View metadata, citation and similar papers at core.ac.uk

Current Biology Vol 24 NO T R12

Chinese groups. In contrast, thirty years ago, it was rare to see an article in any international English journal published by a Chinese group. This unprecedented explosion of research productivity and quality coming out of China can be attributed to a number of factors, including a burst in funding in plant science by the Chinese government, the hunger of Chinese scientists for research productivity and achievements, traditional Chinese values (an emphasis on education), and let's not forget, the critical role that North Americans, Europeans and Japanese have played and continue to play by training Chinese graduate students and postdocs. The trajectory in the productivity of highquality research in plant sciences will continue in China, but the question is whether the trajectory will be followed by the most innovative research at the cutting edge of biology.

This remains to be seen, but there are a number of problems that might constrain a corresponding burst of research of the highest quality and innovation. First of all, education and its evaluation in China do not encourage innovation and creativity, which many believe are linked to the current political system and the traditional Chinese value that emphasizes obedience as opposed to out-of-the-box thinking. Second, for the most part, the current funding systems are not competitive. The majority of research funds are handed out based on reputation and 'quanxi' (connections), with the exception of the Natural Science Foundation of China. As a result, creativity, innovation, and high-risk research are rarely rewarded. Third, related to the funding system, the motivation for productivity (driven by funding and by other incentive systems) discourages scientists from conducting the most innovative and cutting-edge research, which is usually time consuming and risky. Furthermore, there is no good mechanism for the enticement of the best scientists from other parts of the world. Last, but not least, there is a vacuum of research investment from industry and private organizations. To a large extent, the changes and the constraints in plant science research can be applied to other disciplines as well.

Center for Plant Cell Biology, Department of Botany and Plant Sciences, University of California at Riverside, Riverside, CA 92521, USA.

E-mail: yang@ucr.edu

Quick guides

Avian sleep

John A. Lesku¹ and Niels C. Rattenborg²

What is sleep? Each night we enter into a behavioural shutdown that we call sleep. We lie down, become still and surrender awareness of our surroundings. Clues to the purpose of this enigmatic behaviour can be found by comparing sleep across animals. Such an approach has revealed that we are not alone in our imperative for sleep. From zebra to zebra finch to zebra fish, all animals adequately studied have been found to sleep. And yet, not all sleep is the same. In ourselves and most other mammals, there are actually two types of sleep: non-rapid eye movement (REM) sleep - also known as slow-wave sleep (SWS) in non-human animals and REM sleep. During SWS, large slow brain waves dominate the electroencephalogram (EEG), replacing the small fast waves of wakefulness. SWS eventually transitions to, and then alternates with, REM sleep. REM sleep is also known as paradoxical sleep owing to its awake-like pattern of brain activity in a behaviourally asleep animal. But unlike wakefulness, REM sleep is accompanied by eye movements under closed eyelids, reduced skeletal muscle tone and, at least in most humans, is the state associated with vivid dreams. In spite of much research, the functions of SWS and REM sleep remain topics of debate.

Why study avian sleep? Birds are a derived type of dinosaur most closely related to crocodilians. Surprisingly, however, the brain activity of sleeping birds most closely resembles that not of other reptiles, but of distantlyrelated mammals with whom their most recent common ancestor lived 300 million years ago. SWS and REM sleep are common among living birds, having been identified in all avian species studied, ranging from pigeons to penguins to parrots, from songbirds to shorebirds to seabirds. Despite investigations into sleep in non-avian reptiles, amphibians, and other vertebrates and invertebrates, unequivocal SWS and REM sleep

has only been identified in birds and mammals (Figure 1). Collectively, this suggests that SWS and REM sleep evolved independently in the avian and mammalian lineages. Determining the reasons for this convergence might provide insight into the purpose of these states.

