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Behavioural Ecology: Sleeping Safely Carries Energetic Costs

Lauren Tworkowski and John A. Lesku*
School of Life Sciences, La Trobe University, Melbourne 3086, Australia
*Correspondence: J.Lesku@latrobe.edu.au
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Trade-offs shape animal behaviour. For decades, the study of trade-offs has provided insight into how animals make decisions, but they have rarely been explored in relation to sleep. A new study reveals a role for sleep in saving energy in garden warblers on a stopover during a northward migration, but with ecological costs.

Indulge yourself to answer these three familiar questions. Do you spend more time at work to increase your productivity at the expense of spending more time at home? When you leave work late, do you drive faster than you should to recover lost time, but risk getting a fine? When you arrive home, do you cook a more nutritious, but time-consuming meal, or a quick microwaveable meal packed with fattening sugars? You make behavioural decisions, every day, by weighing the benefits of an action against its likely costs, across each possible response. Your decision will (ideally) be the one that has the least cost for the most benefit. In a series of experiments, Ferretti *et al.* [1] demonstrate in this issue of *Current Biology* that a small songbird makes decisions in much the same way. In this case, whether to maximize energy savings by sleeping deeply and suffer increased vulnerability to terrestrial predators, or to sleep more safely, but by doing so, expend extra energy.

Animals, broadly, reach a decision by optimizing the ratio of costs-to-benefits [2]. Notably, small birds in winter must eat a substantial amount of food during the day to stave off starvation at night. However, eating by day increases the risk of being eaten themselves [3]. Leaving the safety of vegetation to find food makes little birds more visible to watchful predators, and keeping their head down to forage makes it harder to look out for those predators [2,4]. Moreover, eating too much can hamper an agile escape

Figure 1. Behavioural decision faced by garden warblers.
Choosing between two sleep postures, head tucked (left) and untucked (right), allows warblers to navigate a trade-off balancing energy homeostasis, sleep intensity, and anti-predator vigilance. The leaner birds choose the former: they sleep more deeply and save more energy, but are also more vulnerable to predators. Conversely, birds with greater energy reserves opt to sacrifice the extra energy in order to better escape approaching threats. Illustration ©Damond Kyllo.

from airborne attackers [3]. Some birds, including mourning doves (*Zenaida macroura*), can lower their night-time body temperature to conserve energy, but in doing so, compromise their ability to fly [5].

Similar trade-offs have long been thought to exist in sleeping animals, but with very little actual research. Firstly, what are the costs of being asleep? The disadvantages of sleep are chiefly its defining characteristics. A sleeping animal is largely unaware of the local environment. Therefore, the decreased responsiveness that best characterizes the behavioural shutdown associated with sleep leaves animals vulnerable to attack [6]. Furthermore, sleep has a 'missed opportunity' cost, as animals aren't performing other vital activities, such as finding food, avoiding predators, defending territory, or securing mates [7]. How do animals mitigate these costs? Rats (*Rattus norvegicus*) delay sleep onset, reduce sleep duration, and shift to safer (lighter) sleep states when threatened [8]. Similarly, barbary doves (*Streptopelia risoria*) sleep less by interrupting sleep more following the brief appearance of a potential predator [9]. Mallard ducks (*Anas platyrhynchos*) keep an eye out for threats while sleeping on the edge of a group, compared to those safely flanked by conspecifics [10]. Great frigatebirds (*Fregata minor*) soaring over the ocean [11], and male pectoral sandpipers (*Calidris melanotos*) on their Arctic breeding grounds [12] sleep very little in favour of long-distance foraging flights and securing mating opportunities, respectively. Thus, when faced with situations that require vigilance or sustained performance, animals commonly resolve the trade-off by simply waking up and reducing sleep.

In a series of experiments, Ferretti *et al.* [1] explore a more nuanced trade-off in the garden warbler (*Sylvia borin*). The garden warbler is a small, long-distance migrant. Normally day active, they switch to flying at night during their spring migration north. Mid-trip, the birds land on the island of Ponza in the Mediterranean Sea. When they arrive, there is substantial variation across birds in terms of body condition, with some birds having greater muscle mass and more body fat, whereas others are leaner. To save energy, lean birds sleep more and tuck their head into feathers on their back (Figure 1). In this posture, they reduce their metabolic rate and conserve heat. Furthermore, the leaner birds sleep more deeply, as revealed by a slower response to the sounds simulating the approach of a terrestrial predator. They respond a fraction of a second slower. The lapse might seem trivial, but when facing predatory attacks from cats and weasels, any advantage matters. Conversely, birds of better condition do not adopt this strategy. Instead, these heavier birds, with their more substantial energy reserves, sleep less deeply with head faced forward, but respond more quickly to the approaching acoustic threat. By doing so, they lose more heat through their exposed head. In this way, each bird solves the trade-off to prioritize either energy homeostasis [13] or anti-predator vigilance [6], depending on its energetic state.

The lean warblers use deep sleep to save energy, but what are other benefits of sleep? The strategy adopted by the heavier birds suggests added value, otherwise they would have remained awake, rather than sleeping lightly. Indeed, the ecological persistence of sleep under risk of predation attests to its undeniable role [6]. In addition to saving energy [13], sleep is also involved in the maturation [14] and upkeep of the brain [15–17]. Although some animals endure extended periods of sleep loss without decrements in performance [11,12], sleep restores the ability to function adaptively in humans (and most other animals) while awake. We are more alert and attentive, better motivated and coordinated, and our memory improves [17,18]. Therefore, beyond reducing energy expenditure, the migrating warblers may encounter neurologically demanding conditions *en route* to Ponza, for which other sleep functions are required.

It is interesting to speculate that the relative value of each sleep function may differ across individuals and species depending on their sex, age, metabolic rate, health, energetic and reproductive state, and broader life-history and ecology [7]. This 'changing priorities' idea with regards to sleep benefits shouldn't

be surprising. There is great diversity in how animals use wakefulness. For example, antelope spend most of their waking effort grazing [19], male sandpipers spend exhaustive time pursing females and deterring rivals during the breeding season [12], and weaverbirds are preoccupied building their structurally complex nests [20]. Similarly, the chief purpose of sleep may differ across ontogeny and between individuals. Lean garden warblers use deep sleep to save energy, while other benefits appear to be ancillary [1], thermally stressed animals might primarily use sleep to reduce body (and brain) temperature [13], and food-caching animals might need to sleep to consolidate spatial memories regarding the locations of thousands of stored food items [7,17]. While time budgets show how awake animals allocate their time, owing to conspicuous behaviours with unambiguous aims, creating analogous visualizations for sleeping animals is much harder. To this end, Ferretti *et al.* [1] provide a window into how animals make decisions with respect to sleep, and by doing so, reveal their priorities with respect to sleep function.

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Plant Development: How Leaves Take Shape

James W. Satterlee and Michael J. Scanlon*
School of Integrative Plant Science, Cornell University, Ithaca, NY, USA
*Correspondence: mjs298@cornell.edu
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Live imaging, genetics, and computational modeling reveal how simple versus compound leaves are formed. Cross-species differences in leaf-wide growth determine the outcome of a locally-acting patterning process.

Deciphering the mechanisms by which genes control form is one of the central goals of developmental biology. Despite the tremendous technical advances made in this field, it remains challenging to relate genetic control of cellular growth to organ-level morphology [1]. New work from Kierzkowski and coworkers combines molecular genetic analysis, live imaging, and modeling to explain how differences in growth give rise to the simple, serrate leaves of *Arabidopsis thaliana* versus the compound leaflets of its close relative *Cardamine hirsuta* (Figure 1A) [2]. The