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1

Why Birds Sleep



Sleep is an essential part of life for jellyfish, snails, octopuses, insects, fishes, and reptiles through to birds and mammals. Indeed, animals could not survive without sleep, even as the portion of each day and of their lifetime in this state differs widely among classes and species. Timing, duration, and intensity of sleep vary in response to each animal's habitat, daily activity, reproductive state, place on a food chain, and other ecological and behavioral factors.

Since animals are often at greatest risk when asleep, sleep must provide benefits that compensate for the danger. Animals that are frequent prey for others have evolved different sleep patterns than predators, just

as those sleeping in exposed places sleep differently from those in secure ones. Similarly, animals living at latitudes with extended daylight or long nights use those hours differently. Migratory animals, such as many birds, alter their sleep regime when traveling and at their destinations.

Sleep's key visible feature is periods of immobility, usually spent in a characteristic posture, during which responses to external stimuli are lower. Among animals in which brain activity has been measured, this also changes. In birds and mammals, with their complex ecologies and behaviors, sleep's aspects and functions increase. The brains and bodies of birds require substantial energy to operate in environments that challenge their ability to find food, to reproduce, to avoid dangers, and, for some, to travel long distances. Rest, when they can conserve and restore energy, therefore has more features than in animals with fewer daily demands.

Functions of Sleep

Sleep's functions and benefits reflect both ecological adaptations and neurological features. For most animals, there are portions of the twenty-four-hour cycle in which light levels make continuation of feeding, other maintenance activities, or reproduction more difficult. During the hours that wakefulness is unproductive and may even be dangerous, inactivity, if not actual sleep, is the most efficient use of this time. For warm-blooded animals—birds and mammals—sleep can also reduce the substantial costs of maintaining endothermy, a higher body temperature than the surrounding atmosphere. In sleep, many endothermic animals lower their body temperature, a significant energy saver that reduces their need for the food that fuels their high metabolic rate. The greater complexity of sleep mechanisms in endotherms may have evolved with warm-bloodedness itself, as a way to offset endothermy's high costs (Berger and Phillips 1995).

Sleep, when the brain is not substantially engaged in directing activity, is also the opportunity for it to restore itself to maintain high waking neurophysiological performance. During sleep the brain strengthens or weakens synaptic connections, effectively creating space for consolidation of learning and for organization of memory. Sleep may also cleanse

the brain of waste and potentially damaging byproducts generated by neuronal activity during wakefulness (Rattenborg and Gonzalez-Martinez 2014). When birds are active, the major activity of their brain is the processing of sensory information, primarily visual. During sleep, when sensory experience and processing are substantially reduced, the brain can refresh memory circuits without conflicting demands.

In the course of animal evolution, the processing of sensory information in brains of ever greater complexity, such as those of birds, created more need for refreshing memory circuits. Sleep became all the more necessary (Kavanau 1998). Laboratory experiments have shown that sleep is involved in, among other things, consolidating imprinting memories for chicks, song learning in finches, auditory discrimination in starlings, and courtship in pigeons. At the same time, some memories may be shed during sleep, preventing saturation in the brain's hippocampus, where memories are stored (Rattenborg et al. 2010; Ungurean et al. 2021). Memory and learning are affected by quality as well as quantity of sleep. For the chicks in memory experiments, nine hours of sleep after imprinting training generated a lasting memory. Six hours of undisturbed sleep achieved almost the same result, but chicks given six hours of disturbed sleep immediately after training did not form any memory of the imprinting stimulus (Vorster and Born 2015).

In oscines (“songbirds”) and suboscines, the muscles controlling the syrinx have bursts of activity during sleep that resemble fragments of the activity during song production; this takes place without respiration, so produces no sound. It may, however, contribute to creating useful muscle memory for subsequent song production (Döppler et al. 2021). In the brain as well, patterns of neural activity during sleep can match what the brain does during certain waking states, thereby reinforcing the motor patterns needed to perform the activity. Zebra Finches (*Taeniopygia guttata*) sleeping in a laboratory were played recordings of their song; the birds responded by producing the same neural patterns that operated when the birds were awake and singing those songs (Dave and Margoliash 2000).

Other tissues may also be restored during sleep. In young animals, sleep is when the central nervous system matures. In adults as well,

growth hormones released during sleep promote the synthesis of protein and RNA (ribonucleic acid, which creates proteins necessary for some cellular processes). These hormones also activate lipid metabolism, which synthesizes and degrades lipids in cells, breaking down fat for storage or energy. Testosterone release increases during sleep, improving skeletal muscle protein synthesis and remodeling of bone. Cell membrane repair, intracellular transport, and clearing of metabolic waste through the kidneys are other important functions that take place during sleep. All these decrease energy demands and cellular stress during wakefulness, so that animals can in those hours perform necessary functions unique to wakefulness (Schmidt 2014).

Phylogeny of Sleep

Animals of every phylum that has been studied for sleep behavior have shown the basic features of a period of immobility during which they have been less responsive to stimulation. Even animals without a brain, such as jellyfish, have a regular rest period where they are harder to stimulate. In animals that have a central nervous system, either a brain or a cephalic ganglion, the definitive signs of sleep are still more pronounced. Flatworms spend their time either swimming or in contraction, where they remain immobile for minutes or hours and are less responsive. Experiments with crayfish, scorpions, spiders, honeybees, fruit flies, snails, and octopuses, among many others, have shown similar but varied results. The next stage of sleep research will be to determine whether any form of sleep exists in organisms without neurons, such as sponges, fungi, or even plants. Among animals, the pervasive evidence of sleep indicates that it must have evolved very early to span such a broad range of phyla with otherwise differing nervous systems (Lesku and Ly 2017; Rattenborg and Ungurean 2023).

Curiously, among vertebrates the recognizable aspects of sleep are less consistent. This is due in part to the definitive features ascribed to sleep having originally come from research on mammals in which measures of neuronal activity in the brain using electroencephalography were the hallmarks. In fishes, for which such measures would be difficult to record

in water, presence of sleep has been evaluated by behavior. Some fishes are continually active in all light conditions, while others have definite periods of immobility. This has been treated as “behavioral sleep.” In studies with nine species of frogs and salamanders, most showed periods of behavioral sleep, when the animals were less responsive, but experiments with an electrograph, measuring the electric activity in the brain, showed patterns different from those of sleeping mammals. Similarly, among sixteen turtles and tortoises, crocodilians, lizards, and snakes studied, electroencephalogram characteristics vary widely and differ from those of mammals. Most tortoises and terrestrial turtles show behavioral sleep, while sea turtles do not; this may be because, like marine mammals, sea turtles must ensure they are on the water surface whenever they need to breath. Various monitored crocodilians, lizards, and snakes slept three to twenty-two hours per day, indicating a wide range of needs and perhaps of functions (Campbell and Tobler 1984).