How did avian sleep evolve? Unlike bones, the brain activity that characterizes sleep does not fossilize. Therefore, we can only infer how SWS and REM sleep came to be through the study of living animals. Characterizing the form of sleep in branches of the mammalian and avian evolutionary trees that have retained 'primitive' traits can provide insight into whether SWS and REM sleep appeared de novo in each lineage or gradually following a similar sequence of steps. The egg-laying monotremes (echidna and platypus) and Palaeognathae (for example, ratites, including the ostrich, which have retained a reptilian sperm structure) are such animals, and may therefore have retained 'primitive' sleep traits as well. Interestingly, ostriches and monotremes share a unique, heterogeneous sleep state that simultaneously combines SWSlike slow waves in the forebrain with REM sleep-related phenomena, such as rapid eve movements and loss of muscle tone generated by the brainstem. Ostriches and monotremes seemingly have little in common that might explain the convergence of this unique sleep state other than their retention of other 'primitive' traits. Consequently, this mixed state may reflect an early stage in REM sleep evolution, with REM sleep originating



Figure 1. Phylogenetic extent of SWS and REM sleep.

Apart from mammals, only birds engage in two sleep states that in most respects are similar to mammalian SWS and REM sleep. Cat painting ©2013 Medimagery, Laura Maaske LLC (www.medimagery.com); pigeon photograph ©N.C.R.



in the brainstem and invading the forebrain over evolutionary time. If so, then the awake-like forebrain activity that is the hallmark of REM sleep in other birds and mammals may be an evolutionarily new feature of REM sleep that supports a new sleep function.

Do birds have to sleep? Our imperative for sleep can be so strong that with only modest sleep loss we will fall asleep even in life-threatening situations, such as while driving a car. Some birds respond to sleep loss similarly, but there are also species that have a remarkable ability to greatly reduce sleep at times of the year when sustained wakefulness is needed. Notably, pectoral sandpipers (Calidris melanotos) migrate annually from the southern hemisphere to above the Arctic Circle where they breed under continuous daylight. Being a polygynous species, the evolutionary fitness of males is determined by mating with as many females as possible. In contrast, female fitness is determined by choosing the genetically best male to sire her only clutch of the year. As a result, males compete to convince choosy females to mate with them (Figure 2). Under the constant light of the Arctic summer, male sandpipers have evolved an unprecedented ability to forgo sleep while maintaining high performance in the tasks leading up to mating (Figure 2). Some males are continuously active for more than 95% of the time for 19 days, and the most active males ultimately sire the most offspring, indicating that the impairments in performance that we and other animals experience after pulling an all-nighter are not a universal outcome of sleep loss.

This example suggests that sleep can be dispensed with, at least by male pectoral sandpipers during the breeding season. However, none of the males actually became entirely sleepless, indicating that the need for some sleep remained. Indeed, the short-sleeping males attempted to compensate for lost sleep by sleeping more 'intensely'.

What does sleep 'intensity' mean? The intensity of SWS is reflected in the EEG by the amount of slow waves, or slow wave activity (SWA). SWA is thought to reflect sleep intensity and need, because in birds and mammals alike, SWA is higher following extended periods of wakefulness and decreases with time spent in SWS. In addition, we are hardest to awaken early in the night when SWA is highest. Such dynamic changes in the level of SWA are thought to reflect homeostaticallyregulated processes, perhaps linked to maintaining optimal brain performance. Indeed, in pigeons, rats and ourselves, the level of SWA is dependent upon how parts of the brain were used during prior wakefulness. Brain regions used more extensively sleep more deeply during subsequent SWS, suggesting that SWS serves a restorative role for the brain itself.

Interestingly, birds can actively modulate the level of SWA through opening one eye, a behaviour associated with reduced SWA in the opposite half of the brain. Such unilateral eye closure is used as an anti-predator behaviour. When ducks are in a row, those safely flanked by their neighbours close both eyes and sleep, whereas those in the potentially dangerous position at the edge of the group open one eye and direct it away from the others, presumably protecting themselves from becoming 'sitting ducks'.

