Chapter

11

Sleep in Nonmammalian Vertebrates

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Chapter Highlights

- Despite being distantly related to mammals, birds exhibit sleep states similar to mammalian non–rapid eye movement (NREM) and rapid eye movement (REM) sleep. Avian NREM sleep is characterized by propagating slow waves that are homeostatically regulated in a local, use-dependent manner, as in mammals. However, some of the NREM sleep brain oscillations implicated in processing hippocampal memories in mammals have not been found in birds.
- As in mammals, avian REM sleep is characterized by electroencephalographic (EEG) activation, diminished thermoregulatory responses, rapid eye movements, and recovery following deprivation, as well as its preponderance early in development. However, unlike mammals, reductions in muscle tone are posture dependent and largely restricted to the muscles supporting the head. Birds experience hundreds of short REM sleep episodes every day.
- NREM and REM sleep either evolved independently in mammals and birds or were inherited from their common ancestor. Studies of reptiles, amphibians, and fish have not yet provided a straightforward answer to this question, largely because of unexpected diversity in the way sleep manifests in reptiles and few studies of amphibians and fish. Notably, sleep states comparable (in part) to NREM and REM sleep in mammals and birds have been found in only some species of reptiles.
- Recent EEG-based studies of birds in the wild have revealed an unprecedented ability to perform adaptively in challenging real-world ecologic circumstances, despite forgoing large amounts of sleep.

Insight into the mechanisms and functions of sleep in humans can be gained through examining sleep across the animal kingdom. Research on animals employs either model-based or comparative-based approaches. Model-based approaches aim to gain insight into human sleep through examining animals with mammalian-like sleep that are amenable to experimental manipulation. The utility of a model species is often viewed as limited by the degree to which its sleep mimics that of humans. By contrast, comparative-based research gives equal emphasis to similarities and differences across *all* taxonomic groups in an attempt to reveal overarching principles that may remain obscure using a narrower approach.[1,2] In addition, this comparative approach can reveal adaptations in unusual animals that inspire new perspectives on sleep in humans. For instance, the recent discovery that poor sleep on our first night in a new environment (i.e., "the first-night effect") is attributable to lighter sleep in parts of the left hemisphere[3] was inspired by ecologically based research on sleep in ducks.[4,5]

In this chapter, we summarize comparative sleep research focused on avian and nonavian reptiles (the latter hereafter referred to as *reptiles*) and amphibians. We also discuss one recent study on zebrafish that has direct bearing on the evolution of sleep states in vertebrates. The evolutionary relationships between these groups are summarized in Box 11.1, and the comparative neuroanatomy of vertebrates, as it relates to the later discussions, is reviewed in Box 11.2.

AVIAN SLEEP

Sleep States

Birds exhibit two sleep states in many respects similar to mammalian rapid eye movement (REM) and non–rapid eye movement (NREM) sleep (Figure 11.1). Wakefulness and NREM sleep, also called slow wave sleep (SWS), are distinguished primarily by the presence of high-amplitude, slow waves with a peak frequency around 2 Hz in electroencephalography (EEG)[6-12] and intra-"cortical" local field potential (LFP) recordings of the hyperpallium (primary visual cortex; Box 11.2) during NREM sleep (Figure 11.2).[13] Although intracellular recordings have not been reported during natural sleep in birds, under anesthesia, pallial neurons show slow oscillations between hyperpolarized "down states" without action potentials and depolarized "up states" with action potentials[14] similar to those described in mammals during anesthesia and natural NREM sleep.[15] The few recordings from birds suggest that the frequency of the oscillation may be higher (1–2 Hz) than in mammals (<1 Hz). During NREM sleep in pigeons (*Columba livia*), LFP slow waves usually originate within and propagate through the hyperpallial regions that receive visual input via the thalamic lateral geniculate nucleus (Figure 11.2).[13] As propagating slow waves have been described in humans and other mammals,[16] they are a fundamental property of NREM sleep.

BOX 11.1 EVOLUTIONARY RELATIONSHIPS OF VERTEBRATES

Our interpretation of the evolution of sleep states in vertebrates depends on an accurate understanding of their phylogenetic relationship. Mammals, birds, and reptiles last shared a common ancestor as recently as 320 million years ago (mya).[135] Although the exact identity of this ancestor is unknown, paleontologists refer to it as the "stem amniote" because the production of amniotic eggs distinguishes mammals, birds, and reptiles from amphibians and fish, which produce anamniotic eggs. The stem amniote, a reptile-like (reptiliomorph) animal, gave rise to two lineages: the synapsids, leading to the evolution of mammals (monotremes, marsupials, and eutherians [formerly placentals], and the sauropsids, giving rise to reptiles, a lineage that includes birds.

Within mammals, monotremes and therian mammals (marsupials and eutherians) diverged 166 mya. Among the living reptilian groups, birds are most closely related to crocodilians,[136] both being members of a group called Archosauria. Fossil evidence indicates that within Archosauria, birds evolved from flightless, feathered theropod dinosaurs more than 150 mya.[137] Living birds include two groups, the Palaeognathae (large flightless ostriches, emus, rheas and cassowaries, the much smaller flightless kiwis, and volant tinamous) and Neognathae (all other birds), which diverged 72 mya.[138] Within Palaeognathae, flightlessness secondarily evolved several times, with only tinamous retaining the ancestral ability to fly.[101]

Contrary to the early view that turtles represented the most basal type of reptiles, recent genetic data indicate that turtles are more closely related to Archosaurs.[139] Instead, Lepidosaurs (lizards and snakes) represent an early split from the lineage that gave rise to turtles and Archosaurs. Finally, amphibians and amniotes last shared a common ancestor 338 mya, and the last common ancestor shared between tetrapods (amphibians and amniotes) and zebrafish, an emerging species in comparative sleep research, lived 430 mya.

Finally, it is important to note that all animals alive today have undergone evolution for the same amount of time.[140] When fish and the ancestor to tetrapods split 430 mya, both lineages continued to evolve. It is also important to recognize that the phenotypes of extant species reflect a mosaic of primitive, derived, convergently evolved, and evolutionarily lost traits.[2,98,101,141,142] Consequently, conclusions about the evolution of sleep drawn from a single species can be misguided by idiosyncrasies of that species' evolutionary history.[40,106] To distinguish between possible evolutionary scenarios and truly identify primitive and derived sleep phenotypes, several species within all taxonomic groups must be examined whenever possible. Only then will we be able to tease apart the evolution of sleep and the functional implications of its diversity.

