arousal thresholds during sleep is perhaps the most important from the antipredator perspective. According to these behavioural criteria, every animal studied to date sleeps in some way (Rattenborg & Amlaner 2002; Lesku et al., in press).

Sleep may also be defined according to the electrophysiological correlates of behaviourally defined sleep. Although several electrophysiological parameters show changes between wakefulness and sleep, the electroencephalogram (EEG) has received the most attention. Unlike simple behavioural criteria for sleep, the EEG of birds and mammals can usually distinguish between two basic states of sleep. The EEG of an awake mammal or bird is characterized by low-amplitude, high-frequency waves (Fig. 1). During a sleep state known variously as quiet sleep, slow-wave sleep, or non-REM (rapid eye movement) sleep, the EEG is characterized by high-amplitude, low-frequency waves (Fig. 1). The other basic sleep state is variously referred to as active sleep, paradoxical sleep, or more typically as REM sleep. This sleep state is characterized by an EEG more typical of a waking animal (Fig. 1), but with a general loss of voluntary muscle tone (except in the ocular muscles). Aside from frequent small twitches, behavioural quiescence is maintained during REM sleep.

In some animals, the EEG can be used to distinguish various stages of non-REM sleep. In humans, non-REM sleep is divided into four stages that represent increasing depth of sleep as indicated by wave amplitude in the EEG and increasing arousal thresholds. The term slow-wave sleep (SWS) traditionally refers only to stages 3 and 4 of non-REM sleep in humans (Horne 1988), whereas SWS refers to all non-REM sleep in most birds and mammals. In rats, two stages of SWS are recognized, with one (stage 2) deeper than other (Neckelmann & Ursin 1993). These stages actually characterize a continuum of changes in the intensity of SWS rather than discrete categories (Borbély & Achermann 2000), and are therefore somewhat arbitrary. Although they do not experience distinct stages of SWS, birds also show variability in the intensity of SWS (Szymczak et al. 1996; Rattenborg et al. 2004). Only one type of REM sleep is typically identified in birds and mammals, although two states of REM sleep, tonic and phasic, are identified in humans (the latter is associated with eye movement and twitching; Hartmann 1973).

In birds and mammals, the two main classes of SWS and REM sleep are organized into ‘sleep cycles’, which are alternating periods of SWS followed by REM sleep. Several such cycles may occur over a given period of sleep (Borbély & Achermann 2000). During an extended period of mammalian sleep, deep SWS usually dominates the early sleep cycles (Fig. 2), with REM sleep and less-intense SWS becoming more prominent as sleep progresses (Horne 1988; Borbély & Achermann 2000). A similar pattern has been observed in some birds (Szymczak et al. 1996; Rattenborg et al. 2004).

The basic classes of SWS and REM sleep apply to most (if not all) birds and mammals, but the existence of these two classes of sleep in other vertebrates is far from clear (see

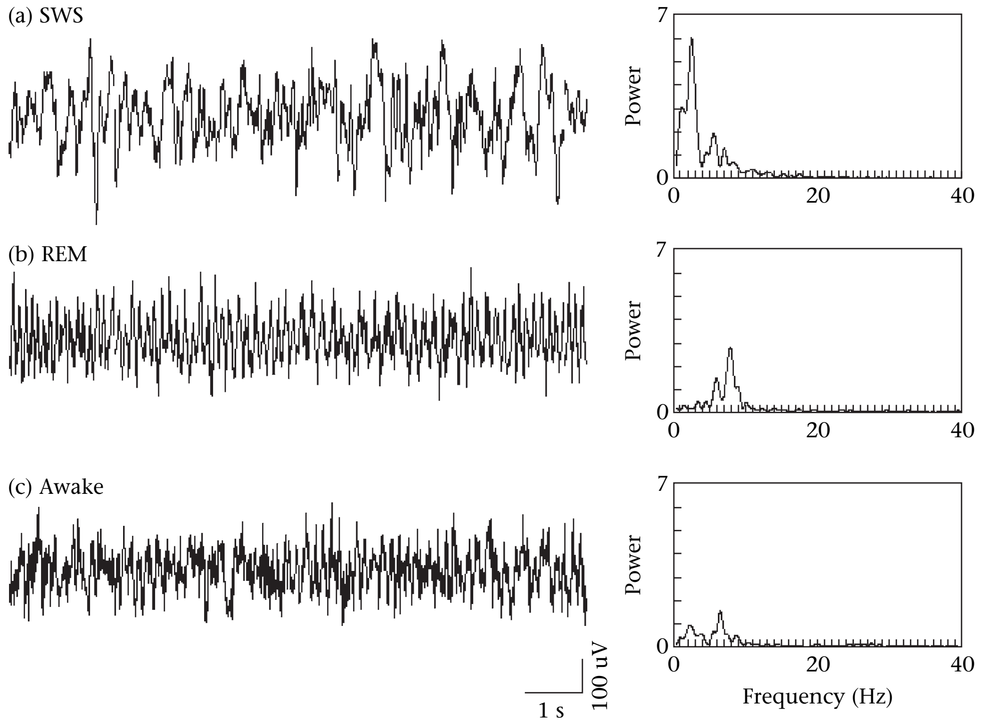

Figure 1. Electroencephalogram (EEG) of sleep in the laboratory mouse. Shown are representative EEGs of the mouse while (a) in slow-wave sleep (SWS) or non-REM sleep, (b) in REM sleep and (c) awake. Plots to the right indicate the relative power (in arbitrary units) of various wave frequencies in the adjacent EEG.

Rattenborg & Amlaner 2002). Obvious behaviourally defined sleep, however, occurs in reptiles (Flanigan et al. 1973, 1974). Several studies have also shown distinctive changes in EEG recordings during reptilian behavioural sleep (Rattenborg & Amlaner 2002; Lesku et al., in press). Whether these distinctive changes are homologous to avian and mammalian SWS or REM sleep remains to be shown. Furthermore, some behavioural states (postures) in sleeping reptiles are sometimes associated with differing degrees of responsiveness to external stimuli and thus probably represent different intensities of sleep (Flanigan et al. 1973). Few studies have examined sleep in amphibians and fish, but clear behavioural sleep occurs in these taxa as well (Tobler 2000; Rattenborg & Amlaner 2002; Lesku et al., in press). Invertebrates also engage in behavioural sleep according to the definition outlined above, and distinct changes in neural activity have been seen in sleeping bees (*Apis* sp.: Kaiser & Steiner-Kaiser 1983; Schuppe 1995) and *Drosophila* (Nitz et al. 2002); however, classes of sleep analogous to SWS or REM sleep have yet to be clearly identified in these taxa (but see Ramón et al. 2004).

