

Primer

Energetic costs and benefits of sleep

John A. Lesku¹
and Markus H. Schmidt^{2,3}

Energy derived from food is a precious resource to animals. Those finite calories are often well-earned through exhaustive foraging effort, which can dominate waking hours, to support physiological processes (e.g. body maintenance and growth) and ecological necessities (e.g. predator avoidance and courting) that are pertinent to the production of progeny. So, it is unsurprising to find that animals have evolved strategies to guard against the gratuitous waste of hard-won caloric energy. Yet, it remains surprising to find such diversity, and elegant creativity, in those solutions. Brief examples of energy-saving innovation could include the very shape of animals and how they move, from streamlined swimming sharks to skyward-soaring seabirds; or the evolutionary appearance of various states of dormancy, such as endothermic animals sacrificing high body temperature through modest (torpor) or severe (hibernation) curtailments to metabolic heat production. Another reversibly dormant state with energetic benefits is sleep.

As with torpid and hibernating animals, a sleeping animal assumes a restful posture, often closes both eyes (when it has eyes), surrenders awareness of its surroundings, and its metabolism slows. Unlike torpor and hibernation, however, animals sleep each day, can be awoken more quickly and with less frenetic stimulation, and the lowering of metabolic rate is less pronounced. Even so, it has long been recognized that the energy savings arising from a night's sleep in an adult human is the caloric equivalent to a cup of low-fat milk. *Don't misunderstand!* This is not said dismissively of paltry energy savings. A cup of milk might seem trivial to post-industrialized, technophilic humans where food is accessible with soft finger taps on a mobile phone, but for archaic humans, and certainly for most wildlife, those calories would have been gained only through hard hours spent foraging. So,

what are the energetic benefits (and costs) of sleep? And if to save energy, then what distinguishes sleep from torpor and hibernation?

Sleep is evolutionarily stubborn

The need for sleep is obstinate. Some animals routinely sleep little, but none go entirely without sleep. Animals will even fall asleep when vulnerable to predators. Rather than evolving sleeplessness, other animals have evolved innovative adaptations to sleep concurrent with behaviors otherwise associated with being awake, such as sleep-watching (e.g. ducks, ostriches, and chevrotains), sleep-standing (horses), sleep-chewing (cows), sleep-swimming (dolphins), and sleep-flying (great frigatebirds); in some cases, by sleeping with just one-half of the brain at a time. A less adaptive example is sleep-driving; nonetheless, this too reveals that the biological necessity for sleep can be dangerously overwhelming.

After extensive scientific study over more than a half-century, we have yet to find a truly sleepless animal. In addition to vertebrates, we know that arthropods, including honey bees (*Apis mellifera*) and fruit flies (*Drosophila melanogaster*) sleep, as do mollusks, such as octopuses (*Octopus* spp.) and cuttlefish (*Sepia officinalis*). Beyond these three 'types' (or phyla) of animals, our understanding of the phylogenetic breadth of sleep gets a little shaky. There exists convincing data for sleep in nematode roundworms (*Caenorhabditis elegans*), platyhelminth flatworms (*Girardia tigrina*), and two cnidarians — upside-down jellyfish (*Cassiopea* spp.) and the freshwater polyp *Hydra vulgaris* (Figure 1). There are also alluring allusions of sleep in other cnidarians, such as soft coral of the family Xenidiidae and at least three species of box jellyfish.

Gaps remain (and even abound) in our understanding of 'what sleeps?'; nonetheless, the presence of sleep in the simplest animals is most intriguing. In vertebrates, sleep helps mature the young brain, optimize the strength of brain cell connections, consolidate (brain-stored) memories, and clear waste produced by brain tissue. But species of the phylum Cnidaria do not have a brain. Instead, they have a rudimentary nervous system, in which nerve cells form into diffuse nets

throughout their radially symmetric bodies. Therefore, the evolutionary appearance of sleep pre-dates that of the brain. While it remains possible that sleep first evolved to support neural processes in brainless cnidarians, it is equally possible that a more foundational purpose explains the early appearance of so vulnerable a state. Much of organismal biology is optimized to conserve caloric energy, raising the possibility that sleep evolved in early animals (or even earlier) to support a similar aim. At the very least, the evolutionary stubbornness of sleep in animals, and restful periods in other organisms, hints that energy conservation may have played an out-sized role in early animal evolution.