Despite these similarities, thalamocortical spindles, a prominent feature of mammalian NREM sleep, have not been detected in EEG recordings in birds.[13,17-26] Early reports of spindles proved to be artefacts from intermittent high-frequency oscillations of the eyes occurring during NREM sleep, REM sleep, and wakefulness[27] (Figure 11.1), which are thought to keep the poorly vascularized avian retina oxygenated.[28] Recently, van der Meij and colleagues used intracerebral LFP recordings of the hyperpallium and thalamus to determine whether spindles might have been missed in the previous (epidural) EEG recordings; however, spindles were not detected.[13]

Hippocampal activity during NREM sleep also appears to differ between mammals and birds. In mammals, the hippocampus exhibits sharp-wave ripples (SWRs), large bursts of synchronous activity, which occur during NREM sleep, as well as while grooming, feeding, and pauses in ambulation in rodents.[29] The few studies that examined hippocampal activity in birds did not report SWRs during wakefulness nor NREM sleep.[22]

As with NREM sleep, avian REM sleep (Figure 11.1, *B*) shares many features with mammalian REM sleep. Avian REM sleep is characterized by EEG activation similar to that occurring during wakefulness.[30,31] However, in contrast to mammals, a hippocampal theta oscillation has not been observed during REM sleep in birds.[10,21-23,25,30-35] EEG activation during avian REM sleep is associated with rapid eye movements and twitches of the bill, wings (unpublished data), head, and body,[19,23,36-38] closure of the eyes (if they were open during preceding NREM sleep),[a] and elevated arousal thresholds when compared with NREM sleep.[25,26,37,41] Changes in respiratory and heart rates between NREM and REM sleep vary considerably among the species examined.[25,42,43]

Behaviorally, REM sleep is typically accompanied by head drops.[b] Drooping of the wings[34] and swaying[11] and tipping of the body[23] have also been observed in standing birds. The behavior of the head depends (in part) on its position at the start of a REM sleep episode: when it is facing forward and unsupported it drops, whereas when the head is turned backward, resting on the bird's shoulder, it may slide off the shoulder or not move at all.[19,24,42] When the head is fully supported on the back, it remains still during REM sleep.[42] Despite the head drops reported in several species, the neck electromyogram (EMG) shows either no change from preceding NREM sleep or only partial reductions (hypotonia) in muscle tone.[c] Mammal-like atonia has been observed only in domestic geese (*Anser anser domesticus*).[42] As in other birds, when geese enter REM sleep with the head facing forward and unsupported, it drops and the neck EMG shows hypotonia or no change; however, mammal-like atonia occurs when the head is fully supported on the back (Figure 11.3).[42] As the duration of REM sleep episodes does not depend on head position,[42] this posture-dependent difference in neck muscle tone is due to other factors. In many species, rather than dropping unabated, the head drops in a slow and controlled manner, often interrupted by pauses.[d] In addition, slow raising of the head can also occur during REM sleep.[11,50] This, and the posture-dependent differences in tone observed in geese, suggest that competitive processes are acting on the neck musculature, one driving reduced tone, and one seemingly limiting or controlling the drop of the unsupported head.[42] Finally, the fact that the head can drop, even when the single EMG recording shows no reduction in activity,[e] indicates that the methods previously used to measure neck muscle tone fail to reflect the full dynamics of muscle tone regulation in birds.

Unlike mammals, birds can engage in REM sleep while standing, even while balancing on one foot. Contrary to the long-held idea that birds rely on a passive locking mechanism in their feet and legs to stand during sleep, recent work in common starlings (*Sturnus vulgaris*) suggests that they need

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[a] References 10, 11, 23, 26, 32, 39, 40.

[b] References 8, 11, 12, 25, 26, 35, 36, 38-41, 44-47.

[c] References 17, 20, 24-26, 30, 32, 39, 40, 47-49.

[d] References 17, 18, 20, 26, 47, 50.

[e] References 20, 23, 25, 26, 35, 45.

BOX 11.2 COMPARATIVE NEUROANATOMY

Interpreting the similarities and differences between sleep in vertebrates requires an understanding of brain evolution. Many of the subcortical nuclei that regulate sleep and wakefulness are conserved between zebrafish and mammals.[143] By contrast, the organization of forebrain pallial neurons has diversified during vertebrate evolution.[135] Although sauropsids lack the six-layered neocortex found in mammals, their forebrains contain homologous pallial neurons organized in a different manner. Based on gene expression profiles and connectomics, amniotes share three general types of pallial neurons: input neurons that receive projections from the thalamus, intratelencephalic projecting neurons, and output neurons that project from the pallium to other brain regions.[135,144]

It is currently debated whether most pallial neurons in sauropsids are homologous to mammalian neocortical neurons, or if only some sectors of their pallia are homologous to the neocortex and others to the pallial claustrum and amygdala.[144-147] This is due (in part) to the manner in which the pallial neurons are organized. The embryonic dorsal pallium, which forms much of the neocortex in mammals, gives rise to the dorsal cortex in reptiles, a three-layered laminar structure.[148] In birds, the dorsal cortex present in their reptilian ancestors evolved into the hyperpallium, or Wulst, a bulge on the dorsal surface of the brain composed of several nuclei stacked one on top of the other.[135,145,146,148] Unlike the reptilian dorsal cortex and the mammalian neocortex, the hyperpallium lacks pyramidal neurons with apical dendrites extending across the layers and toward the surface of the brain; instead, the avian pallium comprises stellate neurons. Although the hyperpallium is involved in processing visual, somatosensory, and olfactory information, most of this region is dedicated to processing visual input from the thalamic lateral geniculate nucleus and therefore is considered functionally homologous to the mammalian primary visual cortex (V1).[148]

In addition to the differences in pallial cytoarchitecture in the dorsal pallium, sauropsids have a brain region called the dorsal ventricular ridge (DVR), a large nuclear structure protruding medially into the lateral ventricle that is not present in mammals, amphibians, or fish.[135] It is still actively debated whether the DVR is homologous to portions of the neocortex or to the claustrum and pallial amygdala. The transcriptomic profiles of DVR neurons have been interpreted as supporting both hypotheses to varying degrees.[135,144,145,149-152] Embryological studies indicate that the DVR develops from the lateral and ventral pallia, regions that give rise to the claustrum and pallial portions of the amygdala in mammals.[147] By contrast, connectomics suggest homology between the DVR and neocortex, with subpopulations of the neurons corresponding to specific layers[152] or, more generally, to specific neuron types (i.e., input, intratelencephalic, and output) in the neocortex.[135,145]