Among the distinctive evolutionary features of sleep in birds is that it occurs in much shorter bouts than in other classes of animals, often running only one to four minutes, with frequent brief wakeups that enable birds to check for any danger around them. Most research demonstrating this, however, has been done in laboratories, where birds are usually kept singly, may be fed *ad libitum*, and are free from signs of danger, all of which may affect sleep duration. Recent experiments with wild Chinstrap Penguins (*Pygoscelis antarcticus*) in Antarctica have shown that sleep can even be a matter of seconds, done frequently throughout the day, and adding up to what for humans would constitute “a good night’s rest.” Using remote sensing monitors, scientists found that during December, when living in constant daylight, penguins slept more than ten thousand times a day, for an average of four seconds at a time. This, however, added up to more than eleven hours of the twenty-four. The birds slept this way both while they were at sea and in their nesting colony. At sea, they need to be alert for predators, while in their colony they are constantly exposed to egg thieves and aggression from neighboring penguins (Libourel et al. 2023).

A defining feature of sleep in birds and mammals is two distinct forms of electric activity in the brain: slow-wave sleep (SWS), or quiet

sleep, and rapid eye movement sleep (REM), or active sleep. In birds, sleep bouts with both these features are much shorter than in mammals. Within birds' typical sleep bouts of one to four minutes, periods of SWS last around fifty seconds during the first hours of sleep, decreasing to about twenty-five seconds in the final hours. REM is less than 10 percent of total sleep time, occurring throughout and generally increasing later (Vorster and Born 2015). REM occurs in periods of two to ten seconds, in clusters, often of hundreds in each sleep session, much more briefly than in mammals, where REM runs uninterrupted for minutes or tens of minutes.

The proportion of sleep time in REM is a mean of 8 percent in birds and 17 percent in mammals. REM sleep, however, varies substantially among birds. It is less than 5 percent of total sleep time in European Starlings (*Sturnus vulgaris*), Rooks (*Corvus frugilegus*), Budgerigars (*Melopsittacus undulatus*), and Turtle Doves (*Streptopelia turtur*), but 16 percent in White-crowned Sparrows (*Zonotrichia leucophrys*) and 25 percent in Zebra Finches (van Hasselt et al. 2020). All these birds, however, were tested in laboratories, which did not replicate aspects of seasonal conditions and reproductive states that may influence extent of REM over the course of the year.

The two sleep states were first measured in birds by connecting electrodes on the brain to a computer via a cable tether, which restricts the bird's movements and may affect normal behavior. Today, laboratory research uses wireless technology that transmits electroencephalographic (EEG) signals to a receiver, leaving the bird unrestrained. And now, lightweight EEG data loggers can be used with animals larger than 100 grams. This has created opportunities to study sleep directly in at least some birds in the wild, especially when data loggers are paired with video cameras (Aulsebrook et al. 2016).

During SWS, EEG readings show low-frequency, high-amplitude activity. SWS originates in the hyperpallium. The pallium is the equivalent of the mammalian neocortex, but it is structurally different. The slow oscillations during SWS support communication between different, sometimes distant, brain regions and integrate processing of information. SWS is also linked to synaptic downscaling and renormalization

that balances synaptic connectivity throughout the brain, preparing the neuronal network for encoding new information in the next wake phase (Vorster and Born 2015).

In REM, EEG activity is similar to that during wakefulness, with low-amplitude, high-frequency activity. For this reason, REM has sometimes been called paradoxical sleep. Some of REM's visible signs are the closing of both eyes, rapid eye movement, occasional bill movements, and, for birds that rest their head on their back, reduced muscle tone (Wellman and Downs 2009). The short duration of each REM sleep, when muscles are relaxed, was once thought to protect perching birds from falling, but it has since also been found in many birds that sleep on the ground (Lesku and Rattenborg 2014). Domestic geese can continue in REM sleep while standing on one leg if their head is resting on their back; if the head is erect, however, muscle tone is higher and the birds are in SWS (Dewasmes et al. 1985).

Body temperature is lowered during REM, which may be a reason for the brevity of each episode as well as the total amount. At the same time, however, the brain warms during REM and cools during SWS (Rattenborg and Ungurean 2023). In both birds and mammals, the time spent in REM sleep increases after sleep deprivation (Lesku et al. 2009). In birds that sleep at night, SWS occurs principally in the first hours of sleep with, in some birds, REM increasing later. Domestic pigeons (*Columba livia*) given twelve-hour periods of darkness slept 81 percent of the time, with REM making up 4 percent of sleep in the first six hours and 8.7 percent in the second six hours, during which sleep overall decreased in the final two hours (Tobler and Borbély 1988). In nature, the relative share of time spent in each form of sleep may depend on local conditions. Geese spend more of their sleep time in SWS when fasting than when well fed; during fasting, each SWS sleep bout is longer and there are more of them. For REM, bouts are briefer and less frequent when fasting (Dewasmes et al. 1984). The same researchers found similar patterns in Emperor Penguins (Dewasmes et al. 1989).

Seeking the origin of SWS and REM, scientists have searched for it in reptiles, but experiments have been inconclusive. Some of the reptiles

tested have two forms of sleep, but the patterns of neuronal activity, durations, and timing in the twenty-four-hour cycle are different from those in birds and mammals. Unlike birds and mammals, reptile limbs do not twitch during sleep and brain temperature does not change in different parts of sleep bouts. In addition, these features differ among species. Thus far, modern tests have used lizards. New research with crocodylians, the closest living relatives of birds, may show more clearly how sleep evolved in birds (Rattenborg and Ungurean 2023).

The parts of the brain involved in sleep in birds and mammals, while having the same origin, are now very different structurally, so sleep features may have evolved independently (Rattenborg 2006a). Comparison of sleep in species from the oldest living groups of birds and mammals—ostriches and platypuses, respectively—show similarities not present in species that evolved more recently. During REM sleep in ostriches, the typical avian rapid eye movements, relaxed muscle tone, and closure of both eyes are evident, but electric activity in the forebrain oscillates between REM sleep-like activation and SWS-like slow waves. This is unlike any other birds that have been tested, but it has also been found in platypuses. In addition, both ostriches and platypuses have relatively more REM sleep than other birds and mammals. These shared features suggest a common, but independent, sequence of steps in the evolution of sleep. SWS and REM likely arose from a single state that later became entirely separated into two distinct states, with the activation of the forebrain as a new feature that performs functions not found in reptiles and other more basal animals (Lesku et al. 2011).

In mammals, factors affecting total sleep time as well as proportions in SWS and REM include body mass, relative brain mass, basal metabolic rate, gestation period, and predation risk. In birds, only predation risk has been found relevant. A literature review of sleep duration in twenty-three bird species (including ducks, turkeys, parrots, owls, doves, penguins, and a range of passerines) found that, in natural situations, the relative safety of their roosting site from predators was the sole feature that correlated with total sleep time (Roth et al. 2006). Eurasian Blackbirds (*Turdus merula*), which in nature sleep in leafy vegetation, were found in a laboratory to spend 6.6 percent of total sleep time

in REM (Szymczak et al. 1993). Five Little Penguins (*Eudyptula minor*), which sleep in burrows, spent a mean of 16.2 percent of total sleep time in REM (Stahel et al. 1984).