Are there any differences between mammalian and avian sleep? Although birds and mammals both engage in SWS and REM sleep, not all aspects of these states are present in each type of animal. In addition to large slow brain waves, mammalian SWS is also associated with sleep spindles - bursts of fast, spindle-shaped EEG activity that are thought to be involved in processing new information. However, spindles appear to be absent in birds, suggesting that the purpose they serve in mammals is either absent or achieved through a different mechanism in birds. Differences also exist between mammalian and avian REM sleep. Most conspicuously, episodes of REM sleep in mammals can be minutes or even tens of minutes long, whereas bouts of avian REM sleep rarely exceed 10 seconds and are packaged into hundreds of episodes per day. It was once thought that short REM sleep episodes prevented perching birds from falling out of trees, but REM sleep is also short in birds that sleep on the ground. Integrating these differences into functional hypotheses



Figure 2. Super-male pectoral sandpipers. Male pectoral sandpipers must remain awake, active, and alert for several weeks during the breeding season in the high Arctic pursuing fertile females (A,B), thwarting competing males (C–E), remaining vigilant for mates, rivals and predators (F), and foraging effectively. Photographs A–E ©Wolfgang Forstmeier; F ©Bart Kempenaers. (Modified from Lesku *et al.* (2012) Science.)

is a necessary challenge for those that seek to identify the universal (or core) function of SWS and REM sleep shared by mammals and birds.

What does avian sleep do? One of the hypotheses for the function of REM sleep with the greatest longevity has been the ontogenetic hypothesis, which proposes that REM sleep is important for the early development of the brain. This idea stems from the observation that altricial newborns, such as kittens, have a lot of REM sleep, which declines throughout early life to plateau at a species-specific adult level. Although evidence for this pattern had been unclear in birds, it was recently demonstrated that young owlets have more REM sleep than older owlets (Figure 3), suggesting that avian REM sleep may too be involved in maturational processes within the developing brain. However, in both birds and mammals, the exact aspects of brain development subserved by REM sleep remain poorly understood.

Sleep appears to also play a role in song learning in juvenile songbirds. Some songbirds, such as the zebra finch, learn their song through imitating a tutor: practising during the day and sleeping (largely) at night. After exposure to the tutor's song, neurons in a part of the brain essential for song production begin to fire in bursts of

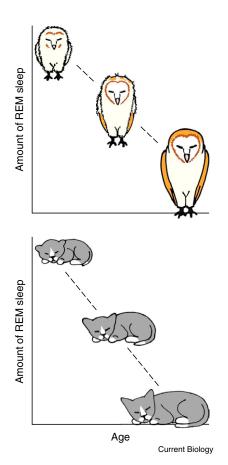


Figure 3. REM sleep ontogeny.

The amount of REM sleep decreases with age in young birds, as it does in young mammals (arbitrary units). Owlet and kitten drawings ©Ninon Ballerstädt.

activity during sleep. Interestingly, the pattern of firing observed is specific to the song heard, suggesting that the neuronal activity carries with it information about the song itself. However, the quality of the juvenile's song actually worsens after sleep, and improves only with practice the next day. Importantly, this effect is dependent upon sleep per se, as it is observed following daytime naps as well. The sleep-dependent deterioration of song quality seems detrimental at first glance; however, those birds whose song deteriorates the most during sleep ultimately reproduce the tutor's song best, indicating that this is an adaptive sleep process.

SWS and REM sleep must serve a purpose beyond developmental processes, however, as they persist into adulthood in both birds and mammals. The observation that SWS is more intense following brain use during wakefulness suggests that SWS serves a use-dependent neurophysiological role; however, the precise nature of this role is debated, with ideas ranging from restoring cellular resources depleted during wakefulness to weakening or strengthening synapses. The purpose of REM sleep in adults remains even more mysterious, as the suppression of REM sleep with anti-depressant drugs does not appear to impair performance in humans, and may even improve performance on motor memory tasks. Nevertheless, the abundance of REM sleep in neonates and its persistence throughout life suggests that REM sleep most likely serves processes prevalent in neonates that are needed less in adults. Ultimately, by determining the reason for the convergent evolution of SWS and REM sleep in birds and mammals, we may provide insight into the purpose of these states in ourselves.

Where can I find out more?