Regardless of which scenario is correct, there is a general consensus that the DVR is involved in performing functions similar to those handled by the neocortex. Although the crocodilian DVR has subregions similar to those making up the avian DVR (mesopallium, nidopallium, and endopallium),[145,153] the DVR reaches its largest size in birds, in which it has been most extensively studied.[154,155] In birds, the independent evolution of large brains comparable in relative size to those in mammals,[156] is due, in large part, to expansion of the DVR.[153,157] Remarkably, the density of neurons in the avian pallium, which mostly comprises the DVR, actually exceeds that of primates with similar-sized brains.[158] The DVR includes primary and secondary sensory (visual and auditory) areas, as well as high-order association regions involved in performing complex cognitive processes, including those performed by the mammalian prefrontal cortex.[154,155,159] Indeed, despite lacking the laminar arrangement of neurons, the avian brain generates complex behaviors in some cases comparable with those performed by primates, including the manufacture and use of tools.[1,154]

to actively maintain some muscle tone to stay upright.[51] Consequently, during REM sleep birds sustain tone in the muscles required to balance while standing,[47] as well as those that actively hold the other foot up. Taken together with the data from geese described previously, this suggests that in contrast to the centralized, largely global regulation of skeletal muscle atonia observed during mammalian REM sleep,[52] muscle tone during avian REM sleep is regulated in a local manner.

Episodes of REM sleep are very short in birds. For 23 species from 9 orders, REM sleep bouts last 11.5 ± 7.8 seconds (mean ± SD). However, the species with the six highest values (mean 22.7 ± 7.1 seconds) originate from one research group. When these unreplicated values are excluded, the mean drops to just 7.6 ± 2.1 seconds.

Transitional States

Quantifying the exact time spent in NREM and REM sleep poses several challenges. This is largely due to the fact that birds engage in hundreds of transitions between states every day. Given that transitional states by definition contain features of the state being exited and the state being entered, they are prone to subjectivity during scoring.

Transitional states have been scored using various approaches. Drowsiness is a poorly defined and inconsistently used behavioral state typically characterized by frequent blinking of the eyes and small head movements occurring in conjunction with slow wave activity (SWA) intermediate between unequivocal wakefulness and NREM sleep and/or SWA rapidly fluctuating between waking and NREM sleep levels.[*] One study also defined a short-lasting intermediate sleep state with spectral features between wakefulness and NREM sleep or NREM and REM sleep that occurred during transitions between states, including REM sleep.[9] Similar transitional states are common in birds because of the daily occurrence of hundreds of short bouts of REM sleep.[†] How these transitional epochs are handled undoubtedly has a large influence on the amount of REM sleep scored.[17] Given these scoring issues, comparative studies based on data from multiple species and laboratories[6,9,55] should be interpreted with caution.

Eye States

Birds rarely close their eyes while awake. However, some species exhibit levels of EEG SWA (typically, 0.5–4.5 Hz spectral power) comparable with NREM sleep during extended periods of immobility with their eyes partially or fully open,[11,23,26,32,39] a state also observed in some mammalian species.[56] This state has been variably categorized as quiet wakefulness, drowsiness,[7] or NREM sleep,[10,39] in some cases

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[*] References 7, 8, 17, 25, 41, 44, 48.

[†] References 9, 17-20, 23, 26, 32, 35, 39, 53, 54.

