PETER RYAN

SLEEPING WITH one eye open

An immature African Penguin snoozes with one eye open for potential threats. Closing its right eye allows the left half of its brain to rest.

WHILE THE exact function of sleep remains elusive, virtually all animals with a nervous system experience periods of reduced activity and awareness. The fact that this occurs despite an increased risk of predation suggests that sleep plays an essential role in enabling the brain to function properly when animals are awake.

Experiments confirm what we know from personal experience – sleep deprivation reduces the ability to concentrate, which has potentially lethal consequences for animals that need to remain alert for predators. Despite this, animals differ in both the amount and type of sleep they experience. **Peter Ryan** reports on recent studies that show that at least some birds have evolved mechanisms to manage with very little sleep for protracted periods.

Although sleep has not been studied in many wild birds, most species sleep for at least six to eight hours every day (see box on page 24). Migrating passerines, however, are unable to do so because they fly for much of the night and need to feed during the day. In 2004, a team of researchers led by Niels Rattenborg showed how captive White-crowned Sparrows sleep about two-thirds less during their period of migratory restlessness than at other times of the year (*PLoS Biology* 7: 924). The migrating sparrows performed behavioural tasks with the same level of accuracy as birds outside the migration period that slept for about eight hours a day, suggesting that they suffered no ill effects from lack of sleep.

Remarkably, the same birds struggled to perform the tasks when they were restricted to three hours of sleep outside the migration period. However, we can't exclude the possibility that the stress of experimentally preventing birds from sleeping may have contributed to their poor performance.

While on migration, the sparrows spent more time drowsing during the day, which may help to offset the lack of sleep at night. In 2006, Thomas Fuchs and colleagues observed how during the migration period, captive Swainson's Thrushes undertook a series of 'micronaps' throughout the day (*Animal Behaviour* 72: 951–958). In 2009 they confirmed with an electroencephalogram (EEG) that the thrushes experienced short sleeps seldom lasting more than 30 seconds (*Biology Letters* 5: 77–80).

The EEG measured activity in both left and right brain hemispheres. Like marine mammals, birds can rest by 'switching off' one half of their brain at a time, known as unihemispheric slow-wave sleep (USWS, see box). Fuchs's team showed that during the day the thrushes often rested only one half of the brain, which enabled them to keep one eye open for danger. Previously, Rattenborg and colleagues demonstrated how the proportion of time Mallards spend in USWS (as opposed to the more efficient bihemispheric slow-wave sleep or BSWS) increases as the risk of predation increases (*Nature* 397: 397–398). The migrating thrushes experienced short bouts of both USWS and BSWS during the day (averaging 11–13 seconds), but rapid eye-movement (REM) sleep only occurred at night and might not occur during migration.

John Lesku and colleagues (*Science* 337: 1654–58) recently reported how male Pectoral Sandpipers sacrifice sleep in order to maximise their reproductive success. Pectoral Sandpipers breed in the high Arctic summer, when day length approaches 24 hours. They are polygamous; males display to females on territories that they defend against other males. There is thus strong selection for males to remain vigilant throughout the day for intruding males and potentially receptive females.

Lesku's team found that males vary considerably in the amount of time that they sleep. Some males are active for nearly 23 hours a >

JOHN VOSLOO

Birds such as this Red-necked Spurfowl are most vulnerable to being killed by predators while asleep, so they have evolved numerous strategies to reduce this risk. These include roosting in groups and in secure locations and taking many short naps rather than undergoing a protracted period of deep sleep.

ALL SLEEP IS NOT EQUAL

Much of what we know about sleep comes from tracing the brain's electrical activity using an electroencephalogram or EEG. When we are awake, the brain's neurons fire irregularly, resulting in very fast, low-amplitude brain waves. During most sleep, however, the neurons alternate between being 'on' and 'off', resulting in slower, high-amplitude waves. This is termed slow-wave sleep (SWS) and the greater the amplitude of the waves, the deeper the sleep.

Mammals typically experience SWS throughout their brain, rendering them largely unresponsive to external stimuli. However, marine mammals are well known to exhibit unihemispheric SWS (USWS), which keeps half of their brain awake. This enables them to continue to breathe while swimming and to remain together in pods. Birds also demonstrate both bihemispheric SWS (BSWS) and USWS, when they can effectively sleep with one eye open to danger and can switch between these two modes of sleep.

Mammals and birds also experience short bouts of paradoxical or rapid eye-movement (REM) sleep, which is accompanied by low muscle tone, rapid eye movements and (at least in humans) dreaming. This type of sleep is always expressed throughout the brain which, coupled with the poor muscle tone, makes it largely incompatible with other activities. For example, large mammals lie down in REM sleep but can remain standing in SWS sleep, and at least some marine mammals apparently never enter REM sleep. However, birds experience less loss of muscle tone in REM sleep than mammals do, which reduces its functional impacts.

HOW MUCH IS ENOUGH SLEEP?

Sleep is a fundamental requirement: when an animal is sleep deprived, the need to sleep overrides even the need to eat or the desire for sex. Reducing the amount of time rats sleep by 70 per cent or more results in their death within a few weeks. Yet surprisingly little is known about sleep duration in birds. A review by Roth et al. in 2006 (*Journal of Sleep Research* 15: 395–402) presented data for only 23 bird species, which slept between six hours (Budgerigar) and 17 hours (Ring-necked Dove) a day.