For both birds and mammals, the time spent in sleep increases when more time has been spent awake. The return to the usual balance of sleep—homeostasis—seems to be internally governed and may be linked to the evolution in both birds and mammals of large, heavily interconnected brains that perform complex cognitive functions and need time to restore and maintain optimal interconnectivity and cognition. In birds, the amount of SWS in an extended sleep bout varies in different parts of the brain based on how intensively each region was used during the prior period of wakefulness. Areas more intensively used have lengthier SWS. If, for example, one eye received more visual input during wakefulness, the visual part of the brain that received input from that eye will have more slow waves during SWS (Rattenborg and Ungurean 2023). Pigeons experimentally deprived of sleep during the day had more SWS during the first three hours of recovery sleep, and they had more slow wave activity during REM sleep (Martinez-Gonzalez et al. 2008). Pigeons deprived of sleep for twenty-four hours then slept longer and with more time in REM sleep (Tobler and Borbély 1988).

Unihemispheric Sleep

The relatively short bouts of sleep typical of birds reflect the balance necessary between the need for neural maintenance and the risks that may be increased by a lengthy complete shutdown of the brain. While a complete shutdown might be the safest and most rapid way to perform neural maintenance, it may also make the bird more vulnerable to predation. In addition to sleeping in bouts far briefer than those of mammals, birds have evolved a way to maintain a degree of alertness during these bouts: unihemispheric sleep. In SWS, birds can sleep either with both eyes shut or with one eye open. EEG activity in the brain hemisphere opposite the open eye is then intermediate between wakefulness and SWS, while the hemisphere opposite the closed eye is in SWS.

Unihemispheric sleep is found elsewhere only in some marine mammals, enabling them to surface and breathe while asleep. Whales and dolphins, eared seals, and manatees have each acquired this ability in their separate evolutions from terrestrial mammals—while sea turtles, in which no sleep of any kind has been found, have not.

For birds, the function of unihemispheric sleep is to enable predator detection while not rousing the entire brain and body. That it occurs only in SWS may be because wakefulness in one hemisphere may interfere with REM sleep in the other. If memory processing occurs during REM sleep, that may require both hemispheres. The brevity of REM sleep, when both eyes are shut and muscles are more relaxed than in SWS, is itself an adaptation to reduce vulnerability. Finally, the loss of muscle tone in REM sleep may counteract what benefits might come from unihemispheric sleep in this state (Rattenborg et al. 2000).

Birds control which hemisphere is asleep. Is one hemisphere given more sleep or wakefulness? The brain's left hemisphere specializes in control of patterns of behavior that occur regularly in familiar situations, while the right hemisphere is responsible for detecting and responding to unexpected stimuli in the environment (Rogers et al. 2013, p. 97). In chicks, which acquire these fundamentals in their first weeks of life, the left hemisphere of the brain is sensitive to major changes in the environment, such as the approach of a predator, while the right hemisphere is sensitive to changes in detail. The left hemisphere is also where memories are consolidated and therefore may require more sleep than the right hemisphere. That could lead to more closure of the right eye, at least during early developmental stages, as has been demonstrated in experiments with chicks raised with or without an imprinting object. Those reared with an imprinting object closed their right eye during sleep more often during their first week, but by the second week after hatching, chicks reared with and without an imprinting object both slept with their left eye closed more than the right (Bobbo et al. 2002).

Later, roosting birds may favor whichever eye and opposite hemisphere is most relevant to the immediate situation, eventually ceding sleep to the other so the entire brain's needs can be met (Rattenborg 2000). In experiments with Mallards (*Anas platyrhynchos*) where four

birds were placed in a row, the birds at the end of each row spent more time in unihemispheric sleep than did the more central birds, and approximately 86 percent of that time they opened the eye on their exposed side. That these birds were vigilant in unihemispheric sleep was demonstrated by their responses in fractions of a second to a video simulating an attacking predator (Rattenborg et al. 1995).

Stimulus for Sleep

Role of Melatonin

The inclination to sleep is governed by several interacting sites, including the retina of the eye, the hypothalamus in the brain, and the pineal gland. The eyes inform the hypothalamus of changes in light level; soon after darkness, the hypothalamus secretes hormones that stimulate the pituitary gland to produce melatonin, which is synthesized from serotonin by one of its enzymes and is released into the bloodstream. Melatonin communicates with pacemakers in the hypothalamus and depresses the synthesis of an avian neurosteroid (7α -hydroxypregnenolone), only recently identified, that stimulates locomotor activity (Tsutsui et al. 2012). The retina also produces melatonin, but this is not released into the bloodstream in all species. For some, that comes entirely from the pineal gland, which in birds, unlike mammals, is sensitive to light. The importance of the pineal gland was shown by experiments in which this gland was removed. House Sparrows (*Passer domesticus*) thus treated lost their regular rhythm of waking and sleeping. Other species require the elimination of both pineal gland and the eyes to abolish the rhythm of melatonin in the bloodstream and in behavior (Gwinner and Brandstätter 2001).

Removal of the pineal gland is more disruptive for some birds than others. Circadian rhythm is totally abolished in House Sparrows, White-crowned and White-throated Sparrows (*Zonotrichia albicollis*), and House Finches (*Haemorrhous mexicanus*), but only partially in European Starlings, and it has far less effect on chickens and Japanese Quail (*Coturnix japonica*). This may indicate that in some species or

orders other factors are involved (Takahishi and Menaker 1980). In experiments where sleep-deprived birds with pineal gland extant are given a twelve-hour infusion of melatonin, they return to normal rhythms. Further demonstrating the power of melatonin, when infusions are given to birds after nocturnal sleep, this stimulates SWS even when the birds are exposed to light (Berger and Phillips 1995).

Under natural conditions, bright light suppresses the synthesis of melatonin and alters or eliminates a bird's normal circadian rhythms of melatonin production, of feeding, and activity. Species living at high latitudes during the season of continuous light produce less melatonin, and they also produce less melatonin during the weeks or months of almost total darkness, when they need to be awake long enough to feed themselves. Similarly, migratory birds that fly at night, and therefore need to be awake more hours than during their breeding season or in winter, then have less melatonin than when fat reserves are too low to enable migration and they are inactive at night (Gwinner and Brandstätter 2001).