Animals may be classified as monophasic or polyphasic sleepers. Monophasic sleepers tend to concentrate sleep into a distinct portion of the day (Tobler 1989; Ball 1992). Humans are classic monophasic sleepers, as are most other primates. Polyphasic sleepers sleep during several periods that may occur at any time of day. Rats are typically polyphasic sleepers, as are many rodents and other small mammals such as insectivores. Some types of mammals

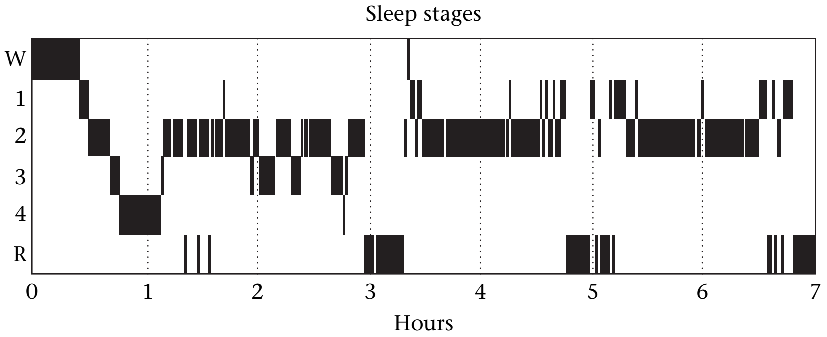

Figure 2. Distribution of sleep states across a typical night's sleep in humans. In humans, non-REM sleep is divided into four distinct stages; stage 1 is the lightest stage and stage 4 is the deepest stage as measured by EEG amplitude and arousal thresholds. W represents the waking state and R represents REM sleep. Reproduced from Borbély & Achermann (2000) with permission from Elsevier.

such as ungulates show no clear tendency towards one category or another (Tobler 1989). Overall, birds are largely monophasic sleepers, but waterfowl and shorebirds (which can feed both day and night) may be largely polyphasic in their sleep (Amlaner & Ball 1983).

Finally, many species of birds sometimes engage in unihemispheric slow-wave sleep (USWS, as opposed to the bihemispheric sleep typical of most mammals) in which one of the cerebral hemispheres is awake (to some extent) while the other sleeps (Amlaner & Ball 1994; Rattenborg et al. 2000). During USWS, the eye contralateral (opposite and neurologically connected to) the awake hemisphere is open and monitoring the environment. Behavioural evidence also suggests that some form of unihemispheric sleep probably occurs in reptiles (Rattenborg et al. 2000). Unihemispheric sleep may be a trait ancestral to both birds and mammals that was subsequently lost in mammals (see Rattenborg et al. 2000).

ANTIPREDATOR CONCERNS AND THE FUNCTION OF SLEEP

As mentioned earlier, there are many theories about the function of sleep. Below are some hypotheses that take a predation-risk perspective. See Moorcroft (1995), Rechtschaffen (1998) and Siegel (2003) for a more complete discussion of the many proposed functions of sleep.

The Immobilization Hypothesis

Prominent among theories of the function of sleep is the ‘immobilization hypothesis’ developed by Meddis (1975, 1977; see also Webb 1975). The basic idea behind this early hypothesis is that sleep serves a protective role during times when an animal cannot be usefully engaged in any other activity. Meddis reasoned that animals not immediately threatened by predators would be safer if they passed the time as quietly as possible, in a state of sleep. Sleep would prevent an animal from moving or responding to nonthreatening stimuli in ways that might attract the attention of predators.

A provocative aspect of the immobilization hypothesis is that sleep serves no restorative function (Meddis 1975, 1977). Sleep is viewed as an optional activity whose duration depends on the opportunities to do something else. For instance, under this hypothesis, animals would sleep longer during longer winter nights to pass the time safely until daylight brings opportunities for useful activity. During the shorter nights of summer, sleep times would be accordingly reduced. There is evidence in humans and other animals that sleep times can vary seasonally in this fashion (Amlaner & Ball 1983; Rattenborg et al. 2004; but see Kohsaka et al. 1992), but a minimum daily core of sleep may be needed for restoration (Horne 1988).

Rechtschaffen (1998) outlined several problems with the immobilization hypothesis. For instance, this hypothesis cannot easily explain why one often observes a rebound in sleep time or intensity following a period of sleep deprivation. The immobilization hypothesis also does not readily explain the existence of various states of sleep, which themselves may be associated with differing functions, such as memory consolidation (Walker & Stickgold 2004; but see Vertes 2004) or energy conservation in endotherms (Berger & Phillips 1995; see also Pravosudov & Lucas 2000). The same holds for several metabolic activities largely unique to sleep (Cirelli et al. 2004). Furthermore, remaining very quietly awake would seem to be safer than sleep, especially if sleep is an optional activity.

Like virtually all hypotheses of sleep under the risk of predation, the immobilization hypothesis has never been modelled formally to determine whether its conclusions actually follow from its assumptions. Here we address the question of whether the profound behavioural ‘blackout’ of sleep provides more safety than quiet wakefulness. From a strategic perspective, two aspects of the immobilization hypothesis are most relevant: (1) the degree to which immobilization prevents detections and attacks by predators and (2) the degree to which an animal can detect or respond effectively to attack as a function of the degree or depth of sleep. We assume (as per Meddis 1977) that a sleeping animal is less prone to detection than is a quietly awake animal (which may be more prone to react to nonthreatening stimuli, as hypothesized). We also assume that a quietly awake animal would be better able to respond to an attack, should one occur.

These two key assumptions are clearly antagonistic and thus, the option favoured evolutionarily is not obvious. The simplest way to approach the problem is to assume that an animal must survive a period T during which it can usefully engage in no activity other than rest or sleep. Assuming that a predator may appear at any time with equal probability, the probability of surviving the interval T is simply $\exp(-aDT)$, where a is the encounter rate with predators and D is the probability of death given an encounter. The variables a and T are fixed; hence, maximizing survival is equivalent to minimizing D. The probability D itself is the product of the probability of being detected and attacked by a predator (d) and the probability of capture given attack (c); each of these probabilities is a function of the intensity of sleep (s), which varies from 0 to 1. Quiet wakefulness and deep sleep are represented by $s = 0$ and $s = 1$, respectively. Intermediate values for sleep intensity are possible, which might represent lighter stages of sleep.