Mammals are better studied and we know that the amount of time spent sleeping depends on age, body size, diet and risk of predation. Sleep duration typically decreases with age; babies sleep more than adults. Sleep duration also tends to decrease as body size increases. This pattern is most evident in herbivorous mammals, with small species spending between eight and 14 hours asleep each day, whereas large species seldom sleep for more than three to five hours a day. By comparison, body size has little effect in carnivores, with most species sleeping for between nine and 20 hours per day. Omnivores fall between these extremes, with humans at about eight hours per day edging towards the lower limit for this dietary group.

Finally, predation risk plays a large role in determining the time spent sleeping. Mammals with secure roost sites can afford to sleep for longer than those that are at risk of being eaten while sleeping. This was the only factor found to affect the duration of sleep among birds.

JOHN VOSLOO

Among the small sample of birds studied, doves, such as this Laughing Dove, are the birds that spend the most time sleeping – up to 17 hours per day.

day, maintaining this hectic pace for almost three weeks, whereas others sleep for more than seven hours a day. Perhaps not surprisingly, those males that remain active longest tend to mate with more females and sire more offspring. There appears to be sexual selection for males that can remain awake for longer. However, this cannot be the only factor. If it were, there would be less variation among males: if the ability to stay awake were the only target of selection, genes for this trait would quickly spread through the population.

Fitting male sandpipers with EEGs revealed that the individuals that spent more time awake experienced deeper sleep during their short resting periods, but this doesn't fully compensate for their limited sleep time. It is likely that they repay their sleep debt once the females are no longer available for mating. Shorebirds probably also suffer sleep deprivation while on their long-distance migrations, which in extreme cases can result in birds flying non-stop for more than a week. Anecdotal evidence suggests that waders arriving in New Zealand after flying across the Pacific Ocean spend more time sleeping than feeding.

Flying on autopilot

Shorebirds, along with other long-distance migrants, might also be able to get some sleep in flight. It has long been assumed that Common Swifts must sleep on the wing, because they apparently remain aloft throughout their non-breeding period, which lasts about nine months. Radar observations confirm that non-breeding swifts climb to about 3000 metres above the ground at night, where they spend the hours of darkness cruising over their colonies. If sleep is indeed essential, they must sleep in flight. In 2006, Rattenborg predicted that birds should be able to sleep in flight, mainly using USWS but perhaps also brief periods of BSWS (*Naturwissenschaften* 93: 413–425). However, he thought that REM sleep was unlikely to occur in flight, as a result of the accompanying lack of muscle tone.

Testing these ideas required the development of an EEG small enough to be attached to a bird that remains aloft for days on end. Frigatebirds are the largest birds to do so and are renowned as seabirds that cannot rest on the sea. A recent paper by Henri Weimerskirch and colleagues (*Science* 353: 74–78) shows how individuals from colonies in the Indian Ocean spend up to two months aloft, circling the edge of the doldrums.

The frigatebirds' extremely long, angled wings and large, deeply forked tails, coupled with a very light skeleton, confer the lowest wing loading of any bird species. This results in very efficient flight; frigatebirds soar effortlessly, routinely rising up to 600 metres above the sea using thermals or trade winds. From these lofty heights, they glide down when they spot a feeding opportunity. They rarely feed at night, when they typically remain 50 to 1500 metres above the sea. However, Weimerskirch's team found that birds only show occasional, brief periods when their

BRYSON VOIRIN

A female Great Frigatebird equipped with a miniature EEG logger on its head and a back-mounted GPS logger soars over its breeding colony in the Galápagos Islands. Niels Rattenborg's recent study of these birds was the first to confirm that birds can sleep in flight.

bodies are completely motionless, suggesting that they seldom sleep.

Rattenborg and colleagues tested whether frigatebirds do actually sleep in flight (*Nature Communications* 7: 12468). They equipped Great Frigatebirds brooding small chicks with an EEG coupled with a tri-axial accelerometer and the birds also carried a GPS logger on their backs. Together these loggers measured the birds' behaviour and brain activity. Only females were studied because they are larger than males, but even so the combined mass of the loggers (55 grams) was about four per cent of a female's body mass – higher than the recommended limit of two to three per cent for loggers on flying birds. Despite this, the birds appeared to behave normally, undertaking foraging trips lasting up to 10 days and travelling as far as 3000 kilometres on long, looping trips north and east of the Galápagos Islands.

The EEG traces showed that frigatebirds sleep while gliding or soaring, but not while flapping. Sleeping occurred mainly when birds were climbing in elevation and were fairly high above the sea – conditions when there is little risk of a collision. As expected, they usually shut down one side of the brain at a time. While soaring, they usually kept the eye open on the side of the head towards which they were circling, to watch where they were going. However, this was not always the case; occasionally both sides of the brain went to sleep at once. More surprisingly, the birds also exhibited brief snatches of REM sleep.

Despite the ability to sleep on the wing, frigatebirds sleep less deeply and spend much less time asleep while flying (less than three per cent of the time) than when they are attending their nests (around 50 per cent of the time). Sleeping on the wing was more frequent at night (five per cent of the time) than during the day (0.4 per cent). Sleep bouts while flying averaged only 11 seconds, but the longest sleep bout was almost six minutes, so flying birds can occasionally take quite long naps.

There was some evidence that the frigatebirds acquired a sleep 'debt' during their foraging trips because of the reduced amount and quality of sleep in flight. On returning to their nests, the amount of time spent sleeping and the depth of that sleep decreased gradually during the first 10–15 hours ashore. Despite this, the average duration of sleep events was still only about one minute, suggesting that birds experience sleep quite differently from how humans do. ◆