In the Rock Ptarmigan (*Lagopus mutus hyperboreus*) on Svalbard, Norway, at 74–81°N, where daylight is continuous between May and August and where from late November to mid-January there is only a short period of civil twilight, melatonin production varies intensely. From May through July, there is no daily rhythm of melatonin production. Around the winter solstice, melatonin production is also reduced, compared to the spring and autumn months. During these months of total darkness, ptarmigans are intermittently active at all hours, but never as much as during the months with daylight. They retain some of the daily rhythm from the light months, with melatonin level lowest at noon and slightly higher during the other hours (Reierth et al. 1999). Similarly, Emperor Penguins (*Aptenodytes forsteri*) at 66°S in Antarctica have a well-defined pattern of melatonin production during spring and autumn, but they produce hardly any during summer or winter (Miché 1991).

Few nocturnal birds have been studied for melatonin rhythms, but the results have been consistently different from those of normally diurnal species. Barn Owls (*Tyto alba*) and Ural Owls (*Strix uralensis*) have low melatonin levels both by day and night and no discernable

rhythm. The Swallow-tailed Gull (*Larus furcatus*) of the Galapagos Islands, the world's only fully nocturnal gull, forages at sea on fish and squid during the night, when these are closer to the surface. By day during the breeding season, the Swallow-tailed Gull is on land and intermittently active, preening, displaying, etc., while during the non-breeding months it is continually at sea, mostly between the islands and the South American mainland. It has low melatonin levels throughout the twenty-four-hour cycle, while the similarly sized diurnal Black-headed Gull (*L. ridibundus*) of Eurasia has a clear rhythm with more melatonin in the bloodstream at night (Wikelski et al. 2006).

Light levels also affect the production of other hormones that influence activity. Corticosterone regulates energy, immune reactions, and stress responses. For birds at temperate latitudes, corticosterone level is linked to the hours birds typically sleep: in diurnal species it is higher at night and in nocturnal ones higher during daylight. During the continuous light of the Antarctic summer, however, Adelie Penguins (*Pygoscelis adeliae*) at 64°S have consistently lower corticosterone concentrations (Vleck and Van Hook 2002).

Internal and External Temperature Changes

While melatonin secretions are making a bird drowsy, its body is undergoing another change that promotes sleep: body temperature. Birds routinely lower their body temperature during periods of sleep to conserve energy through the hours they cannot feed and replenish their energy stores. In birds, metabolic heat production is set in the central nervous system by spinal cord temperature, not, as in mammals, by temperature of the hypothalamus. During sleep, spinal thermosensitivity lowers, first during SWS and still more during REM sleep. The change in body temperature may be related to changes in breathing rate, which is slower when sleeping, and in acid-base balance. At the onset of sleep, more carbon dioxide is retained in the body; this is reversed when birds are aroused (Heller 1988).

Ambient temperature also has an influence. A study of Great Tits (*Parus major*) that use nest boxes in southern Germany found that

temperature affects the length of each sleep bout, experimentally confirming what had already been noted, that birds in warmer climates waken more frequently. Under natural February conditions, the birds woke up 4.5 times per hour. When the temperature in the nest boxes was raised experimentally by 5°C, they awakened 30 percent more frequently, an additional 1.3 awakenings per hour, with the greatest effect in the first part of the night, when more time is in SWS than REM. The birds kept under normal conditions also woke more frequently in the first part of the night than later. Frequent wakenings during these hours may be because the first part of the night is when nocturnal predators are most active and birds can maintain more vigilance in SWS. As the night progresses, the drive to restore sleep balance increases and overrides vigilance behavior (Stuber et al. 2017).

Emperor Penguins, during their fasts of several weeks while incubating during the Antarctic winter, increase the time they spend sleeping and thereby lower their metabolic rate while reducing body temperature only slightly in the extreme cold (Groscolas 1990). Similarly, Dark-rumped Petrels (*Pterodroma phaeopygia*) nesting on high, cold mountains in Hawaii, with incubation bouts of eight to twenty-three days before they are relieved by their mate and can return to the sea to feed, spend about 95 percent of this time asleep, during which their respiratory rate falls from twenty-four to twelve breaths per minute (Simons 1985).

Effects of Sleep Deprivation

The duration and intensity of a bird's activity influences the need for rest and the time given to it. To restore sleep balance, homeostasis, after particularly intense or lengthy activity, birds may sleep longer or more deeply. In a Herring Gull (*Larus argentatus*) colony in Cumbria, England, adults that were provided food at their nest remained sedentary and slept less than neighbors that had to fly and search for food (Shafery et al. 1985a). Glaucous-winged Gulls (*L. glaucescens*) at a colony in Puget Sound slept more during the most demanding stages of feeding their young, starting when these were twenty days old and required

more foraging commutes to a garbage dump; the gulls then slept 61.3–93.6 percent more at night than in the earlier stages of chick-rearing (Shaffery et al. 1985b). Great Frigatebirds (*Fregata minor*) returning to their colony from several days spent entirely in flight over the ocean sleep longer and with more time in REM sleep, where muscles are most relaxed, than do ones that have remained at the colony (Rattenborg 2017). Among Chinstrap Penguins in Antarctica, which were found to sleep in bouts of seconds when incubating, those returning from more than twenty hours at sea spent more time in SWS during their first two hours on land than during later periods of sleep (Libourel et al. 2023). Barnacle Geese (*Branta leucopsis*) experimentally deprived of four or eight hours of sleep during the night in summer and winter showed different seasonal responses: in summer, they made up for lost sleep with an increase in sleep the following day. By the end of the twenty-four-hour cycle, they had slept almost as much as the control geese, which were not disturbed; during winter there was no response. Evidently, at least for geese, the need for homeostasis varies at different times during the annual cycle (van Hasselt et al. 2020).

Sleep deprivation has been found to affect immune function, neurogenesis in the adult brain, consolidation of recently acquired information, ability to acquire new information, and alertness, among other features (Roth et al. 2010). Birds have evolved ways to restore homeostasis after deprivation. Laboratory experiments giving birds varying amounts of sleep deprivation have shown similar results in different species. California White-crowned Sparrows deprived of six hours of sleep and then monitored over twelve hours of recovery showed that total SWS did not increase compared with their normal sleep. Instead, the SWS was more intense than normal, as measured by the increase in low-frequency EEG, known as slow wave action. REM sleep decreased during the first two hours; through the recovery period, REM bouts overall were briefer than in normal sleep (Jones et al. 2008).

Pigeons have been used to reveal further refinements of slow wave action: during sleep it may increase only in the parts of the brain that need extra restoration during sleep. Pigeons that were kept awake watching David Attenborough's *The Life of Birds* with only one eye were

then found to have increased slow wave action only in the part of the hyperpallium (which processes visual information) that is neurologically connected to the eye that had been stimulated. As in unihemispheric sleep, this was the side of the brain opposite the open eye. For these birds, there was also more REM sleep in the final hours of sleep afterward (Lesku et al. 2011).