The animal has behavioural control over the intensity of sleep; hence, we seek the value of s that minimizes $D = d(s)c(s)$. The optimal sleep intensity (s^*) depends strongly on the form of the functions chosen to describe the probabilities $d(s)$ and $c(s)$. For instance, if both $d(s)$ and $c(s)$ are linear in s, then D will be minimized at one of the extremes (Fig. 3a). That is, the animal would be either quietly awake ($s^* = 0$) or deeply asleep ($s^* = 1$). These two extreme solutions also hold when d and c are both concave-downward functions of s (Fig. 3b). The extreme favoured is determined by the details of the functions. Furthermore, an intermediate value of s^* is possible when both d and c are concave-upward functions of s (Fig. 3c).

This simple exercise in modelling suggests that immobilization can indeed be superior to quiet wakefulness as a predator avoidance strategy. However, quiet wakefulness

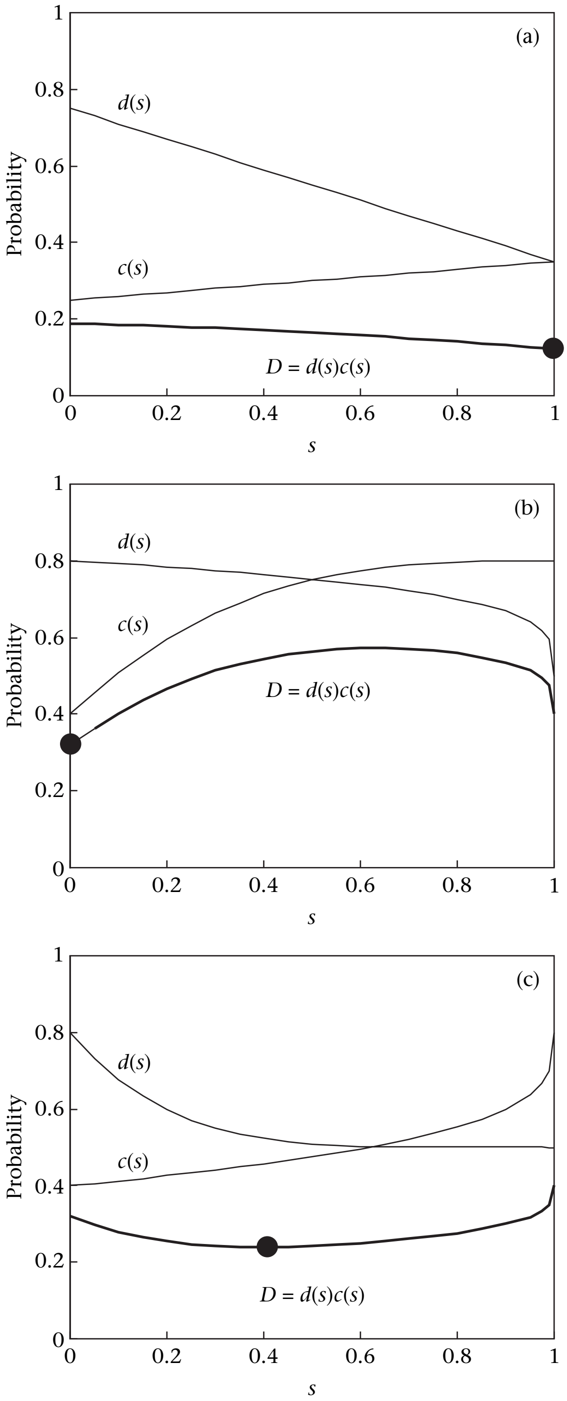

Figure 3. Representative views of the immobilization hypothesis for the function of sleep. Shown is the probability of death (*D*) given an encounter with a predator as a function of the intensity of sleep (*s*). *D* is the product of the probability of being detected and attacked by a predator ($d(s)$) and the probability of capture given attack ($c(s)$). Quiet wakefulness is represented by $s = 0$, and deep sleep by $s = 1$. The large dots indicate the value of *s* minimizing *D* (or s^*). (a) Case in which both $d(s)$ and $c(s)$ are linear. Here, s^* occurs at one of the extremes of 0 or 1; $s^* = 1$ for the functions shown. (b) Case in which both $d(s)$ and $c(s)$ are concave-downward functions of *s*. Here, s^* also occurs at one of the extremes of 0 or 1; $s^* = 0$ for the functions shown. (c) Case in which both $d(s)$ and $c(s)$ are concave-downward functions of *s*. Here, s^* may occur at an intermediate value of *s*.

or even an intermediate degree of sleep can also be favoured under some circumstances. Thus, it is clear that immobilization (defined broadly as $s > 0$) is not a unique outcome of the assumptions put forth by Meddis (1975, 1977). Unfortunately, we do not have nearly enough information on the behavioural events surrounding attacks on sleeping animals to assess which of the above outcomes would be more likely (see also Lima 2002). It does seem reasonable, however, to conclude that the immobilization hypothesis cannot account generally for the existence or maintenance of sleep. We nevertheless suspect that immobilization is an important aspect of the nature of sleep.

A New Hypothesis: 'Blackout' Sleep Makes Sleeping Safer

Here, we outline a simple strategic model that views the whole-brain 'blackout' nature of sleep as an antipredator response. More specifically, the function of blackout sleep may be to achieve the specific functions of sleep as safely as possible. Our approach differs from (and is complementary to) the traditional approach to the subject, in which insights into the function of sleep are sought by comparing various neural/metabolic processes between the sleeping and waking brain. We believe that theories of the function of sleep must also address why these sleep-associated processes are best accomplished via a behavioural blackout. Without the blackout and resulting vulnerability of sleep, there would not be anything enigmatic to explain. Space limitations require that this model be presented in full elsewhere, so here we will simply summarize its main points.

We take the position held by a plurality of sleep researchers and assume that sleep has some sort of critical maintenance or restorative effect on neural tissue (see Siegel 2003). We assume that the brain is composed of distinct neural units that are linked to other such units to perform various functions for the organism in question. We further assume that these units could 'sleep' separately from other units (Mahowald & Schenck 1992; Huber et al. 2004). Sleep in a given unit would require that the unit be taken off-line much as envisioned by Krueger & Obál (1993, 2002; see also Tononi & Cirelli 2003). With this configuration, it would be possible for one part of the brain to sleep while another part is awake and in a relatively good position to react to threats.