A suite of sleep strategies

For half a century, sleep scientists have been puzzled by substantial variation in the amount of sleep across mammals. For example, ruminants and other large herbivores sleep only a few hours per 24-h day, while adult humans sleep about eight hours each night. Conversely, most Rodentia sleep more than they are awake, and more extreme still, some armadillo and opossum are *awake* just a handful of hours each 24-h day. This rich diversity, which is mirrored by the amounts of the two mammalian sleep states, rapid-eye movement (REM) and non-REM sleep, beckons explanation. Such datasets are perfectly suited for comparative analysis, which tries to explain across-species trait variation through correlation with variation in other traits. In this way, one can reveal broad evolutionary patterns that might otherwise remain obscured.

Comparative datasets have been well-mined over the decades. The more fruitful studies have been those which employed phylogenetic comparative methods. Most statistical analyses, including correlation, require datapoints to be independent. However, species are inherently non-independent owing to their shared evolutionary history: a mouse is more closely related to a hamster than to a monkey. Phylogenetic comparative methods statistically account for this variable ancestry amongst members of the dataset.

The resulting analyses have revealed energetically relevant patterns. The correlation between sleep amount and basal metabolic rate, after controlling



for the confounding effect of body mass, is decidedly negative. Species with a relatively high metabolic rate sleep less than those with a lower relative metabolic rate. Put another way, species with relatively high metabolism are awake more, presumably to carry out wake-related activities, such as foraging, to sustain their demanding energetic requirements. Accordingly, herbivores, whose nutrient-poor diet requires voluminous consumption, are awake more than carnivores. These relationships might imply that the energy gained through foraging is valued more than the energy saved by sleeping. Nonetheless, this is a bird's-eye view of evolutionary outcomes. Observations on individual species, including birds, might provide more specific and nuanced insight.

Energetic economies of avian sleep

Here, we focus attention on three compelling case studies of animals with variant solutions to a sleep–energy problem. First, a recent study on garden warblers (*Sylvia borin*) found an original, and probably widespread, trade-off between body condition (or energetic state) and sleep depth. The garden warbler is a small songbird, similar in size to a house sparrow, and a long-distance migrant. Each spring, the typically diurnal warblers switch to flying at night during their migration from north Africa, over the Mediterranean Sea, to Europe, where they breed. Many birds stop to seek respite on the island of Ponza, 100 km to the west of Naples, before continuing northward. Upon landing on Ponza, some birds are lean (less fat and muscle), and others are more robust. Interestingly, warblers adopt different sleep postures depending on their energetic state. Robust birds, with their surplus energy reserves, sleep with their head facing forward. In doing so, they maintain a higher metabolic rate than leaner birds and lose added heat through their exposed head, but they also respond more quickly to an acoustic playback of the sounds of crunching leaves, which mimic the sounds of an approaching terrestrial predator. Conversely, leaner birds, depauperate of energy stores, sleep with their head tucked into the feathers over their back. They enjoy an energetic savings via heat conservation and lower metabolic rate, compared