Yawning

Yawning is associated with the onset of sleep and the initial stages of waking, as well as with other transitions such as when rest is interrupted, at the initiation of a new phase of activity, and with a reduction in stress level. It can cool the brain, thereby improving alertness and mental processing efficiency. Together with stretching, yawning is widespread in birds and mammals, frequently following one another or occurring together. Yawning is preceded by a rise in temperature in the brain and skull, where it drops after yawning. Experiments with Budgerigars showed that they are more inclined to yawn when ambient temperatures are rising, especially at higher levels, than when temperatures are descending.

Yawning is found both in social and in nonsocial animals and in seclusion, indicating it has a physiological function. In some birds, yawning is contagious. The benefit of contagious yawning may be that by cooling the brain it improves group vigilance. Budgerigars seeing neighbors yawn then themselves yawned more often than otherwise, but in similar experiments Common Ravens (*Corvus corax*) did not respond to others yawning (Gallup 2022).

A study of yawning behavior in Ostriches (*Struthio camelus*), where this can be observed more easily than in smaller or less continually conspicuous birds, found that chicks yawned as soon as they had recovered from the effort of hatching and ridding themselves of the eggshell. The yawn was in the same form as used through all later stages of life. When older, nestlings walking a few paces from their nest yawn, stretch, squat, and settle for a nap. Then and as adults, they awaken with a deep yawn

associated with neck stretching, followed or preceded by a complete stretch. For Ostriches, yawning also has a social function connected with rest or sleep. At the beginning of a period of rest for a herd of Ostriches, higher-ranking birds are the first to yawn, indicating absence of danger. Contagious yawning then induces a general relaxation of tension and triggers sleepiness in the group. After any disturbance during a rest, yawning by dominant birds assures more nervous ones that the danger has passed and stimulates them to continue their rest or sleep. At the end of a period of rest, yawning stirs up the group, initiating and synchronizing the new activity cycle (Sauer and Sauer 1967).

Circadian Rhythms

For all birds, perhaps for all animals, presence or absence of light is the principal factor in circadian rhythms, the daily pattern of activity and rest. The morning's increase in light intensity is a positive signal to diurnal species and a negative one to nocturnal ones, with different species beginning or adjusting their activities in response to different light levels, sometimes associated also with temperature. Light level is not directly correlated with duration in time. At most latitudes, light level and extent move forward and backward on the clock with the earth's rotation over the course of the year. At all latitudes, even near the equator, where day length hardly changes, local conditions, such as variations in cloud cover, affect light level and extent on a daily basis. Finally, hormonal levels, which may be triggered by changes in day length, also influence the circadian rhythm, as in shifting activity patterns during the breeding and nonbreeding seasons.

The time birds sleep during the twenty-four-hour cycle depends on the rest of their ecology as well as on seasonal changes governing light level. Compared with winter, birds sleep less during the breeding season if this is at a latitude of longer day length. The season of longest days correlates, for most birds, with the breeding season, so parents that feed or guard their young are active more hours than when they are tending only themselves.

Under Long Hours of Light

In the high Arctic summer when light is continuous, male Pectoral Sandpipers (*Calidris melanotos*) at Point Barrow, Alaska (71°N), sleep hardly at all during the three-week period when each is competing to mate with as many females as possible. The males defend a territory, sometimes with physical fights against other males, and display in flight and on the ground for females, chasing them as well—all energetically demanding activities. A study with marked individuals found that the males slept, in many short bouts, between 2.4 and 7.7 hours each day. The males that slept least sired the most offspring and were most likely to return to the same territory the following year. Later in the season, since the males have no role in incubation or raising the young, their sleep increased to the same levels as in females. For at least a few weeks, however, minimal sleep did nothing to reduce fitness; in fact, it enhanced it (Lesku et al. 2012).

Also at Point Barrow, Semipalmated Sandpipers (*C. pusilla*), in which both sexes incubate, members of a pair replace each other at consistent intervals, but these vary from pair to pair, ranging from twenty-one to nearly twenty-eight hours. For them, the twenty-four-hour circadian cycle is abandoned for at least the weeks of continuous light. Blood samples taken from these sandpipers and also from Red Phalaropes (*Phalaropus fulicarius*) and Snow Buntings (*Plectrophenax nivalis*) sharing this habitat found no detectible levels of melatonin at any hour (Steiger et al. 2013). At 73°N on Bylot Island, Canada, Snow Geese (*Chen caerulescens*) at the beginning of their nesting season rest only 8 percent of the twenty-four-hour day and this in short bouts at any hour (Gauthier and Tardif 1991). Still higher, at Spitsbergen, 77–80°N, Northern Fulmars (*Fulmarus glacialis*) feed at all hours during summer, but more rest on water between 9 p.m. and 6 a.m. The amount of time each fulmar rests, however, is not known (Cullen 1954).

In Antarctica as well, the continuous summer daylight affects sleep patterns. At a colony of King Penguins (*Aptenodytes patagonicus*) on the Crozet Peninsula, birds returning from or departing for the sea spend time sleeping in a resting area away from their breeding territory. They

stand close to one another, with at least two penguins per square meter. The depth of their sleep varies at different hours. At all hours, the walkers prefer to pass near sleepers to avoid being attacked by awakened birds defending their territory. Birds sleep more deeply during the afternoon than in the morning, when more birds are walking about. The morning traffic rouses more neighbors from sleep than the lower-activity afternoons (Dewasmes and Loos 2002).

At lower latitudes in Alaska, Rufous Hummingbirds (*Selasphorus rufus*) require less than all the 20.3 hours of available daylight for feeding, courtship, and nesting. Their total resting time, based on observations that could not distinguish quiet wakefulness from actual sleep, was 4.7–5.7 hours per day. Wintering in Jalisco, Mexico, where midwinter daylight is 11.4 hours, they feed for 10.5–10.9 hours; during the actual night, they are presumed to be sleeping (Calder 1993). Similarly, in Churchill, Manitoba, where summer daylight runs twenty hours, American Tree Sparrows (*Spizella arborea*) are active for less than eighteen hours (Baumgartner 1937). Experiments keeping high-latitude Pine Grosbeaks (*Pinicola enucleator*) and Common Redpolls (*Acanthis flammea*) at constant levels of low light found that they shifted their sleep phase from a single period to two or three (Palmgren 1949).

Seasonal Shifts

Birds living year-round at one latitude also have seasonal sleep patterns. As with migratory species, among sedentary birds there is no absolute amount of time they require for sleep. European Starlings in Germany sleep 7.5 hours per day during summer and 12.5 hours in winter, and in summer take naps at midday. Experiments with starlings kept in semi-natural conditions showed that REM sleep averaged only 1.3 percent of total annual sleep time and was most extensive during winter nights (van Hasselt et al. 2020).

Blue Tits (*Cyanistes caeruleus*) in southern Germany sleep 4.8 hours longer in winter than in spring. From November through January, they begin to sleep after sunset; in February and March somewhat before sunset; and in April, when the days were much longer and they were feeding

young, again at sunset. Throughout the study period, the birds woke up each morning after the start of civil twilight but before sunrise. Individuals monitored through the night woke up between sleep bouts 23 to 230 times, but this did not change seasonally (Steinmeyer et al. 2010).