The form of sleep favoured evolutionarily depends on the nature of the interactions between neural units. With additive interactions among units, if 50% of the units are online (awake), then the animal has a 50% chance of surviving attack. If interactions are multiplicative, then having 50% of units online leads to much less than 50% survival. Given additive interactions, it matters little whether sleep is concentrated into one blackout period or spread out evenly over a much longer time spent partially awake. However, multiplicative interactions among units would lead quickly to blackout sleep; that is, survival is maximized if all units sleep at the same time. Simply put, it is safer to sleep by consolidating sleep into one single (short) block, which increases the time spent awake and fully able to deal with predators. The option of spending time partially awake will not lead to greater safety when interactions between units are multiplicative. A model addressing the actual time spent asleep should also consider the various 'states of vigilance' that exist in sleeping animals (see below) and the fact that the level of risk experienced while sleeping will determine (in part) the total time spent asleep. Factors related to the benefits of immobilization may also influence total sleep time.

Overall, blackout sleep may simply be the safest way to deal with the fact that neural units must be taken off-line for maintenance and restoration in an interconnected and interdependent brain (multiplicative interactions are undoubtedly the rule in a real brain). It may indeed be the case that the need for restoration ultimately is responsible for blackout sleep, but simply demonstrating the need for restoration will not, in itself, be sufficient to explain the blackout. As noted by Moorcroft (1995), Rechtschaffen (1998) and others, many of the proposed restorative functions of sleep could conceivably be performed to a large extent while awake. Our simple model suggests, however, that such a 'waking' strategy of sleep organization is unlikely to be favoured by natural selection. Finally, we note that our ideas are compatible with many of the proposed restorative functions of sleep (Rechtschaffen 1998; Siegel 2003), provided that such restoration can be done more effectively if neural units are taken off-line.

ARCHITECTURE OF SLEEP

Thinking about sleep under the risk of predation has usually focused on the architecture of sleep. By 'architecture', we mean the states of sleep, the distribution of such states within sleep bouts, length of bouts, timing of sleep across the day, and so forth. Regardless of whether a predation-risk perspective will ultimately shed much light on the function of sleep, predation risk has many important implications for the architecture of sleep.

The Sentinel Hypothesis and REM Sleep

In an early paper, Snyder (1966) proposed the idea that REM sleep serves a sort of sentinel function because it is in many respects a state of much neural activity. The basic idea is that episodes of REM sleep allow an animal to be ready to escape should an attack occur, and that the brief arousals to wakefulness that may precede or follow REM sleep also serve an antipredator function. Voss (2004) has recently recast the sentinel idea to include other sleep states and their distribution over time. She suggests that the arousals associated with REM sleep establish a 'protective field' around the (human) sleeper.

The sentinel hypothesis is appealing in many respects. Mammals in REM sleep are clearly more physiologically prepared for wakefulness than are those in deep SWS (Tolaas 1978). A recent study also suggests that rats are in a relatively alert state when awakened from REM sleep (Horner et al. 1997; see also Van Twyver & Garrett 1972). Furthermore, humans (Nashida et al. 2000; Cote 2002; Perrin et al. 2002) and rats (Maho & Hennevin 1999) can detect and process information to a surprising degree during REM sleep (Bastuji & Garcia-Larrea 1999; Nashida et al. 2000; Cote et al. 2001; see also below). Paradoxically, however, arousal thresholds in REM sleep tend to be higher than in SWS (Dillon & Webb 1965; Van Twyver & Garrett 1972; Amlaner & McFarland 1981; Neckelmann & Ursin 1993); hence, time in REM sleep could be relatively dangerous (see below). In addition, the brief arousals sometimes associated with REM sleep (Van Twyver & Garrett 1972) may not be frequent enough to have much benefit from an antipredator perspective (see Bednekoff & Lima 1998).

Overall, the validity of the sentinel hypothesis is not yet established. This hypothesis has never really been tested, and its predictions are not obvious. One simple prediction might be that REM sleep would become more prominent in species that suffer higher predation, or when the perceived risk of predation increases. As we will show in the next section, however, this prediction does not hold. Perhaps a more direct prediction would be that an increase in predation risk would lead to shorter cycles of REM sleep and thus, more arousals to wakefulness (see also Voss 2004).

Comparative Perspectives on Sleep Architecture

Allison & Van Twyver (1972) and Allison & Cicchetti (1976) published early papers that defined some important aspects of the architecture of mammalian sleep under the risk of predation (also see Meddis 1983). These authors sought insight into the evolution of sleep by relating key structural features of sleep, such as total sleep time and percentage of time in REM sleep, to constitutive traits of animals such as brain and body mass. In addition to these constitutive variables, Allison and colleagues also included key features of the environment, including the degree to which the mammals in question are vulnerable to predators and the determinants of relative exposure to predators. Their analyses indicated a strong role for the predatory environment as a determinant of sleep architecture, a role that was roughly as important as factors such as brain mass and body size. In general, mammals living in relatively exposed environments had short sleep times and a low density of REM sleep in both absolute and relative measures. Predatory mammals were most likely to show large amounts of REM sleep. These results apparently reflect the fact that arousal thresholds tend to be higher in REM sleep than in other states, making REM sleep a relatively dangerous form of sleep. Adding to the problem with REM sleep is the fact that large animals like ungulates must lay down during REM sleep (due to loss of muscle tone), which might advertise their vulnerable state to predators (Ruckebusch 1972). The predatory environment also appears to influence sleep patterns in birds (Amlaner & Ball 1983). However, the relative lack of detailed information on REM sleep and SWS in birds limits inferences about the effects of predators on avian sleep architecture.

None of the comparative studies conducted to date have made any inferences about changes in the relative intensity of SWS with increasing predation risk, because such data are unavailable for many species. Presumably, however, species with less REM sleep would also show a less intense form of SWS as well (see below).

These comparative studies also demonstrate some important points about the states of sleep and REM sleep in particular. First, the amount of REM sleep and SWS can each vary greatly across the phylogenetic spectrum of mammals, and thus, there are no fixed requirements for either state (at least in an evolutionary sense). Other comparative studies of sleep architecture (Zepelin & Rechtschaffen 1974; Elgar et al. 1988) also reported much interspecific flexibility in the distribution of SWS and REM sleep. Second, given the apparent dangers associated with REM sleep, it appears that mammals require at least some REM sleep (but see Lyamin et al. 2000 on the possible lack of REM sleep in cetaceans). Lastly, these comparative studies suggest that the dangers imposed by certain states of sleep are largely unavoidable constraints on vertebrate sleep. That is, natural selection has not ‘found a way’ to circumvent these constraints except through altering the time spent in certain dangerous states like REM sleep.