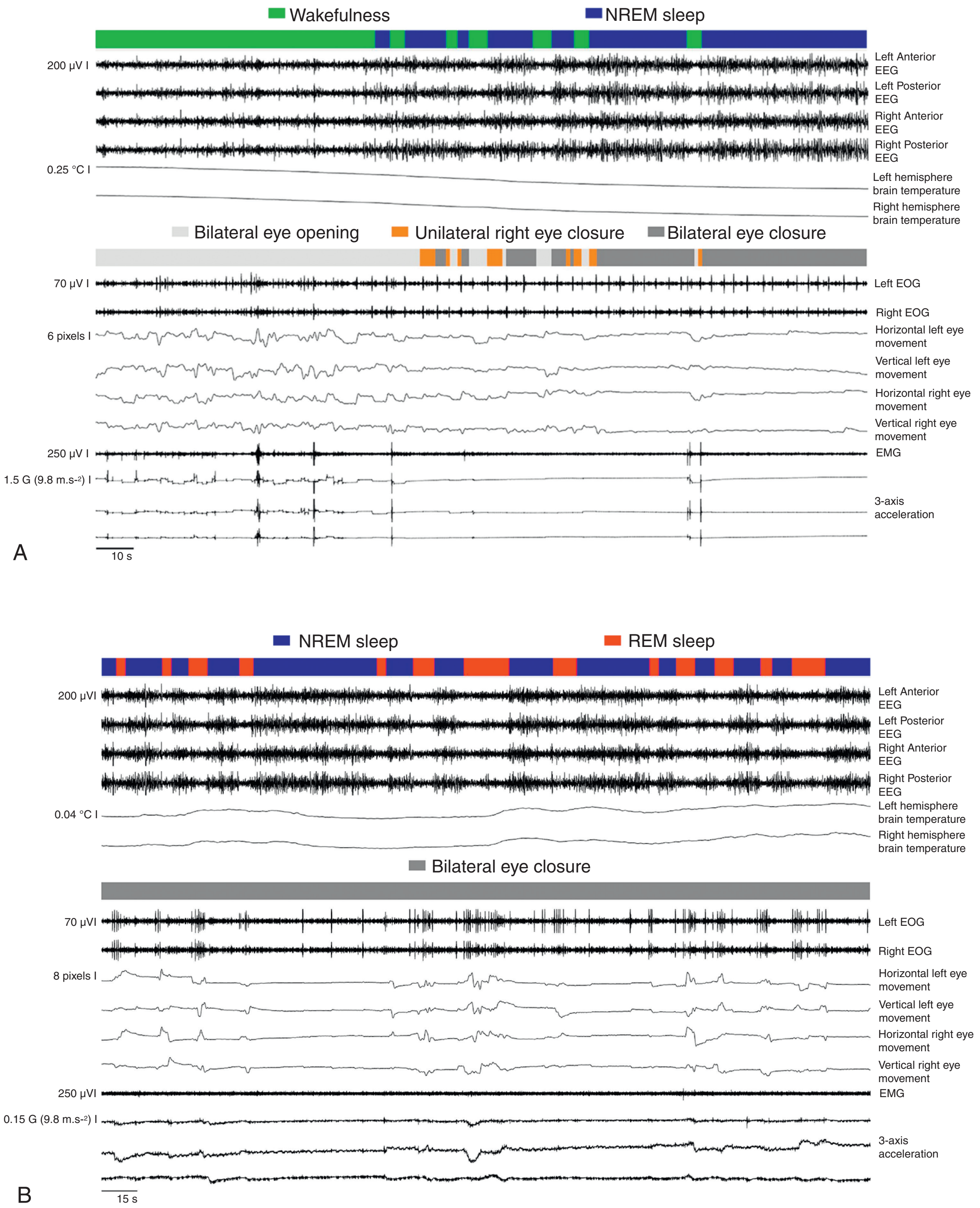

Figure 11.1 Avian sleep states. **(A)** Transition from wakefulness to non-rapid eye movement (NREM) sleep, and **(B)** alternations between NREM and rapid eye movement (REM) sleep in a pigeon. *Top bar,* Hypnogram showing wakefulness (*green*), NREM sleep (*blue*), and REM sleep (*red*); electroencephalogram (EEG) recorded from the anterior and posterior hyperpallia of the left (L) and right (R) hemispheres; brain temperature recorded from the L and R hyperpallia; eye state, both open (*light grey*), both closed (*dark grey*), and left open and right closed (*orange*); electrooculogram (EOG) recorded from the L and R eyes band-pass filtered (25–39 Hz) to show occurrence of high-frequency eye oscillations present in all states; L and R eye movements along horizontal and vertical axes defined relative to the plain of eyelid closure calculated from pupillometry (positive increases in signal values represent rostral and dorsal movements, respectively); neck electromyogram (EMG); head movements along three axes recorded with an accelerometer. Trace duration: A = 210 s and B = 320 s. (From Gianina Ungurean, unpublished data.)

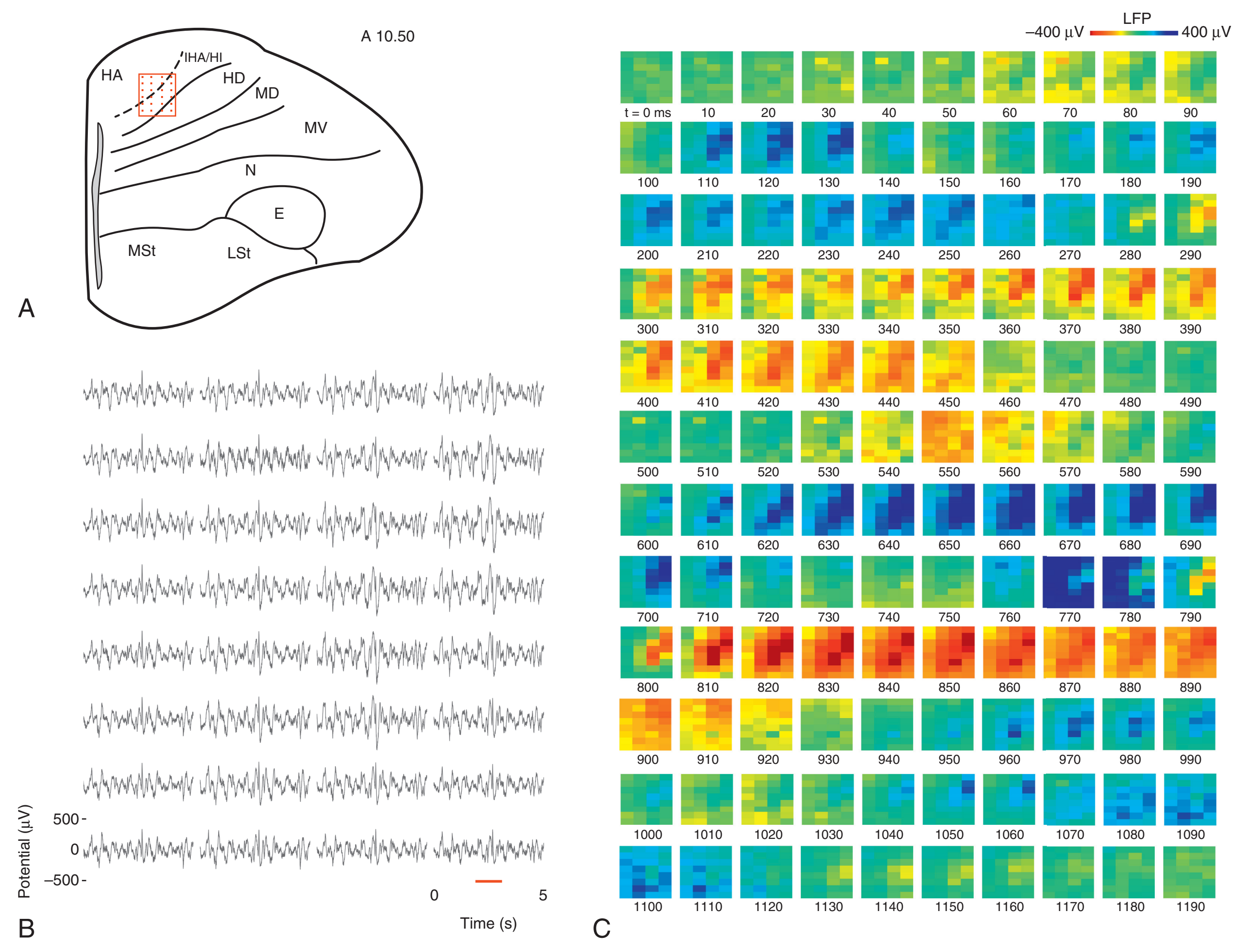

Figure 11.2 Neurophysiology of the avian "primary visual cortex" (hyperpallium) during non-rapid eye movement (NREM) sleep. **(A)** Position of a 32-channel silicon electrode grid (*red*) in the hyperpallium of a pigeon (*medial, left* and *dorsal, top*). Input from the avian lateral geniculate nucleus (LGN) projects primarily to the interstitial part of hyperpallium apicale (*IHA*) and the hyperpallium intercalatum (*HI*). The underlying hyperpallium densocellulare (*HD*) receives relatively little input from the LGN. The hyperpallium overlies and is interconnected with the dorsal and ventral mesopallium (*MD* and *MV*) and nidopallium (*N*). **(B)** Five-second example of local field potentials (LFPs) showing the spatial distribution of slow waves in the hyperpallium during NREM sleep. **(C)** Propagating slow waves during NREM sleep: *red underlined* 1.2-second episode from panel **(B)** is visualized in a sequence of image plots where pixels represent electrode sites and electrical potential is coded in color. Both negative and positive potentials are largest in amplitude in the thalamic input layers. They also propagate most prominently within these layers and, to a lesser extent, the overlying hyperpallium apicale (HA). E, Entopallium; LSt, striatum lateral; MSt, striatum medial. (Reproduced from van der Meij J, Martinez-Gonzalez D, Beckers GJL, et al. Intra-"cortical" activity during avian non-REM and REM sleep: variant and invariant traits between birds and mammals. *Sleep.* 2019;42:zsy230.)