- Abel, T., Havekes, R., Saletin, J.M., and Walker, M.P. (2013). Sleep, plasticity and memory from molecules to whole-brain networks. Curr. Biol. 23, R774–R788.
- Derégnaucourt, S., Mitra, P.P., Fehér, O., Pytte, C., and Tchernichovski, O. (2005). How sleep affects the developmental learning of bird song. Nature 433, 710–716.
- Lesku, J.A., Meyer, L.C., Fuller, A., Maloney, S.K., Dell'Omo, G., Vyssotski, A.L., and Rattenborg, N.C. (2011). Ostriches sleep like platypuses. PLoS ONE 6, e23203.
- Lesku, J.A., Vyssotski, A.L., Martinez-Gonzalez, D., Wilzeck, C., and Rattenborg, N.C. (2011). Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? Proc. R. Soc. B 278, 2419–2428.
- Lesku, J.A., Rattenborg, N.C., Valcu, M., Vyssotski, A.L., Kuhn, S., Kuemmeth, F., Heidrich, W., and Kempenaers, B. (2012). Adaptive sleep loss in polygynous pectoral sandpipers. Science 337, 1654–1658.
- Margoliash, D., and Schmidt, M.F. (2010). Sleep, off-line processing, and vocal learning. Brain Lang. *115*, 45–58.
- Rattenborg, N.C., Lima, S.L., and Amlaner, C.J. (1999). Half-awake to the risk of predation. Nature 397, 397–398.
- Rattenborg, N.C., Martinez-Gonzalez, D., Roth, T.C., and Pravosudov, V.V. (2011). Hippocampal memory consolidation during sleep: a comparison of mammals and birds. Biol. Rev. 86, 658–691.
- Scriba, M.F., Ducrest A.-L., Henry, I., Vyssotski, A.L., Rattenborg, N.C., and Roulin, A. (2013). Linking melanism to brain development: expression of a melanism-related gene in barn owl feather follicles covaries with sleep ontogeny. Front. Zool. 10, 42.
- Shank, S.S., and Margoliash, D. (2009). Sleep and sensorimotor integration during early vocal learning in a songbird. Nature 458, 73–77.
- Siegel, J.M., Manger, P.R., Nienhuis, R., Fahringer, H.M., and Pettigrew, J.D. (1998). Monotremes and the evolution of rapid eye movement sleep. Philos. Trans. R. Soc. B 353, 1147–1157.
- Siegel, J.M. (2011). REM sleep: a biological and psychological paradox. Sleep Med. Rev. 15, 139–142.

¹Department of Zoology, La Trobe University, Melbourne, Australia. ²Avian Sleep Group, Max Planck Institute for Ornithology, Seewiesen, Germany. E-mail: j.lesku@latrobe.edu.au, rattenborg@orn.mpg.de

Mosquitoes

Ralph E. Harbach¹ and Nora J. Besansky²

What are mosquitoes? Mosquitoes are delicate, long-legged twowinged flies (order Diptera, family Culicidae) that are easily recognized by their long proboscis and the scaly wings and legs (Figure 1). More than 3,500 species inhabit the temperate and tropical regions of the world. Females of many species suck blood - all males and many other females feed exclusively on nectar, fruit juices and plant exudates. Blood-sucking females require blood for egg development. Warm-blooded animals are a common source of blood, but many mosquito species also attack coldblooded animals such as snakes, turtles, toads, frogs and other insects. Some species are active at night or twilight while others are active during the daytime.

How do mosquitoes reproduce? Females lay their eggs in water, where they develop into larvae, pupae and adults. Many species inhabit temporary or permanent bodies of ground water, but many others utilize container habitats such as tree holes, leaf axils and discarded tires. The larvae of most species feed on microorganisms and organic debris, but some are predators that feed largely on larvae of other mosquitoes. Mature larvae transform into pupae, which do not feed. Extensive anatomical changes take place within the pupa, and the adult emerges in two or three days.

The deadliest bite? Some bloodseeking mosquitoes attack only one or two host species, but most have no host preference and are opportunistic in their feeding behavior. Beyond simply annoying humans with their bites, fewer than 100 mosquito species are important because the females transmit ('vector') the viruses, filarial worms and protozoa that cause diseases such as yellow fever, lymphatic filariasis (elephantiasis), and malaria, respectively. The most important vectors have a marked tendency to feed on humans and inhabit domestic environments,