An important matter regarding quantitative comparative work on sleep is the lack of analyses that explicitly take into account the phylogenetic relationships among animals (Harvey & Pagel 1991). Virtually all existing comparative work on sleep simply takes each species as statistically independent of all others, but this approach is largely unacceptable given the current understanding of such analyses (Martins 2000). Only Elgar et al. (1988) provide any sort of phylogenetically based comparative study on mammalian sleep. We do not wish to imply that existing comparative studies are necessarily wrong or misleading, but it is possible that some of the inferences derived from such analyses will not hold up under the scrutiny of modern techniques.

Plasticity in Sleep under the Risk of Predation

Distribution of sleep states

The literature on behavioural plasticity under the risk of predation is replete with examples of graded behavioural responses to changes in the perceived risk of predation (Sih 1987; Lima & Dill 1990). Furthermore, many studies show that the behaviour of feeding animals represents a trade-off (or adaptive compromise) between the benefit of energy intake and the obvious fitness costs of an early death (Lima 1998). Analogous trade-offs also apply to mating and other forms of reproductive behaviour (Sih 1994). So far, however, this ‘trade-off’ concept has largely bypassed the study of sleep.

There are many ways in which sleep responses to changes in the perceived risk of predation might be adaptive. Under an increase in the perceived risk of predation, we might expect less time spent sleeping and a disproportionate decrease in REM sleep. We might also expect more frequent arousals, less time in deep SWS, more time in unihemispheric sleep (if possible), and perhaps a reallocation of sleep to different times of day. However, without a clear understanding of the function of sleep, we cannot be very specific about either the trade-offs involved or the predicted changes in sleep behaviour (such trade-offs are much more straightforward in the study of feeding animals; Lima & Dill 1990). We could base quantitative predictions on empirical demonstrations of lowered performance as a result of differing degrees of sleep deprivation (which might occur given any of the above responses to increased risk), but such studies are not easily done with animals. At this point, we can say that sleep seems to serve a vital function, and that there are negative consequences of losing sleep short of some sort of ‘target’ (Rattenborg et al. 2004). However, we would not expect most aspects of sleep to be absolutely ‘protected’ any more than energy intake is absolutely protected in feeding–predation trade-offs.

As mentioned earlier, this sort of predation-risk ‘trade-off’ perspective is rare in the study of plasticity in sleep architecture. Lendrem (1984) provides a unique exception to this rule. He studied changes in the sleep of doves, *Streptopelia risoria*, in response to the brief, controlled appearance of a predator (ferret, *Mustela putorius*). Following their brief encounter with the predator, the doves showed a marked increase in the rate at which sleep was interrupted by ‘peeking’ (eyes open) to scan the local environment. These doves also spent less overall time sleeping after the encounter with the predator. Furthermore, doves in the safer setting of a group spent more time sleeping with lower rates of peeking while asleep. Lendrem (1983) also found that mallards, *Anas platyrhynchos*, sleeping in relatively vulnerable places showed increased rates of sleep interruptions (peeking), and that mallards in larger groups showed longer bouts of sleep. Similar effects have been observed in other ducks (Gauthier-Clerc et al. 1998, 2000, 2002) and a shorebird (Dominguez 2003).

Studies demonstrating plasticity in sleep architecture are most valuable when they involve the manipulation of predation risk in conjunction with EEG recordings of sleep states. We know of only a few such studies. Sanford et al. (2001) examined the distribution of sleep states in rats after electric shock conditioning; although not predation per se, electric shocks probably mimic many aspects of it. The main effect on sleep was a substantial reduction in the prevalence of REM sleep for several hours (also see Sanford et al. 2003). The functional consequences (if any) of this long-term reduction in REM sleep were not studied. One effect of severe REM sleep deprivation may be a general decrease in fear (Hicks & Moore 1979; Martínez-González et al. 2004), but this degree of deprivation is probably not normally observed in free-living animals.

A study of unihemispheric sleep in mallards (Rattenborg et al. 1999a, b) demonstrated a different sort of plasticity in sleep architecture under variable risk. Ducks, like most birds, sleep either unihemispherically or bihemispherically (Amlaner & Ball 1994). When sleeping in a relatively risky situation (on the edge of a group versus within the group’s interior), mallards engage in less overall sleep and show a large relative increase in the prevalence of USWS (Fig. 4; Rattenborg et al. 1999a, b), although bihemispheric sleep is still the dominant form of sleep. This suggests that bihemispheric sleep is more valuable than

USWS, but that the latter is used to aid in predator detection under an increased threat. During USWS, the open eye (contralateral to the awake hemisphere) is readily able to detect incoming threats (Rattenborg et al. 1999a, b). The REM state is a minimal component of overall sleep in mallards and is not significantly affected by an individual's position in the group. As with the study by Sanford et al. (2001), the functional consequences of a decrease in the riskier (i.e. higher-quality) form of sleep were not determined.

Although there are few studies that both manipulate risk and record EEGs, there is a fairly large literature on sleep states under various forms of stress (in both humans and rats; Van Reeth et al. 2000) that might shed light on predation-related trade-offs (also see Voss 2004). Human patients suffering from high levels of stress or anxiety show sleep patterns that are much diminished in deep SWS and REM sleep (Fuller et al. 1997; Voss 2004). An increase in stress hormones in rats causes a fragmentation of sleep and a decrease in the deeper stages of SWS (Dugovic et al. 1999). These sorts of studies usually do not deal with life-threatening stimuli such as predators (but see Lavie et al. 1991), but the general phenomenon of stress-induced changes in sleep almost certainly forms the basis for at least some predator-induced changes in sleep architecture.

Timing of sleep

The timing or 'phasing' of sleep (that is, the distribution of sleep over the daily cycle) should also be influenced by trade-offs between the quality of sleep and the risk of predation (also see Ball 1992), but there are no studies on the topic. As a possible example of this phenomenon, Fenn & Macdonald (1995) showed a dramatic shift in the activity patterns of free-living rats from nocturnal to diurnal in response to changes in activity of red foxes, *Vulpes vulpes* (who were, in turn, responding to changes in the activity patterns of humans). This shift in activity presumably also resulted in a switch to a more nocturnal sleep pattern in the rats. Similar sorts of shifts in sleep have been demonstrated in laboratory rats in response to changes in feeding schedules (see Tobler 1989).