A comparison of several British tits found that, throughout the year, the smallest species were the first to leave their roost site in the morning and the last to enter it at the end of the day (Perrins 1979, p. 123). This is probably because they need more time to feed to maintain their high metabolic rate, since heat dissipates faster from small bodies than larger ones. In winter, when foraging hours are most reduced and energetic demands are highest, the smallest birds must make the most of all the time they have to find food. Small birds like tits, which are active through all the daylight hours because their food source and foraging method require it, are more likely to have a single, long sleep session when they cannot forage.

Influence of Food Availability

This contrasts with birds such as raptors and carcass scavengers that are active only intermittently during the day, because their food comes in large packages or unlimited quantities. Raptors and scavengers—vultures, storks, and some gulls—may spend hours of the day perched and immobile, in a mix of quiet wakefulness and actual sleep. At Lake Naivasha, the African Fish Eagle (*Haliaeetus vocifer*), which hunts only by day, spends 94 percent of daylight hours perched, and the night as well; actual fishing time is often less than eight minutes per day (Brown 1980, p. 53). A similar condition can be created in the laboratory: pigeons with unlimited food slept 37.7 percent of a twelve-hour light period and 81.6 percent of a twelve-hour dark period (Tobler and Borbély 1988). Likewise, birds that have to travel far from their nest to forage but capture large items may also spend much of the day resting or sleeping. During the breeding season, Northern Gannets (*Morus bassanus*) spend 50 percent of their time asleep while at or near their nest at intervals during the long daylight hours and through most of the night (Mowbray 2002).

Shorebirds in tidal environments, especially those that probe for food rather than searching visually and therefore can forage at night, have a sleep regime governed by tides rather than the sun. They are often polyphasic sleepers, with discontinuous rest periods. Just as with the birds that sleep less during the seasons of longer daylight—including many of the same Arctic-nesting shorebirds—so they may during other seasons on an almost daily basis adjust their hours of sleep in response to feeding opportunities made possible by the tides. Over the course of the year, the extent, timing, and regularity of their sleep changes in response to local conditions. For shorebirds, and likely for other birds as well, age and the experience that comes with it may also influence resting time. Among Bristle-thighed Curlews (*Numenius tahitiensis*) wintering on Laysan Island, adults spend more than 80 percent of daylight standing still, sleeping, or preening, while those in their first year spend 61 percent of daylight performing these activities (Marks et al. 2002).

Sleep Postures

Head and Neck

Most of the nonlaboratory information on bird sleep comes from knowing the characteristic postures birds assume in different stages of sleep and how these differ from the ways birds stand, sit, perch, or float while awake. Many birds begin sleep with the neck relaxed and the head facing forward, sunk between the shoulders. This is the most vigilant posture for most birds; at any distance, they may look awake to a potential predator, even more so if they are sleeping with one eye open. Some birds, including grebes, storks, hornbills, and pigeons, always sleep this way (Thomson 1964, p. 710). Hummingbirds do as well, with the bill tilted upward (Skutch 1973, p. 58).

Many other birds, when feeling secure, then turn their neck so that the head rests on the back, often with the bill buried in the scapular feathers. Birds can maintain both the head-back and the head-forward positions when they are standing, sitting, perched, or on water. The head-back posture reduces heat loss from the head and neck, but is a

more vulnerable position, even when the bird has an eye open. When geese sleep with their head facing forward, their muscle tone is higher than when the head rests on the back. They may be in SWS or REM when in either position, but when facing forward in REM, the head drops. Even when the head is supported on the back, and neck muscles are relaxed, however, REM is very brief, with more than 90 percent of REM episodes lasting less than ten seconds, and REM comprising only 10.2 percent of total sleep time (Dewasmes et al. 1985). Some birds, including Eurasian Blackbirds only turn their head back when sleeping in darkness, which may likewise be when they are least vigilant (Szymczak et al. 1983).

The evolutionary antiquity of sleeping with the head turned to rest on the back has been demonstrated by two recent, separate discoveries of fossils of a newly described species of small non-avian dinosaur, *Mei long*, in the same position. They were found in the lower Yixian Formation in Liaoning Province, China (*mei* is Chinese for “to sleep soundly,” *long* means dragon). Each is about 53 cm in length, the same size as *Archaeopteryx lithographicus*, the most ancient of known fossil birds, and was preserved in volcanic ash or mud of an early Cretaceous formation 128–139 million years old. Both sit on their hind limbs, with their forelimbs directed rearward (as are bird wings), the neck curved back, and the head resting on the side of the body. While *Mei long* is not an ancestor of birds, the posture with the body and limbs compressed suggests that it too was warm-blooded and had the head against the back to reduce heat loss (Xu and Norell 2004; Gao et al. 2012).

Birds that normally perch by clinging to vertical surfaces sleep with the head forward or back. Woodpeckers, with stiff tail feathers, use these as well as their feet to cling to a tree trunk or the wall of a cavity; several species have been observed with their head back among their shoulder feathers (Villard 1999). Among passerines, the Rock Wren (*Salpinctes obsoletus*) is known to roost on vertical rock faces, propped up by its tail (Brewer 2001, p. 109). Other songbirds living in similar environments, or like tree-creepers and the Neotropical woodcreepers feeding on the trunks of trees, may do so as well. Carolina Parakeets (*Conuropsis carolinensis*) observed by Alexander Wilson and John James

Audubon slept in tree cavities, clinging vertically, with their bill hooked into the cavity wall and feet pressed against it (Snyder and Russell 2002). Swifts, which have relatively short necks, sleep with the head facing forward. Those with stiff tail feathers use these to brace themselves, while the Black Swift (*Cypseloides niger*), which, unlike the rest of its congeners and many other swifts, lacks very stiffened rachises, holds its body away from the rock wall on which it rests (Marin and Stiles 1992).

Most of the birds that sleep on water, such as waterfowl and gulls, also sleep on land, and use the same familiar positions—albeit they are less likely to turn their head to their back if in water with waves or any turbulence. Loons, which normally never set foot on land except on their nest, also sleep with the head on their back. Grebes, similarly aquatic, have distinctive resting postures. They face forward, tucking their bill between the feathers at the base of the neck, most often to the right. One foot, usually on the side where the head rests, may be tucked under the wing to conserve heat. Grebe chicks may turn their head backward, which may recall the way the neck was bent when still in the egg (Fjeldså 2004, p. 78).

Legs and Feet

A posture unique to birds is sleeping on one leg. Birds in many families do it, including some small songbirds, but unipedal standing, when awake or asleep, is best known in storks, flamingos, waterfowl, and shorebirds. It is also seen frequently in herons, hawks, gulls, and owls. Sleeping waterfowl standing on one leg rest their head on the opposite shoulder, while flamingos put the head on the same side as the supporting leg. The benefits or functions of this posture may include reduced muscle fatigue (by shifting weight from one leg to the other) and heat retention, especially if the retracted leg and foot are held among the belly feathers (Clark 1973).