with the qualification that the eyes are open.[11] Despite this awake-like behavior, these slow waves appear to reflect NREM sleep because they often terminate with a transition to REM sleep characterized by closure of both eyes, behavioral signs of reduced muscle tone, and EEG activation.[11,24,26,32] By keeping their eyes open while exhibiting EEG slow waves, birds may be able to maintain some responsiveness to threatening visual stimuli in the environment while still obtaining some of the benefits of NREM sleep.

A trade-off between visual vigilance and NREM sleep processes is suggested by birds sleeping with only one eye open. Many birds often engage in unilateral eye closure, a behavior associated with high levels of SWA in the hemisphere contralateral to the closed eye, and SWA levels intermediate between unequivocal wakefulness and NREM sleep with closed eyes in the hemisphere contralateral to the open eye.[4,5,9,21,57-61] This state has been referred to as asymmetric SWS (ASWS) or unihemispheric SWS (USWS).[61] Birds are able to switch between bihemispheric SWS (BSWS) with both eyes closed and ASWS with one eye open in response to ecologic demands for wakefulness.[4,5] In mallards (*Anas platyrhynchos*), when compared with individuals flanked by other birds, the ratio of SWS with one versus both eyes closed increases when the birds are positioned at the edge of a group.[4,5] Moreover, when sleeping with one eye open, mallards at the edge direct the open eye away from the other birds, as if watching for approaching predators. This, and the finding that the open eye is responsive to threatening visual stimuli, suggests that sleeping with one

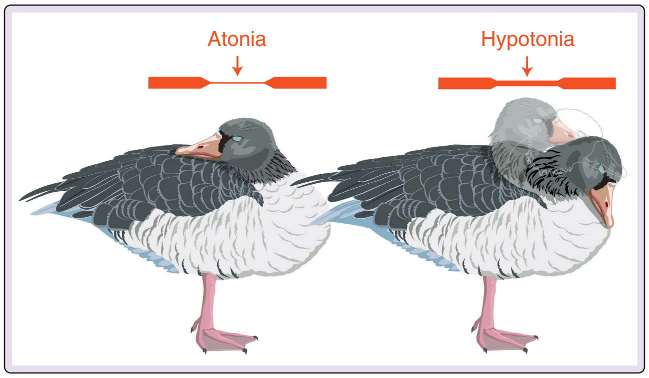

Figure 11.3 Posture-dependent regulation of muscle tone during rapid eye movement (REM) sleep in geese. Like many other birds, geese can engage in REM sleep while balancing on one foot. The head can face backward, supported on the bird's back (*left bird*) or forward and unsupported (*right bird*). When the head is supported, it usually remains still, and the neck electromyogram (EMG) shows atonia. By contrast, when the head is unsupported, it drops in a controlled manner and the neck EMG shows hypotonia. Birds only occasionally show behavioral signs of reduced tone in the muscles involved in holding the wings against the body and balancing on one foot. (Illustration by Damond Kyllo based on Dewasmes G, Cohen-Adad F, Koubi H, et al. Polygraphic and behavioral study of sleep in geese: existence of nuchal atonia during paradoxical sleep. *Physiol Behav.* 1985;35:67–73.)

eye open reflects a visually based anti-predator strategy.[4,5,60,62] (Reptiles also keep one eye open and on the lookout in risky situations, although the neural correlates of this behavior have not been systematically investigated.[59,63-65]) The fact that mallards at the edge of the group only open one eye, rather than both, suggests that a trade-off exists between visual vigilance and processes linked to EEG SWA. Consequently, NREM sleep with both eyes open may reflect a similar strategy used when threats are perceived in all directions.

NREM Sleep Regulation

In mammals, the level of EEG SWA during NREM sleep increases as a function of time spent awake and decreases as a function of time spent in NREM sleep. This relationship, and the positive correlation between SWA and arousal thresholds,[66] suggest that SWA reflects homeostatically regulated processes occurring during NREM sleep. Although a direct link between the level of NREM sleep SWA and arousal thresholds has not been determined in birds (but see the work by Szymczak and colleagues[43]), the temporal pattern of SWA suggests that NREM sleep is more intense early in the night in diurnal songbirds.[8,43,44] In pigeons, however, changes in NREM sleep SWA across the night are either absent[7,11,67]or weak,[10] possibly because of their propensity to take frequent naps across the day.[67] Although pigeons that are sleep deprived by gentle handling for 24 hours did not show an increase in SWA during recovery NREM sleep,[11] depriving them of daytime naps for 8 hours resulted in a significant increase in SWA during recovery sleep at night.[10] An increase in NREM sleep SWA was also observed after 4 to 8 hours of nighttime sleep deprivation in songbirds,[8,68] suggesting that this is a general feature of avian sleep.[69]

Berger and Phillips[7] reported that constant light suppressed sleep greatly in pigeons for up to 74 days but failed to cause an increase in SWA when the birds were switched to constant dim light. However, when quantified irrespective of scored sleep state, SWA in pigeons kept in constant light was maintained at 94.5% of the level occurring during the 12:12 light:dark schedule.[7,8,10] Consequently, it is perhaps not surprising that SWA did not increase in dim light.

Local NREM Sleep Homeostasis

Lesku and colleagues used unilateral visual stimulation and total sleep deprivation to determine whether NREM sleep-related SWA is homeostatically regulated in a local, use-dependent manner in birds (Figure 11.4).[70] In contrast to the symmetric increase in SWA observed after sleep deprivation without asymmetric visual stimulation,[10] a pronounced asymmetry in SWA was evident during recovery NREM sleep with the hyperpallium previously visually stimulated showing a large increase in SWA, and the visually deprived hyperpallium showing no change in SWA. As in humans,[71,72] the former likely reflects a homeostatic response to extended time awake and taxing brain use, whereas the latter probably reflects the summation of factors with opposing effects on SWA: increased time awake increasing SWA and decreased visual input decreasing SWA. Importantly, this asymmetry was restricted to the visual hyperpallium, underscoring the specific link between visual stimulation and local SWA homeostasis.