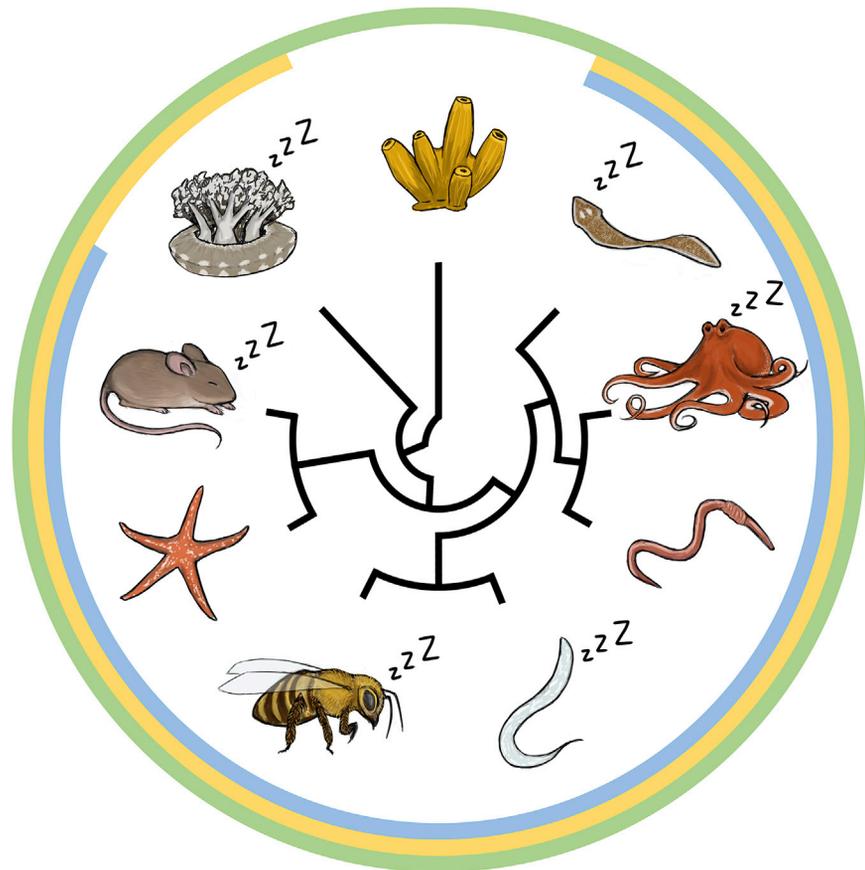


Figure 1. Evolutionary breadth of sleep.

Here we see a pruned phylogenetic tree of the animal kingdom, emphasizing the nine most species-rich groups, including chordates (represented by the mouse), echinoderms (starfish), arthropods (honey bee), nematodes (roundworm), annelids (earthworm), mollusks (octopus), platyhelminths (flatworm), cnidarians (upside-down jellyfish), and poriferans (sponge). Together, these nine groups constitute 95% of all animal life. The outer-most green circle, and inner yellow and blue arcs, denote animals with a nervous system, and animals with a centralized nervous system, respectively. Sleep has been observed in animal phyla marked by 'zzz', including brainless jellyfish with their radially diffuse nerve net; unmarked phyla have yet to be studied by sleep scientists. Illustrations by Laura X. Tan.

to untucked birds, but show slower responsiveness to the playback sounds. In this way, body posture provides a window into each bird's priority during sleep: energy conservation versus anti-predator vigilance (Figure 2A). Presumably such decisions are made to maximize reproductive success.

Pectoral sandpipers (*Calidris melanotos*) are avian extremists. They are small, trans-hemispheric migratory shorebirds. In austral autumn, the birds leave the southern hemisphere and fly above the Arctic circle to breed under continuous daylight of the midnight sun. The breeding season is short, just three weeks, and intense. Males establish territories from which they deter marauding males and court fertile

females with hopes of maximizing paternity. To fulfill those hopes, some males become super-active. In the most extreme case, one male was active more than 95% of the time for 19 days. Males are not entirely sleepless, however. Recordings of brain activity of birds on their tundra territories reveal that super-males sleep some, albeit not much; some just 10% of the 24-h day. This sleep is packaged into hundreds of naps each seconds or tens of seconds long, and characterized by the most intense form of non-REM sleep. Only after females are occupied incubating eggs do males decrease their vivacity. Is it worth it? *Absolutely!* Males that sleep the least — and expend the greatest energy in near-continuous activity for