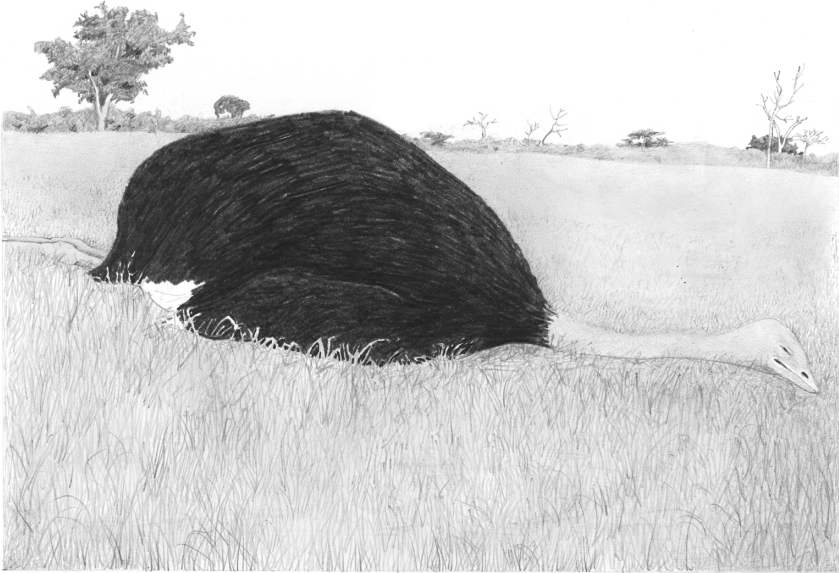
Observation of a flock of captive Caribbean Flamingos (*Phoenicopterus ruber*) at the Philadelphia Zoo showed that they stood unipedally more often at lower temperatures. Conversely, flamingos in the wild in

extremely hot environments will lose more body heat with both legs exposed. Another benefit of unipedalism for wild flamingos living in extremely salty or alkaline water is that keeping one leg off the ground some of the time may reduce parasitism and general tissue exposure. The Philadelphia birds were bipedal in windier conditions, because that increased their stability. There was no difference in the length of time resting in one position or the other, suggesting that, for these birds, muscle fatigue from bipedalism was not a factor (Bouchard and Anderson 2011). Resting on one leg is not fatiguing either, which is important if this posture is used during sleep. Specialized structures of the flamingo's limb lock the knee and hip of the supporting leg without any muscular activity (Chang and Ting 2017).

It is likely that a similar mechanism operates for other long-legged birds that often rest unipedally. The thermal benefits have been demonstrated for shorebirds. On the coast of southern Victoria, Australia, observation of nine species from four families, a mix of Eurasian winterers and locals, showed that the longer-legged species roosted more often on one leg than the smaller ones, and six of the nine increased unipedal roosting to over half the time as temperatures decreased. For the smallest and lightest in weight of the sandpipers in these aggregations, balancing on one leg may be more difficult if there is any wind than it is for larger, heavier species (Ryeland et al. 2019). When the temperature is 30°C or above, however, some shorebirds shift to bipedal standing, and those with long bills, such as Dunlin (*Calidris alpina*) also hold the head forward so that heat can be lost through the exposed bill as well as through both legs (Playà-Montmany et al. 2023).

Passerines also sometimes sleep while standing on one leg. British finches, with many cold months to every year, sleep with their head turned back and tucked beneath the shoulder feathers, their body feathers fluffed, and often with one leg raised into the feathers (Newton 1973, p. 130). A Eurasian Blackbird fitted with EEG monitors was on one leg 68.2 percent of the time it was in REM sleep, and 43.9 percent of that time the bird had its head on its back (Szymczak et al. 1993).

Other birds with long legs have several distinctive sleep positions. Standing Painted Storks (*Mycteria leucocephala*) of India and Southeast



Ostriches in brief episodes of REM sleep lose all musculature coordination in the head and neck, which then come to lie on the ground.

Asia often rest on one leg and clasp the tarsus of that leg with the other foot (Hancock et al. 1992, p. 56). Ostriches and rheas sometimes sit with their legs underneath them and their head erect. Other times, they may extend their legs behind them. When their head is erect, ostriches are in SWS, sometimes with one eye open, giving the impression of alertness and maintaining some visual processing. In the transition to REM sleep, both eyes close and the head falls forward, sometimes to the ground. At the end of a REM bout—which, unlike in other birds, may last up to five minutes—muscle tone is restored and they raise their head (Lesku et al. 2011). The Greater Rhea (*Rhea americana*) similarly sometimes holds its head erect or extends its neck on the ground while sleeping, but more often it folds the neck in a tight S-curve, with the nape resting on the back or the base of the neck (Davies 2002, p. 199).

Storks and plovers, which rest most of the time while standing, will also half-squat, putting their weight on their tibio-tarsal joints (Campbell

and Lack 1985, p. 104). Among the birds that squat fully are the New World vultures, harriers (which sometimes lie down), and the Secretary-bird (*Sagittarius serpentarius*). All of these except the vultures bury their head in the scapulars when in deep sleep. For the vultures, with their unfeathered head and neck, keeping the head forward may be a way to prevent any parasites acquired when feeding on carrion from reaching feathered areas—the unfeathered head and neck of both New World and most Old World vultures in itself being an adaptation to reduce parasite load (Brown and Amadon 1968, p. 46). Among Old World vultures, the Bearded Vulture or Lammergeier (*Gypaetus barbatus*) sleeps while resting on its belly, with the feet covered by feathers and the head and neck hunched; it does not lie down (Mundy et al. 1992, p. 209). Young birds of many kinds squat by resting on their breast, and adults may do so as well when feeling particularly free from danger; this is seen most often in gallinaceous birds, gulls, and babblers (Thomson 1964, p. 285).

Perching

The general understanding is that birds can sleep while grasping a perch because the stretching of tendons between the ankle and the toes when the leg is flexed causes the toes to curl tightly, with no muscular effort. The more the leg muscles relax, as in REM sleep, the more tightly the toes grip the perch. This has not been tested experimentally, however, and close examination of the legs in some sleeping perching birds shows that this is not always so. Sleeping European Starlings only slightly flex the knees and ankles, and the distal two-thirds of their toes are not flexed to grip a perch. The birds are then balancing their weight over the central pad of their feet—unlike when awake and the toes actively grasp a perch. Starlings that had the relevant tendons or the locking mechanism removed surgically were not able to flex their toes perched in the same manner when sleeping. In other experiments, starlings that inhaled an ether anesthetic were not able to remain perched, indicating that the locking mechanism prompted by the stretched tendon was not in fact automatic (Galton and Shepherd 2012).