We agree with Tobler's (1989) suggestion that animals with polyphasic sleep patterns and an ability to feed at any time probably have the greatest flexibility in sleep phasing (e.g. the rats in Fenn & Macdonald 1995). We also suggest that prey facing generalist predators (such as foxes) are most likely to show major changes in the temporal patterning of sleep with changing risk. Specifically, animals that are mainly incidental prey of generalist predators are most likely to benefit from a major change in sleep times. A predator that specializes on a given prey species will most likely match any change in the prey's activity pattern (also see Kotler et al. 2002); hence, major changes in prey sleep phasing in specialized predator–prey systems are unlikely.

Where to sleep

An animal's choice of a sleep site is probably one of the most important determinants of predation risk experienced during the sleep period, and thus sets the stage for many of the issues discussed so far. As might be expected from the preceding discussion, however, there are few studies on plasticity in the choice of sleep site. There is virtually no experimental work, or even systematic observational work, on the topic. There currently exist only anecdotal observations of sleep-site selection in dangerous situations (e.g. Skutch 1989). Such observations from primates, however, suggest that safety is paramount in the choice of where to sleep (Anderson 1998). Ramakrishnan & Coss (2001) provide a particularly detailed treatment of the topic in a macaque.

We naturally would expect animals to choose safe sites for sleeping, but the picture is undoubtedly more complicated. The choice of sleep site will depend on (among other things) the safety of available sites, choices made by others (degree of crowding, attraction of predators to groups, etc.), proximity to profitable feeding areas, as well as thermodynamic considerations (Bakken 1992). 'Shell game' considerations, in which animals frequently shift sleeping sites to avoid predators (Mitchell & Lima 2002; also see Day & Elwood 1999), may also apply. The expected quality of sleep in a given location could itself be an important consideration in choice of a site.

It is likely that most animals routinely sleep in relatively secure, thermodynamically favourable places. However, the safest sites will not necessarily allow for deep sleep. Under some circumstances, the safest available sites might be exposed spots where predators have trouble approaching unseen (e.g. starlings roosting on open power lines). Thus, the safety of such places may be reflected in a bias towards the more shallow sleep states. Animals choosing to sleep in such situations will tend to form groups for safety (Krause & Ruxton 2002). Such exposed spots are often not the most thermodynamically favourable sites, and this fact may dictate changes in sleep irrespective of antipredator considerations. Since endotherms cannot thermoregulate well in REM sleep (Heller et al. 1983;

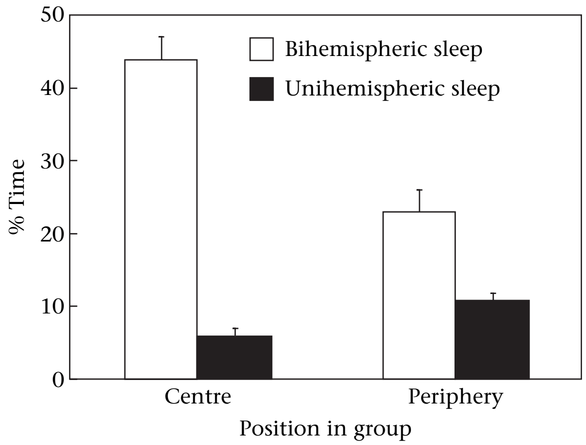

Figure 4. Percentage of time spent in bihemispheric or unihemispheric sleep by mallard ducks (as determined by electroencephalogram power analyses, see Rattenborg et al. 1999a, b). Ducks slept in linear groups of four birds such that two were in the centre and two were on the periphery of the group. Data are averaged over 16 ducks. Time not spent in one of these two states of sleep was spent awake.

Parmeggiani 2003), diminished REM sleep is expected under thermodynamically stressful conditions. Thus, thermodynamic and antipredator considerations may interact to determine choice of sleep site and its effect on sleep architecture.

States of Vigilance while Sleeping: Some Conceptual Issues

The various states or stages of sleep (and wakefulness) are referred to as 'states of vigilance' by sleep scientists. Compared to the literature on antipredator vigilance (Elgar 1989; Bednekoff & Lima 1998), the sleep literature uses the term 'vigilance' more in reference to awareness of the environment in general than attention directed towards predators, but there is an obvious connection between the two usages. As implied above, deep SWS and REM sleep are low states of vigilance (high arousal thresholds; Dillon & Webb 1965; Van Twyver 1969; Neckelmann & Ursin 1993), whereas drowsiness might be considered the highest state of vigilance while still sleeping to some extent (Tobler 2000). Similarly, in birds, bihemispheric sleep would be considered a lower state of vigilance relative to unihemispheric sleep. Quiet wakefulness (deep rest) is also considered a high state of vigilance, and active wakefulness is considered the most vigilant state.

Here we address two related questions: (1) why are there different states of vigilance/sleep? and (2) why not always sleep at maximum intensity? Regarding the latter question, it seems clear that some deep (intense) sleep is essential in the long term, and it is in many ways a superior form of sleep. Furthermore, following significant sleep deprivation, the sleep debt is often mitigated by a substantial increase in deep SWS (Horne 1988; Tobler 2000). It therefore seems possible that all or most of the functions of SWS, at least, could be accomplished during a relatively short but intense period of deep sleep. However, a considerable amount of time is actually spent in the shallower states of SWS (see Fig. 2), at least in humans, and deep SWS may represent only a relatively minor portion of overall sleep (Horne 1988; Borbély & Achermann 2000).

There are at least three reasons why an animal might not sleep at the maximum intensity. First, perhaps the less intense forms of sleep are states through which an animal must pass when progressing through the sleep cycle. For instance, the less intense forms of sleep may unavoidably occur when passing from deeper SWS to the more neurologically active REM sleep and vice versa. In humans, there is a tendency to pass into REM sleep from stage 2 non-REM sleep (Fig. 2; Borbély & Achermann 2000), but the predominance of stage 2 sleep seems much greater than one would expect if it were simply a transitional sleep state. Second, perhaps different aspects of the function of sleep are accomplished in the different stages such that all stages are necessary to realize the full benefits of sleep.