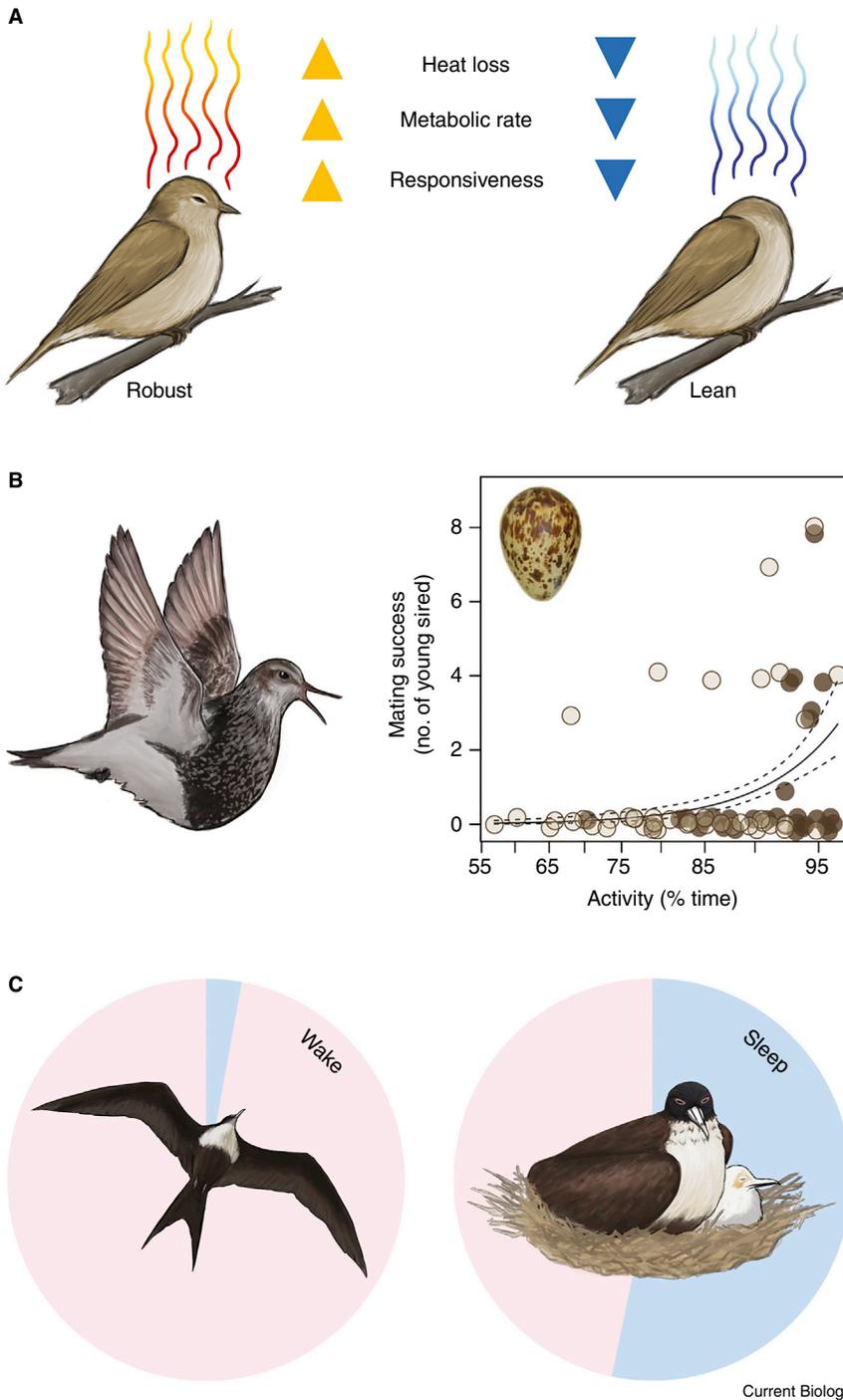


Figure 2. Sleep strategies with energetic consequences.

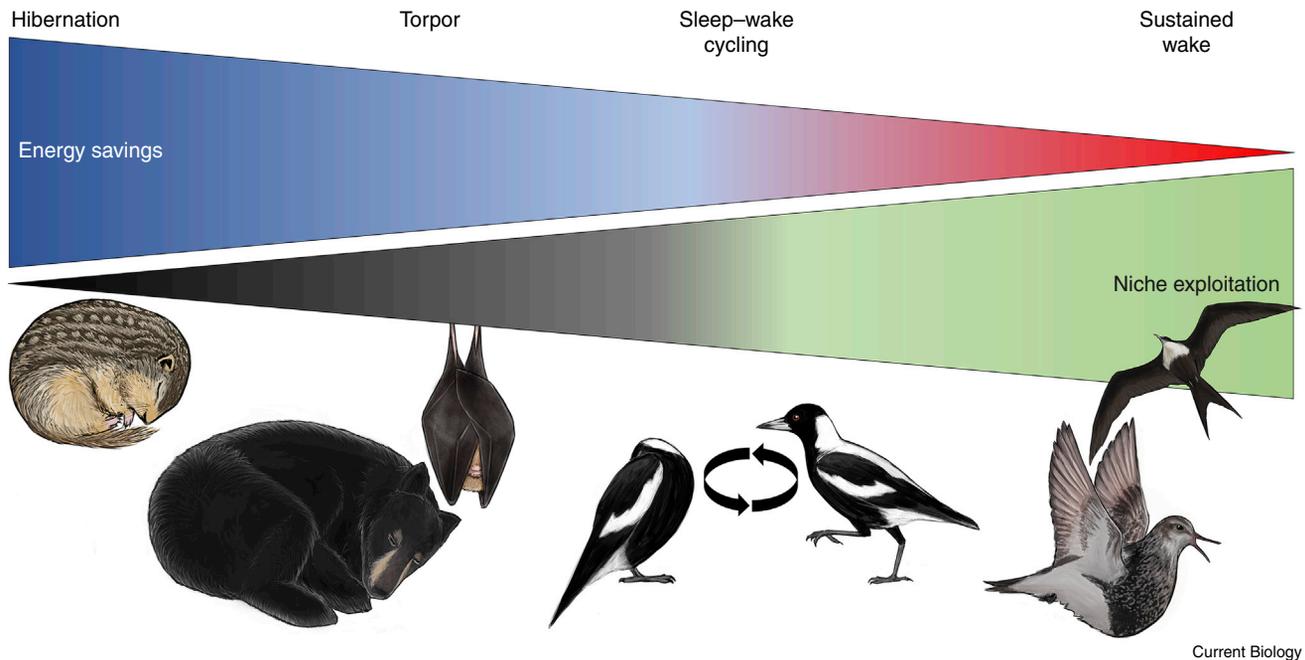
(A) Migratory garden warblers can adopt one of two sleep postures. Robust warblers sleep with the head forward (left) and endure higher metabolic costs, but this affords a faster response time to acoustic stimuli; lean warblers sleep with the head tucked over the back (right), and in doing so, save energy, but respond to sounds more slowly. (B) Intra-sex variation in wakefulness in male pectoral sandpipers breeding in Alaska predicts reproductive success. Males that are awake the most sire the most offspring. (C) Female great frigatebirds undertake long foraging sojourns over the ocean to provide food for their chicks. During these flights, they sleep just a sliver of the 24-h day, just 0.7 h (left). Upon returning to the nest, the birds sleep 18 times as much (right). Illustrations by Laura X. Tan. The sandpiper painting was inspired by a photograph taken by Katharina Kapetanopoulos, Max Planck Institute for Ornithology; line graph is from Lesku *et al.* (2012) *Science* 337, 1654–1658.