Sleeping Blue-crowned Hanging Parrots blend in with the foliage around them at the tips of slender branches, where they are already harder to reach by predators and can easily fly off if disturbed.

Whether or not the toes are actually grasping a perch tightly, on many birds the toes have another feature that keeps a perched bird steady, awake or asleep. Birds that routinely grasp twigs or similar structures usually have a rougher underside of the toes than birds that normally stand on flat surfaces. This is true not just in “perching birds,” the Passeriformes, but others as well. Among the ground-dwelling tinamous of the Neotropics, the species that roost on the ground have smooth undersides to the tarsi while those that ascend to trees to sleep have rough ones. There, they do not grip a branch but balance on the rough soles of their feet (Davies 2002, p. 76). As Theodore Roosevelt recounted it, when William Beebe reared the seeds found in the rough tarsi of a Great Tinamou (*Tinamus major*) from Guyana, they were all from arboreal plants (Beebe et al. 1917, p. xi).

Some small parrots sleep while perched hanging upside down. These include the genus *Loriculus*, known in English as the hanging

parrots, with ten species ranging from India to the Philippines and New Guinea, as well as the African lovebird genus *Agapornis*, and several species in Neotropical genera. Hanging upside down requires circulatory and musculature adjustments; these may initially have evolved to enable the birds to reach fruit and nectar while clinging head downward. When the ancestral forms could sustain this position—sleeping among leaves at the end of slender twigs that could not support their weight when erect—it would make them inconspicuous and possibly unreachable by predators. When sleeping at night, the head and neck of *Loriculus* are pulled back into the body, and one foot may be tucked into body feathers. When these parrots rest by day, they are upright, with eyes partly closed and feathers slightly fluffed (Buckley 1968).

Fluffing the Feathers

Since birds lower their body temperature at night, they often fluff their feathers to insulate themselves without expending energy. This augments the energy saving some birds are receiving by covering their bill in the scapular feathers, inserting one leg among the belly feathers, or sitting so that both legs are covered. For birds roosting on the ground in open areas, a different strategy is common. These birds seek a slight depression that insulates them on their sides while they sleek down their feathers to make themselves level with the surface and as inconspicuous as possible. Birds roosting in open areas, whether trying to be less visible or not, face into the wind to avoid having their feathers ruffled and therefore less insulating.

Fluffing the body feathers can serve other functions as well, especially in regions where significant heat loss is not a risk. Alexander Skutch (1996, p. 73) observed several species of antshrikes and antbirds in Panama on their nest at night spread their feathers loosely, thereby obliterating their body form; this could be to prevent nocturnal predators from recognizing the shape of the nest or the bird in it. In Southeast Asia, the Fairy Pitta (*Pitta nympha*) roosts on the ground, standing on one leg and putting its head in the fluffed feathers of the back, looking

like a ball, which may not match any predator's search image of a bird (Erritzoe and Erritzoe 1998, p. 138).

The Hawaiian honeycreepers are an exception to the usual passerine sleeping position of tucking the head in the back feathers and crouching on their feet to cover them or lifting one of them to conceal it. Relatively warm night temperatures and an absence of biting insects and most nocturnal predators may have led to the loss of habits that their mainland ancestors likely had. As a result, when *Culex* mosquitoes and avian malaria arrived on the islands in the nineteenth century, the honeycreepers were especially vulnerable. The extinction of many species and the severe reduction in the populations of the surviving species have been attributed to avian malaria. Introduced Japanese White-eyes (*Zosterops japonica*), which sleep in the typical passerine position, are only rarely bitten by mosquitoes, while the honeycreepers are bitten extensively. At the time this analysis was made, in 1968, honeycreepers were found on the islands only above 600 m, the upper limit of mosquitoes (Warner 1968). More recently, some species have developed a degree of immunity and have repopulated lower elevations—while mosquitoes have advanced to higher elevations, where avian malaria has decimated honeycreepers there. One species, the Hawai'i Amakihi (*Hemignathus virens*), roosts singly rather than in flocks and sleeps with its head tucked behind its back and one foot raised; these habits may have helped reduce its vulnerability (Lindsey et al. 1998).

Eyes

Finally, a few nocturnal birds have eye features used when resting or sleeping during the day. These may deter predators or reduce their conspicuousness. The Northern Pygmy-Owl (*Glaucidium gnoma*) has a whitish lower eyelid that it raises when sleeping, giving the appearance that the owl is awake (Holt and Petersen 2000). Potoos have especially large eyes, most with a bright yellow iris; their upper eyelids have two or three small folds on their edge, creating notches or slits. When the eyes are closed, these small gaps still enable the bird to detect motion. This so-called magic eye may help camouflage the bird, allowing it some

vision while resting or in unihemispheric sleep without keeping the entire eye open as would most other birds (Cohn-Haft 1999, p. 289).

Summary

All animals that have been tested—from jellyfish, mollusks, and insects, to birds and mammals—are known to sleep. Sleep's seeming universality suggests that it arose very early in animal evolution. Its key features include a period of immobility, a characteristic posture, and lower response to external stimuli. Sleep must therefore have benefits that compensate for this vulnerable state. In birds, these include consolidating memory, clearing waste from the brain, and restoring other tissues and bones. It is also a time when they can lower their body temperature, thereby reducing energy expenditure during the period when darkness or other conditions prevent them from finding food to maintain their high metabolic rate.

Avian sleep has many distinctive features. Notable among them is sleep's brevity, typically in bouts of several seconds or a few minutes. In between, birds wake up and may check for any sign of danger then immediately revert to sleep. Two patterns of brain activity have been found in sleeping birds: slow-wave sleep, when electroencephalogram readings show low-frequency, high-amplitude activity, and rapid eye movement sleep, when brain waves are similar to wakefulness, with low-amplitude, high-frequency activity. Duration of each REM episode is much shorter than those of SWS, with muscles more relaxed. Over the hours of sleep, the relative proportion of REM increases. When birds are deprived of sleep, they have more REM sleep at their next opportunity, indicating REM's vital restorative functions. Another avian feature is the capacity to sleep with either one or both halves of the brain shut down. Unihemispheric sleep enables birds to maintain a degree of alertness. The eye opposite the awake part of the brain is open. Unihemispheric sleep occurs only in SWS; the greater relaxation of both brain and muscles in REM makes this impossible and may be among the reasons REM is usually so much briefer than SWS.

The inclination to sleep is governed by several interacting sites, including the retina of the eye, the hypothalamus in the brain, and the

(continued...)

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- Zenaida auriculata*. *See* Dove, Eared
- Zenaida macroura*. *See* Dove, Mourning
- Zonotrichia albicollis*. *See* Sparrow,
White-throated
- Zonotrichia capensis*. *See* Sparrow,
Rufous-collared
- Zonotrichia leucophrys*. *See* Sparrow,
White-crowned
- Zosterops lateralis*. *See* Silvereye