A third possible reason concerns the antipredatory consequences of sleep outlined so far: the continuum of sleep/vigilance states may allow sleep to be tailored to the prevailing risk of predation and current sleep debt such that survival (fitness), rather than the benefits of sleep per se, is maximized. In nature, bouts of high risk are episodic (as per Lima & Bednekoff 1999), and the use of the vigilant states of sleep during such periods would allow sleep to proceed to some extent (as long as some or most of the functions of sleep can be served by the relatively high-vigilance states of sleep). Furthermore, if the sleep debt is minimal, then extensive reliance on deep SWS may not be necessary.

There is considerable evidence for adaptive changes in sleep states in response to changes in the risk of predation. We have already discussed several ways in which changes in the perceived risk of predation (or perceived threats in general) influence the distribution of sleep states (especially REM sleep). Observations on the effects of stress/fear on human sleep are also consistent with the idea that sleep states can be tailored to prevailing perceptions of risk (also see Voss 2004).

Further support for the 'tailoring-of-sleep' hypothesis comes from empirical observations on the distribution of sleep states (or the intensity of sleep) across the sleep period. Distribution of sleep states across time has not been studied in many animals, so we focus our attention on humans and rats. During a long bout of sleep, there is typically a strong bias towards deep sleep early in the sleep period, followed by less deep (more vigilant) states and an increase in REM sleep as the end of the bout approaches (Fig. 2; also see Horne 1988; Borbély & Achermann 2000). This general temporal pattern in changing sleep (vigilance) states is analogous to changes in antipredator vigilance in feeding animals as their energetic states change (McNamara & Houston 1986). As we argue below, the similarity in these two vigilance-related phenomena suggests that deep sleep is high-quality sleep, and that a major function of sleep is restorative in nature (as per Rechtschaffen 1998; Siegel 2003).

Our reasoning here is based directly on dynamic models of antipredator vigilance (e.g. McNamara & Houston 1986; Clark & Mangel 2000). In these models, energetic state and the passage of time combine to determine antipredator vigilance. These models assume that feeding functions to redress the energetic deficit incurred during the overnight fast. Feeding can be interrupted at any time during the day for unknown lengths of time due to encounters with predators or bad weather. The fastest way to erase this energetic deficit is to feed at the maximal rate, but this option precludes any antipredator vigilance (vigilance and feeding are often mutually exclusive activities). These models predict that a hungry animal should devote much effort to feeding and relatively little to vigilance. As its energetic reserves increase, the animal should devote increasing effort to vigilance at the expense of feeding rate. In other words, as the energetic deficit is eliminated, the animal takes fewer risks by engaging in greater vigilance. Changes in antipredator vigilance allow the behavioural sequence to be tailored to changing energetic states such that overall fitness is maximized.

Different states of vigilance in sleeping animals may play the role of antipredator vigilance in the above conceptual scenario, with the sleep deficit as the analogue of the energetic deficit. Assume further that unpredictable events (e.g. predators, general disturbance) can disrupt sleep for much of the night. Assume that sleep is essential for some sort of restorative function, and that deep SWS can erase this deficit faster than the more vigilant states of SWS. In a dynamic model of sleep, an animal would accept the risk of relatively intense SWS early in the sleep period when the sleep deficit is greatest (e.g. Fig. 2); this ensures that enough high-quality sleep takes place on most nights, even if interruptions occur occasionally. A shift towards less-deep sleep will occur as high-quality sleep accumulates. As mentioned earlier, the observation that intense SWS occurs early in the sleep period is consistent with the idea that sleep serves a restorative function. The tailoring-of-sleep hypothesis also seems similar to the 'changing priorities' idea presented by Voss (2004) to explain changes in sleep states over time. This sort of dynamic model of sleep would predict a greater degree of intense SWS following sleep deprivation, which is commonly observed in mammals (Tobler 2000). The corresponding phenomenon in birds of less unihemispheric sleep and more bihemispheric sleep in response to sleep deprivation has recently been observed (Boerema et al. 2003).

The above analogy may help to explain the existence of various states of SWS sleep, but REM sleep presents a problem for which there is no real analogue in the above feeding–vigilance trade-off. The late portion of the sleep period is indeed dominated by less-intense SWS, but there is also a relative increase in REM sleep as well (Fig. 2). As mentioned earlier, arousal thresholds are higher in REM sleep than for most or all intensities of SWS. Thus, an overall theory for the distribution of sleep states over time must address the issue of why REM sleep is most prevalent late in the sleep period. Perhaps there is some antipredator value to 'packaging' REM sleep with relatively vigilant forms of SWS sleep (Voss 2004). The relatively late appearance of REM sleep may also be explained by assuming that deep SWS and REM sleep are antagonistic states, and that the function of REM sleep is not as important as that of SWS (at least on a short-term basis). However, severe REM sleep deprivation may well cause problems with memory consolidation (Walker & Stickgold 2004; but see Vertes 2004) and perhaps a shift in REM sleep to the earlier portions of a sleep bout. Alternatively, Voss (2004) suggests that REM sleep occurs late in an undisturbed period of sleep because that is when (humans) are most secure in their sleeping arrangements (reflecting the lack of disturbance).

Drowsiness as a state of vigilance

Drowsy animals are usually immobile, relatively unresponsive, and usually have their eyes at least partially opened. Drowsiness is taxonomically widespread, and is known to occur in many species of mammals (Allison & Cicchetti 1976; Meddis 1983) and birds (Amlaner & Ball 1983). Many workers have grappled with the question of whether to categorize this state as a form of sleep or quiet wakefulness (e.g. Allison & Cicchetti 1976; Meddis 1983; Campbell & Tobler 1984; Tobler 1995; Zepelin 2000), and all have chosen not to treat it as a form of sleep. However, drowsiness is in many ways a particularly vigilant form of sleep (Makeig et al. 2000; Noser et al. 2003), and might be an effective way of dealing with the problem of predator detection.

If drowsiness has a significant antipredator function, then we might intuitively expect more drowsiness in a risky environment (but not when dealing with an acutely risky situation with a predator present). More generally, the degree of drowsiness should respond to changes in the risk of predation. The degree of drowsiness might even influence the distribution and density of various states of sleep during 'true' sleep. However, these issues surrounding drowsiness will be unresolved until the sleep-related benefits (if any) of drowsiness can be determined.