three weeks — interact with the most females and ultimately sire the most offspring (Figure 2B).

The great frigatebird (*Fregata minor*) is another Herculean derived dinosaur. They are well adapted to life aloft. Frigatebirds are large seabirds with very long, pointed wings best suited to soaring. They are adept at finding and exploiting marine thermals to minimize the energetic cost of flight. Frigatebirds, however, are not well adapted to life on the sea. Short legs, poorly developed foot webbing, and inadequate waterproofing make taking off from the water difficult, and even momentary contact with the water can be lethal. To catch food the birds rely on large sub-surface predatory fish and cetaceans to drive prey, such as flying fish and flying squid, near, or above, the surface of the sea. This is a rather unpredictable and ephemeral food resource, however, and the birds must travel long distances (thousands of kilometers) over long periods (weeks and months) without alighting on the water. Frigatebirds do not become entirely sleepless during this time at sea. While it is true that the birds sleep very little — *less than any sandpiper* — they obtain their sleep while soaring (Figure 2C). Here, the birds engage in REM and non-REM sleep, including a cetacean-like ability to engage in non-REM sleep with one-half of the brain at a time. Importantly, this sparse sleep strategy is not a fixed feature of frigatebirds: when the birds return to their nest, they sleep nearly 13 h per day. Thus, frigatebirds, like sandpipers, endure sustained wakefulness for extended periods of time, seemingly without detriment.

Energy conservation, allocation, or both?

Energy savings during sleep have long been recognized. Not surprisingly, energy conservation as a hypothesis for the function of sleep enjoys an equally long history. Under this idea, sleep saves energy by reducing metabolic rate, and by not doing something more demanding. As clearly demonstrated by garden warblers (Figure 2A), the energy saved by a sleep strategy must be weighed against the heightened vulnerability the strategy demands. More broadly, sleeping carries many costs: the loss of awareness brings forth increased risk, but there is also a so-called missed



Current Biology

Figure 3. Trade-offs of energy allocation strategies.

Hibernation (shown by the thirteen-lined ground squirrel) and torpor (black bear, little brown bat) are strategies of global metabolic downregulation that provide the greatest energy savings, but other biological processes and niche exploitation are compromised. Conversely, sustained wakefulness (pectoral sandpiper, great frigatebird) is a state of global metabolic upregulation that maximizes niche exploitation, but carries the greatest energetic cost. Between these extremes, sleep-wake cycling (Australian magpie) saves energy during sleep, and alternates with wake-dependent niche exploitation. This strategy promotes metabolic rate reduction and metabolic partitioning, which together contribute to energy savings and balance. In doing so, sleep-wake cycling generates a wide range of species-specific optimization strategies that manifest as diverse sleep quotas and the expression of one or more sleep states. Illustrations by Laura X. Tan.

opportunity cost by not engaging in another adaptive behavior, such as foraging, territorial defense, courting, sex, or provisioning for young. Under the energy conservation hypothesis (or indeed any hypothesis for the function of sleep), the benefit of sleeping must be greater than the sum of these costs.

Does sleeping save energy? Yes. Energy savings during sleep have been measured in diverse animals from cats and rats to fishes and flies. As mentioned earlier, the calories saved for humans following a night of 8-h sleep amounts to a cup of milk. Yet the energy conservation hypothesis struggles to explain the existence of, and alternation between, multiple sleep states in some animals. Rather, this hypothesis assumes that sleep is a passive process whereby biological functions are globally downregulated compared to the waking state. Much research shows just the opposite. Sleep is a highly active state wherein some biological operations are upregulated. Notably, the REM sleep state itself is difficult to reconcile with the energy conservation hypothesis.