REM Sleep Homeostasis

Sleep-depriving pigeons for 8 or 24 hours caused a significant increase in REM sleep.[10,11] However, this occurred during the second half of the night after 8 hours of daytime sleep deprivation, and during the first half of the night after 24 hours of sleep deprivation. A similar relationship between the duration of sleep deprivation and the timing of REM sleep during recovery sleep has also been described in rats.[73] REM sleep homeostasis has also been demonstrated in response to changes in housing conditions that likely influence the birds' perceived risk of predation.[67] Finally, as in rats, pigeons deprived of sleep using a modified version of the disk-over-water method also show a large rebound in REM sleep.[74] Interestingly, however, for the variables measured, pigeons did not develop signs of the sleep deprivation syndrome described in rats using the disk-over-water method.[75]

Sleep Architecture

Birds from diverse orders exhibit sleep architecture similar to mammals. In many diurnal birds, NREM sleep, as a proportion of sleep time, declines and REM sleep increases across the night, largely because of an increase in the number of REM sleep episodes* and, in some species, their duration.[9,10,40] However, this pattern is not a universal finding in diurnal birds.[35,76,77] In nocturnal barn owls (*Tyto alba pratincola*), the number and duration of REM sleep episodes increase across the daylight hours.[78]

The duration of the "sleep cycle" between episodes of NREM and REM sleep has not been systematically quantified in birds. Although REM sleep becomes more prevalent later in the major sleep phase in several species, the interval between individual episodes is highly variable. Qualitatively, this arises from the fact that birds alternate between periods of sleep with infrequent and frequent episodes of REM sleep.[44]

Sleep Ontogeny

In most mammals examined electrophysiologically, the time spent sleeping, particularly in REM sleep, is high early in life

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*References 9, 10, 17-19, 24, 40, 44, 49.

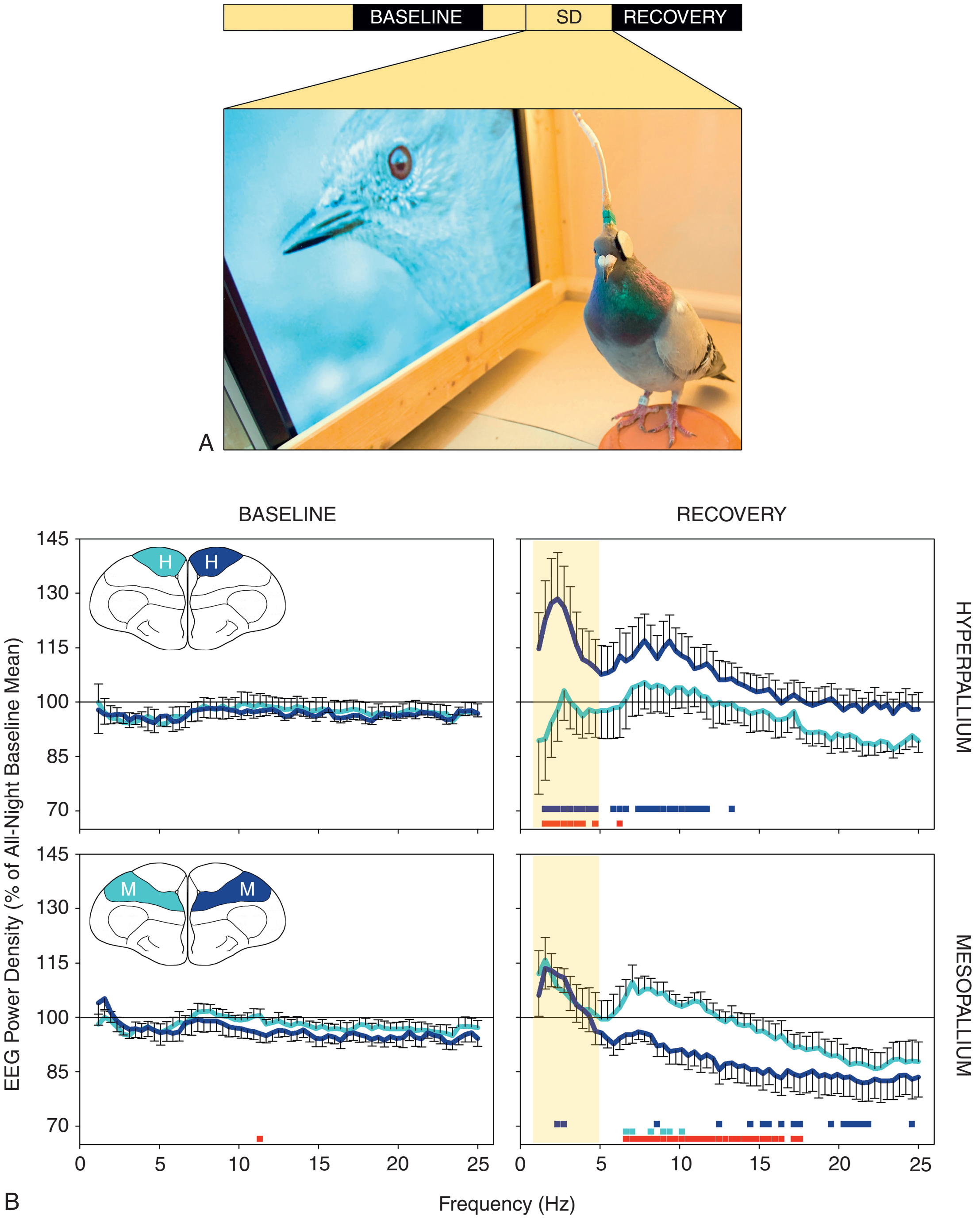

Figure 11.4 Local sleep homeostasis in the avian brain. **(A)** Experimental design: a 12-hour baseline night, 8-hour period of bihemispheric sleep deprivation (SD) with unilateral visual stimulation and a 12-hour recovery night. Photograph shows the experimental environment during the treatment. **(B)** Normalized spectral power density (0.78–25.00 Hz) during non-rapid eye movement sleep for the first quarter of the baseline and recovery nights for the stimulated (*dark blue*) and visually deprived (*light blue*) hyperpallia and mesopallia. Data are presented as mean ± standard error. *Colored squares* at the bottom of each recovery night plot reflect a significant pairwise comparison between the baseline and recovery night of the stimulated (*dark blue*) and visually deprived (*light blue*) hyperpallia; *red squares* denote a significant asymmetry between the left and right brain region during recovery sleep. Although the experimental treatment induced interhemispheric asymmetries across a wide range of frequencies, slow wave activity (*yellow shading*) in the hyperpallium showed the largest asymmetry. *Insets*, Frontal view of a transverse section through the cerebrum of a pigeon highlighting the hyperpallium (H) and mesopallium (M). (Courtesy of Axel Griesch.)