ANTIPREDATOR INFORMATION AVAILABLE TO A SLEEPING ANIMAL

Alert and awake animals use several cues and sensory modalities to gain information about the local risk of predation (Lima & Steury, in press). Is a similar range of information also available to sleeping animals? Are information-rich predator cues more likely to cause an arousal from sleep than are other types of cues? Are arousal thresholds in the various stages of sleep a function of the information content of particular cues? We know that a sleeping animal is monitoring the environment for relevant stimuli to some extent (Velluti 1997; Coenen & Drinkenburg 2002), and that the magnitude of stimuli necessary to awaken an animal varies with different sleep states. Beyond these simple facts, however, little is known about the monitoring and assessment of potential predatory threats by sleeping animals.

The degree to which information-rich cues might alter arousal thresholds is a particularly important question for our purposes. It seems likely that meaningful predatory stimuli would have a markedly greater effect than would other stimuli that may trigger arousals. It is also conceivable that important cues may be linked to unexpectedly low arousal thresholds in deep sleep. It has long been known that rats do indeed show greater arousal thresholds in deeper sleep even when the cue in question is a tone associated with foot shocks (Van Twyver & Garrett 1972), but the relevance of this result to their natural predator cues is unclear. It does seem likely that arousal thresholds are greater in deep sleep, but arousal thresholds for key predatory stimuli are likely to be lower than expected based on current available work. There are almost certainly specific neural structures devoted to monitoring the predatory environment during sleep (Lang et al. 2000, Öhman & Mineka 2001; also see Lima & Steury, in press), making these lower thresholds a real possibility.

Of course, arousal from sleep reflects a process of not only information detection but also a degree of information processing. Thus, a lack of arousal from sleep does not necessarily reflect a lack of information available to the sleeping animal; some sensory information can undoubtedly be received without overt arousals. Separating these two processes is not easy, but techniques designed to detect an evoked or event-related potential (ERP) may yield some insights. These techniques allow one to record neural responses to stimuli that are detected but do not necessarily lead to arousals or wakefulness (see Bastuji & Garcia-Larrea

1999 for a review). They can be used to show that the sleeping human brain can (during shallow SWS and REM sleep) differentiate the subject's own name from general speech (Bastuji et al. 2002). Analyses of ERPs have shown that the sleeping avian brain can also detect and 'acknowledge' song playbacks (Nick & Konishi 2001). During REM sleep, humans can detect odd items in a string of auditory stimuli without awaking (Nashida et al. 2000; Cote 2002; Perrin et al. 2002). In some respects, ERPs during sleep can be similar to those evoked by the same stimuli during wakefulness (but this is often not the case; Cote 2002).

Humans and rats show ERPs that are much diminished or absent during deep SWS (Bastuji & Garcia-Larrea 1999; Nashida et al. 2000; Cote et al. 2001). This result suggests that during deep SWS (1) information detection or processing (or both) is greatly limited, and (2) interactions between the vertebrate sleeping brain and the external environment are stemmed early in the detection and processing of information (Voss 2004). Such limitations may well apply to the detection and processing of predator cues, but this remains to be shown. It would be valuable to apply this ERP technique and more recent imaging techniques (Portas et al. 2000) to the detection and processing of predatory stimuli in a diverse array of animals.

The work on ERPs illustrates an apparent paradox regarding the detection of threatening stimuli while in REM sleep. As noted earlier, EEG patterns during REM sleep are more like those in awake subjects than those in SWS. Thus, it may not be surprising that many sorts of stimuli evoke neural responses during REM sleep (in addition to cardiac responses in rats; Maho & Hennevin 1999). This apparent neural interaction with the external environment, along with the fact that animals aroused from REM sleep are more alert and ready to deal with threats (Horner et al. 1997), is suggestive of the sentinel hypothesis (see above) for the function of REM sleep. The only problem for this hypothesis is the fact that arousal thresholds are high during REM sleep. Portas et al. (2000) suggested that these relatively high arousal thresholds reflect a deactivation of the higher-level processing of information during REM sleep. Future work should establish whether this 'REM paradox' really applies to the detection of predatory stimuli under ecologically relevant conditions.

SUMMARY AND CONCLUSIONS

Sleep (broadly defined) appears widespread in the animal world. The functions of sleep remain elusive but one fact is clear: sleep renders an animal more vulnerable to predatory attack than just about any other behaviour. However, sleeping animals are not helplessly turned-off, and certain states of sleep and ways to sleep are safer than others. We are certain that a research programme focused on predation-related consequences of various sleep patterns will yield new insights into the nature of sleep in general.

Relatively little work has been conducted on sleeping under the risk of predation, despite several early studies focused on this topic. All of the areas that we covered need a great deal more attention, and many areas are virtually unstudied. Regarding comparative work, the classic studies of Allison & Cicchetti (1976), Meddis (1983) and others need to be updated using modern phylogenetically based statistical techniques. These studies also need to be expanded where possible to cover nonmammalian taxa. Comparative work on sleep in ectothermic vertebrates and invertebrates would be particularly valuable. Indeed, there is a great need to simply characterize sleep in a wide variety of invertebrates. From ecological and evolutionary perspectives, it is essential to expand the current view of sleep beyond the mammalian paradigm.

We suspect that the most rapid advances will be made in the study of the flexibility in sleep architecture. Experimental work focusing on the dynamic changes in sleep states or intensity over the sleep period and under various levels of predation risk should prove valuable. Thresholds of arousal from various states of sleep must also be characterized relative to important predator-based stimuli. Flexibility in the phasing of sleep over the circadian cycle and the choice of sleep sites under the risk of predation should prove relatively easy to study. We also need to address the issue of the degree to which drowsiness is a state of vigilant sleep. The trade-off approach to studying flexibility that we advocate will be greatly enhanced by an increased understanding of the link between the quality of sleep and daytime performance. Collectively, this work on sleep architecture will illustrate the dynamic environmental challenges under which sleep evolved, and extend the striking patterns in sleep seen in the early comparative work.

In summary, we advocate an ecologically and evolutionarily based view of sleep and its consequences. In doing so, we echo the suggestion of Horne (1988), Tobler (1989) and others that more work is needed on sleep in ecologically realistic settings. The vast majority of work on sleep behaviour is done in highly simplified laboratory environments that may not capture all of the salient features of sleep. We have little doubt, however, that many productive collaborations between behavioural ecologists, sleep scientists and neurophysiologists will be forged in studying sleep under the risk of predation. Neurobiological information and insights will be key to the success of this new paradigm. This is particularly apparent when determining the sorts of information available to sleeping animals and the mechanisms with which the brain processes information about risk while sleeping. Perhaps such collaborations will ultimately help forge an understanding of the functions of sleep itself.

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