During REM sleep, brain metabolism and temperature increase during a time of vivid dreaming where numerous dynamic processes take place, such as the consolidation of emotionally rich memories, sensory-motor integration, and reproductive physiology as evidenced by penile erections in human males and rodents. The upregulation of biological processes is not limited to REM sleep. Non-REM sleep is associated with neural plasticity, protein synthesis, cellular housekeeping, and repair. Finally, it could be argued that if saving energy is the *raison d'être* for sleep, then there are better dormant states (e.g. shallow torpor) to achieve that lauded aim.

Although the energy conservation hypothesis has some support and intuitive appeal, its limitations have led to alternative proposals. The adaptive inactivity hypothesis puts forth that sleep is a strategy to keep an organism out of harm's way when it is outside its temporal niche of specialization. This is an interesting idea because it implies that sleep, not wakefulness, is the safer

state. But sleeping is dangerous, and attacks on sleeping animals have been documented (and are almost certainly under-reported). Adaptive inactivity, by itself, cannot explain why sleep would be favored over restful wakefulness where astute awareness and rapid responsiveness could be maintained. Moreover, adaptive inactivity, like the energy conservation hypothesis, does not provide a clear rationale for two sleep states in birds, mammals, and a handful of other animals. Lastly, if we accept the premise that sleeping is safe, then sleep would again be the wrong strategy, as torpor would be equally safe, but with enhanced energy savings.

In contrast to these ideas, the energy allocation hypothesis proposes that sleep-wake cycling has evolved to balance energy savings during sleep with energy acquisition (or more broadly, niche exploitation) while awake (Figure 3). In this way, the alternation between sleep and wake promotes energy optimization by coupling certain biological processes to certain behavioral and physiological

Table 1. Contrasting three energy-centric hypotheses for the function of sleep.

Hypothesis	Amount (%) of energy saved	Emphasis	Role of multiple sleep states
Energy conservation	<10%	Reduced MR	None
Adaptive inactivity	Unclear	Predator avoidance	Unclear
Energy allocation	20–30%	MP and reduced MR	Energy optimization

Abbreviations: MR, metabolic rate; MP, metabolic partitioning. Calculations of energy saved are based on 8-h sleep per 24-h day.

states. Sleep saves energy via reduced metabolic rate — and also by state-dependent metabolic partitioning. Mathematical modelling suggests that consigning metabolic processes to either sleep or wake can increase energy savings four times over the observed metabolic rate reduction alone.

The energy allocation hypothesis overcomes the limitations of other energy-centric hypotheses, and is consistent with the view of sleep as an active physiological process (Table 1). Consider REM and non-REM sleep: these two states can be viewed as alternative energy allocation strategies in which unique menus of biological processes are up- or downregulated. REM sleep promotes a cost-neutral energy allocation to favor activation of the nervous system by sacrificing thermoregulatory defense. Heat production to sustain high body temperature in birds and mammals is the most energetically expensive process. Perhaps not surprisingly, (unequivocal) REM sleep, and associated cessation of thermoregulation (panting, shivering), is found only in endotherms. Consistent with expectations under the energy allocation hypothesis, the lateral hypothalamus promotes REM sleep in mice at the moment the environment warms to their most comfortable (thermoneutral) temperature, as if to make better use of available energy when thermoregulation is no longer needed. Accordingly, as observed in mice and man, individuals engage in more REM sleep bouts, and shorten inter-REM sleep intervals, as ambient temperatures approach thermoneutrality. In contrast, REM sleep precipitously decreases (much more than non-REM sleep) as ambient temperatures deviate from

thermoneutrality. Overall, the energy allocation hypothesis suggests that selective pressures have driven resource optimization strategies that manifest as species-specific phenotypes of sleep architecture. These species differences may include not only the timing of multiple sleep state cycling, but also the type of functions that coalesce during the state(s) of sleep.

Conclusions

Not only is food energy a finite and fundamental resource ultimately needed for procreation, but organisms have a finite capacity to process food, even when abundant. Therefore, selection favors resource optimization. Animals typically use energy only frugally, and as such, have an arsenal of energy-saving strategies, including sleep. Sleep is an evolutionarily widespread state, found even in brainless polyps and jellyfish, and may have evolved to alternate high energy expenditure and acquisition (wake) with truncated energy use (sleep) during which unique menus of metabolic processes become upregulated and downregulated. Indeed, sleeping animals save energy by slowing metabolism and generally avoiding more energetically taxing behaviors, but also amplify energy savings by partitioning biological functions by state.