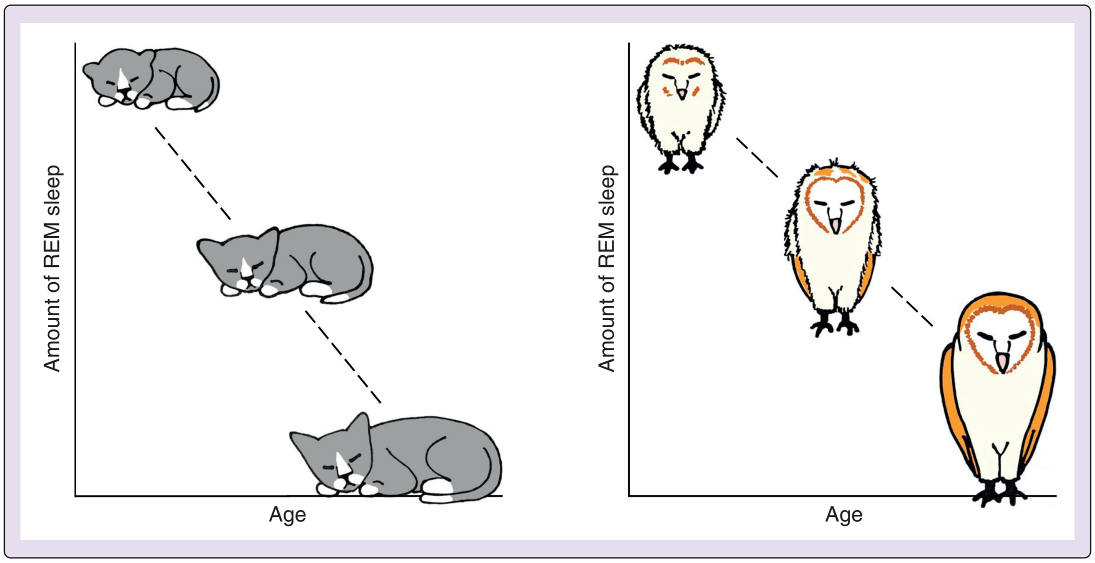

Figure 11.5 Mammalian-like rapid eye movement (REM) sleep ontogeny in barn owls. In both altricial mammals, such as cats, and altricial barn owls, REM sleep as a proportion of recording and sleep times is high early in life and progressively declines to adult levels.[12] The figure conveys the general pattern and not absolute values. (Courtesy of Ninon Ballerstädt.)

and then gradually declines to adult levels[79] (see Scriba and colleagues[12]). Until recently it had been unclear whether REM sleep also declines with age in young birds (see the review by Scriba and colleagues[12]). Sleep ontogeny was recently examined in barn owls (*Tyto alba guttata*) in the wild.[12] REM sleep expressed as a percent of total recording or sleep time declined with age (Figure 11.5), suggesting that, as in mammals, REM sleep is involved in brain maturation.

Temperature and Photoperiod

Mammals and birds, both homeotherms, show similar changes in thermoregulation across states. Although birds pant or shiver during NREM sleep when thermally challenged, these thermoregulatory behaviors diminish when they enter REM sleep.[12,80,81] As in many mammals,[82] brain temperature in birds declines and increases during NREM and REM sleep, respectively (Figure 11.1, *B*).[83]

Adaptive Sleeplessness

Pectoral sandpipers (*Calidris melanotos*) reproduce in the Arctic Circle under continuous daylight during a 3-week breeding season. The males are polygynous and as such their reproductive success is determined by their ability to mate with as many females as possible. Conversely, a female must choose the best quality male to sire her only clutch of the year. Consequently, competition among males for access to choosy fertile females is intense. Males establish and defend territories against rival males and display to females with aerial and ground displays (Figure 11.6, *A, B*), which precede copulation when performed effectively.

The biologic drive to sleep on a daily basis is so strong that humans will fall asleep even in life-threatening situations, such as while driving a car. Moreover, sleep restriction and fragmentation impair waking performance in humans[84-87] and other animals,[88] suggesting that sleep performs restorative processes that maintain adaptive brain function.[84,89,90] Thus were it not for a biologic drive for sleep, and the dependence of waking performance on prior sleep, male pectoral sandpipers would be able to secure mates around the clock. Accordingly, in this highly competitive environment, sexual selection has favored males with an ability to perform well on the tasks leading up to mating while getting little sleep. Using actigraphy and EEG/EMG recordings in the wild, Lesku and colleagues determined that some males had a remarkable ability to sleep very little for several weeks.[91] In the most extreme case, a male was active more than 95% of the time for 19 days. In addition, the little sleep some males obtained was highly fragmented, and although these males attempted to compensate for lost sleep by sleeping more intensely (i.e., higher SWA), they nevertheless maintained a large sleep debt. Surprisingly, however, these males were best able to convince choosy females to mate with them and ultimately sired the most offspring (Figure 11.6, *B*), indicating that their waking performance was not impaired in any meaningful way. Importantly, these findings indicate that impaired performance is not an evolutionarily inescapable outcome of sleep restriction and fragmentation.[91]

Migration

Normally diurnal songbirds switch to flying at night during migration.[92] In response to an endogenous circannual rhythm, captive songbirds exhibit nocturnal migratory restlessness (*Zugunruhe*), consisting of hopping and wing flapping, during the spring and fall, when their conspecifics in the wild would be migrating.[92] Captive songbirds exhibiting nocturnal migratory restlessness reduce the time spent sleeping at night by two-thirds but may compensate (in part) for lost nighttime sleep by increasing the time spent drowsy or napping in the day.[44,50,57]

Recently, sleep behavior and physiology were examined in garden warblers (*Sylvia borin*) caught at a migratory stopover site immediately after crossing the Mediterranean Sea.[93] Interestingly, at night, birds with low body fat, body mass, and muscle mass spent more time sleeping, were more likely to assume a heat-retaining sleep posture with the head tucked in the feathers, and had a lower metabolic rate during sleep but were less responsive to a sound simulating an approaching