Diverse strategies for balancing energy requirements have been observed. Mammals with higher relative metabolic rates, and herbivores, are awake longer, presumably to spend more time in labour intensive foraging for their low-quality forage. When faced with energetic shortfalls, garden warblers adopt energy-saving postures and sleep more deeply. In this way,

warblers divert stretched resources away from anti-predator vigilance and tap into the energetic benefits of sleep, presumably to reallocate some of those energetic savings to maintenance and repair. Conversely, pectoral sandpipers and great frigatebirds recognize the significant missed opportunity cost of sleep, and instead endure the energetic burden of near-continuous wakefulness for weeks. That said, these are all natural systems, in which solutions have been shaped by selection. As human populations expand, the frontiers of urban spaces move outward, transforming natural ecosystems into modified environments. Species inhabiting such places might struggle to find energetically adaptive solutions. For instance, light pollution disrupts sleep in birds, which must compound their metabolic demands. How diurnal animals cope with unnatural nocturnal wakefulness is unknown, but important for understanding how cityscapes influence animal physiology and health.

Hypotheses have been proposed to explain the variety of energy optimization strategies. The energy conservation hypothesis has appeal, but fails to acknowledge the dynamic, energy-consuming features of sleep, or to explain the existence of multiple sleep types. The energy allocation hypothesis is an attractive amendment, because it adds an energy-saving mechanism — state-dependent metabolic partitioning. In doing so, it explains variant optimization strategies that manifest as divergent sleep amounts, and in some animals, more than one kind of sleep. Going forward, more study is needed to reveal the full diversity of sleep-wake strategies, which will bring forth a more complete understanding of the energetic costs and benefits of sleep.

DECLARATION OF INTERESTS

The authors declare no competing interests.

FURTHER READING

- Aulsebrook, A.E., Connelly, F., Johnsson, R.D., Jones, T.M., Mulder, R.A., Hall, M.L., Vyssotski, A.L., and Lesku, J.A. (2020). White and amber light at night disrupt sleep physiology in birds. *Curr. Biol.* 30, 3657–3663.
- Berger, R.J., and Phillips, N.H. (1995). Energy conservation and sleep. *Behav. Brain Res.* 69, 65–73.
- Ferretti, A., Rattenborg, N.C., Ruf, T., McWilliams, S.R., Cardinale, M., and Fusani, L. (2019). Sleeping unsafely tucked in to conserve energy in a nocturnal migratory songbird. *Curr. Biol.* 29, 2766–2772.
- Kelly, M.L., Collins, S.P., Lesku, J.A., Hemmi, J.M., Collin, S.P., and Radford, C.A. (2022). Energy conservation characterizes sleep in sharks. *Biol. Lett.* 18, 20210259.
- Komagata, N., Latifi, B., Rusterholz, T., Bassetti, C.L.A., Adamantidis, A., and Schmidt, M.H. (2019). Dynamic REM sleep modulation by ambient temperature and the critical role of the melanin-concentrating hormone system. *Curr. Biol.* 29, 1976–1987.
- Lesku, J.A., Roth, T.C., Amlaner, C.J., and Lima, S.L. (2006). A phylogenetic analysis of sleep architecture in mammals: the integration of anatomy, physiology, and ecology. *Am. Nat.* 168, 441–453.
- Lesku, J.A., Rattenborg, N.C., Valcu, M., Vyssotski, A.L., Kuhn, S., Kueppel, F., Heidrich, W., and Kempenaers, B. (2012). Adaptive sleep loss in polygynous pectoral sandpipers. *Science* 337, 1654–1658.
- Nath, R.D., Bedbrook, C.N., Abrams, M.J., Basinger, T., Bois, J.S., Prober, D.A., Sternberg, P.W., Gradinaru, V., and Goertzen, L. (2017). The jellyfish *Cassiopea* exhibits a sleep-like state. *Curr. Biol.* 27, 2984–2990.
- Omond, S.E.T., Hale, M.W., and Lesku, J.A. (2022). Neurotransmitters of sleep and wakefulness in flatworms. *Sleep* 45, zsac053.
- Rattenborg, N.C., Voirin, B., Cruz, S.M., Tisdale, R., Dell’Omo, G., Lipp, H.P., Wikelski, M., and Vyssotski, A.L. (2016). Evidence that birds sleep in mid-flight. *Nat. Commun.* 7, 12468.
- Schmidt, M.H. (2014). The energy allocation function of sleep: a unifying theory of sleep, torpor, and continuous wakefulness. *Neurosci. Biobehav. Rev.* 47, 122–153.
- Schmidt, M.H., Swang, T.W., Hamilton, I.M., and Best, J.A. (2017). State-dependent metabolic partitioning and energy conservation: a theoretical framework for understanding the function of sleep. *PLoS One* 12, e0185746.
- Siegel, J.M. (2009). Sleep viewed as a state of adaptive inactivity. *Nat. Rev. Neurosci.* 10, 747–753.
- Stahl, B.A., Slocumb, M.E., Chaitin, H., DiAngelo, J.R., and Keene, A.C. (2017). Sleep-dependent modulation of metabolic rate in *Drosophila*. *Sleep* 40, zsx084.
- Xie, L., Kang, H., Xu, Q., Chen, M.J., Liao, Y., Thiyagarajan, M., O’Donnell, J., Christensen, D.J., Nicholson, C., Iliff, J.J., et al. (2013). Sleep drives metabolite clearance from the adult brain. *Science* 342, 373–377.

¹School of Agriculture, Biomedicine and Environment, La Trobe University, Melbourne, Australia. ²Department of Neurology, Center for Experimental Neurology, Bern University Hospital (Inselspital), Bern, Switzerland. ³Ohio Sleep Medicine Institute, Dublin, OH, USA. E-mail: J.Lesku@latrobe.edu.au (J.A.L.); Markus.Schmidt@insel.ch (M.H.S.)

Primer

Elastic energy storage and the efficiency of movement

David Labonte¹ and Natalie C. Holt^{2,*}

Movement is an integral part of animal biology. It enables organisms to escape from danger, acquire food, and perform courtship displays. Changing the speed or vertical position of a body requires mechanical energy. This energy is typically provided by the biological motor, striated muscle. Striated muscle uses chemical (metabolic) energy to produce force, to move this force over a distance to do work, and to do this work within some time to generate power. The metabolic energy consumed in producing these mechanical outputs is a major component of an organism’s energy budget, particularly during repetitive, cyclical movements. This energy could otherwise be used for maintenance, growth, and reproduction. Hence, fitness may be enhanced by improving locomotor efficiency — the ratio between work done and metabolic energy consumed. This may be achieved by reducing the need for muscle to do work, and by increasing the efficiency with which muscle does work.

Early work on locomotor efficiency measured mechanical energy fluctuations and the metabolic energy consumed in animals moving at various speeds. The results of these experiments were puzzling: locomotor efficiency seemed to be far higher than the efficiency measured in isolated muscle. In addition, large animals seemed to be more efficient than small animals. Either there were experimental errors, or an additional source of mechanical energy, one that varied systematically with body size, had been overlooked. Elastic elements — biological springs — were identified as a suspect because they can cyclically store and release mechanical energy. In this primer, we discuss if and how biological springs can reduce muscle work

and power demands during cyclical movements such as flight, running, and sound production, and whether these reductions decrease metabolic costs. We examine evidence for elastic energy storage and associated changes in the efficiency of movement across vertebrates and invertebrates, and hence across a large range of body sizes and diversity of spring materials.

Mechanical energy fluctuations in cyclical movements

Changing the speed or vertical position of a body part or the center-of-mass of the body requires changes to its kinetic (E_{kin}) or gravitational potential (E_{gp}) energy, respectively. Any change in energy requires work. This work is typically done by muscle. When muscle actively shortens, it does positive work, which increases the energy of the body. When an active muscle is lengthened, it does negative work, which dissipates the mechanical energy of the body as heat.

Many biologically important movements occur cyclically, for example, downstrokes and upstrokes of wings during flapping flight, swinging of legs during terrestrial locomotion, and vibration of internal membranes during sound production. Such cyclical motion is often associated with characteristic fluctuations of the kinetic and gravitational potential energy of the moving body. A textbook example is walking in bipedal animals, which is often likened to the motion of an inverted pendulum: the kinetic energy of the center-of-mass is maximal when the gravitational potential energy is minimal and *vice versa*. These out-of-phase energy fluctuations enable a cyclical exchange between E_{kin} and E_{gp} without the supply of work by muscle; walking is energetically efficient because it is controlled forward falling. But not all cyclical movements share such favorable energy fluctuations. For example, in running, E_{kin} and E_{gp} of the center-of-mass characteristically fluctuate in-phase during stance, suggesting that muscle has to do positive and negative work with every step. There is, however, another energy form which may help to reduce muscle work demands: elastic energy.