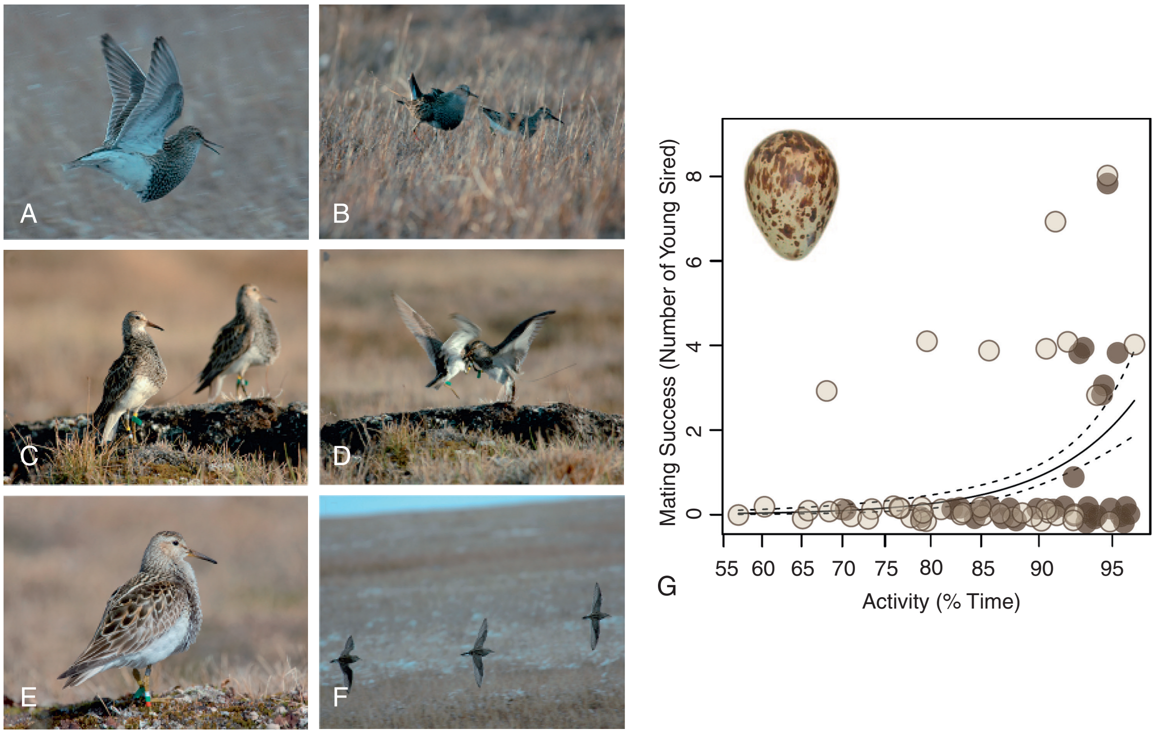

Figure 11.6 Adaptive sleep loss in polygynous male pectoral sandpipers. Male pectoral sandpipers engaging in various behaviors during an intense period of male–male competition for territories and females. Male displaying in flight **(A)**. Male displaying to a female (smaller bird) on the ground **(B).** Territorial displays between two males **(C)** leading to a physical fight **(D).** A male standing vigilant for intruding males, available females, and predators **(E)**. Males engaged in an aerial chase **(F).** The graph **(G)** shows the positive relationship (*fitted line*, with the dotted lines showing the 95% confidence intervals) between time spent active (awake) and the number of young sired for 2 years (*light and dark grey circles* reflect raw data). *Inset,* A pectoral sandpiper egg. (A-D, F: Courtesy of Wolfgang Forstmeier, Max Planck Institute for Ornithology. E: Courtesy of B.K.)

predator than birds in better physical condition. In addition, birds in better condition exhibited more migratory restlessness,[93] suggesting that they would have continued their migration that night in the wild.[92] Collectively, these findings indicate that birds in poor condition invest in deep nocturnal sleep at the expense of antipredatory vigilance, to conserve energy and, possibly, recover sleep lost during the adverse environmental conditions (e.g., difficult foraging or prolonged flights) that caused their poor physical condition.

Sleep in Flight

In contrast to most migrating songbirds, which have opportunities to land and sleep each day, recent advances in tracking and actigraphy have confirmed that several other types of birds fly nonstop for periods lasting several days to months (reviewed in Rattenborg[94]). For example, great frigatebirds (*Fregata minor*) spend up to 2 months foraging over the ocean[95] but cannot land on the water without becoming waterlogged, and therefore fly continuously.[95] Given the universal need for daily sleep,[89] it has been assumed that these birds sleep in flight.[94]

By deploying EEG data loggers on great frigatebirds, Rattenborg and colleagues established for the first time that sleep can occur in flight (Figure 11.7, *A*).[96] Sleep occurred primarily during the first hours of the night while the birds were soaring in circles, to the left or right, on rising air masses, but never during flapping flight (Figure 11.7, *B*). NREM sleep was categorized as BSWS or ASWS based on the degree of interhemispheric asymmetry in EEG SWA; USWS was a subcategory of ASWS with an asymmetry exceeding the threshold used to define USWS in marine mammals.[97] Most SWS was ASWS, with nearly half of it consisting of USWS; however, BSWS also occurred in flight. Although episodes of sleep lasted on average just 12 seconds (versus 52 seconds on land), bouts of USWS, ASWS, and BSWS occasionally lasted for several minutes. The accelerometry recordings revealed that when sleeping deeper (based on SWA) with the left hemisphere, the birds circled to the left and when sleeping deeper with the right hemisphere they circled to the right (Figure 11.7, *B* and *C*). Interestingly, interhemispheric asymmetries in gamma (30 to 80 Hz) showed the opposite relationship with turning direction (Figure 11.7, *C*). Given that each hyperpallium primarily receives input from the contralateral eye, and gamma has been implicated in visual processing, this suggests that the birds kept the eye facing into the turn open (Figure 11.7, *D*), possibly to avoid collisions with other birds. Finally, in addition to engaging in BSWS, frigatebirds also exhibited REM sleep in flight. During bouts of SWS, brief periods of EEG activation occurred in conjunction with accelerometry signals indicative of head dropping similar to that observed during REM sleep on land.

Surprisingly, during their 6-day flights, frigatebirds only slept on average for 42 minutes per day, whereas after landing they slept over 12 hours each day. The low amount of sleep in flight suggests that frigatebirds face unexpected demands for attention at night that usually exceed that afforded by ASWS or USWS. In addition to sleeping more, in longer bouts, and more symmetrically, during all types of SWS, sleep intensity

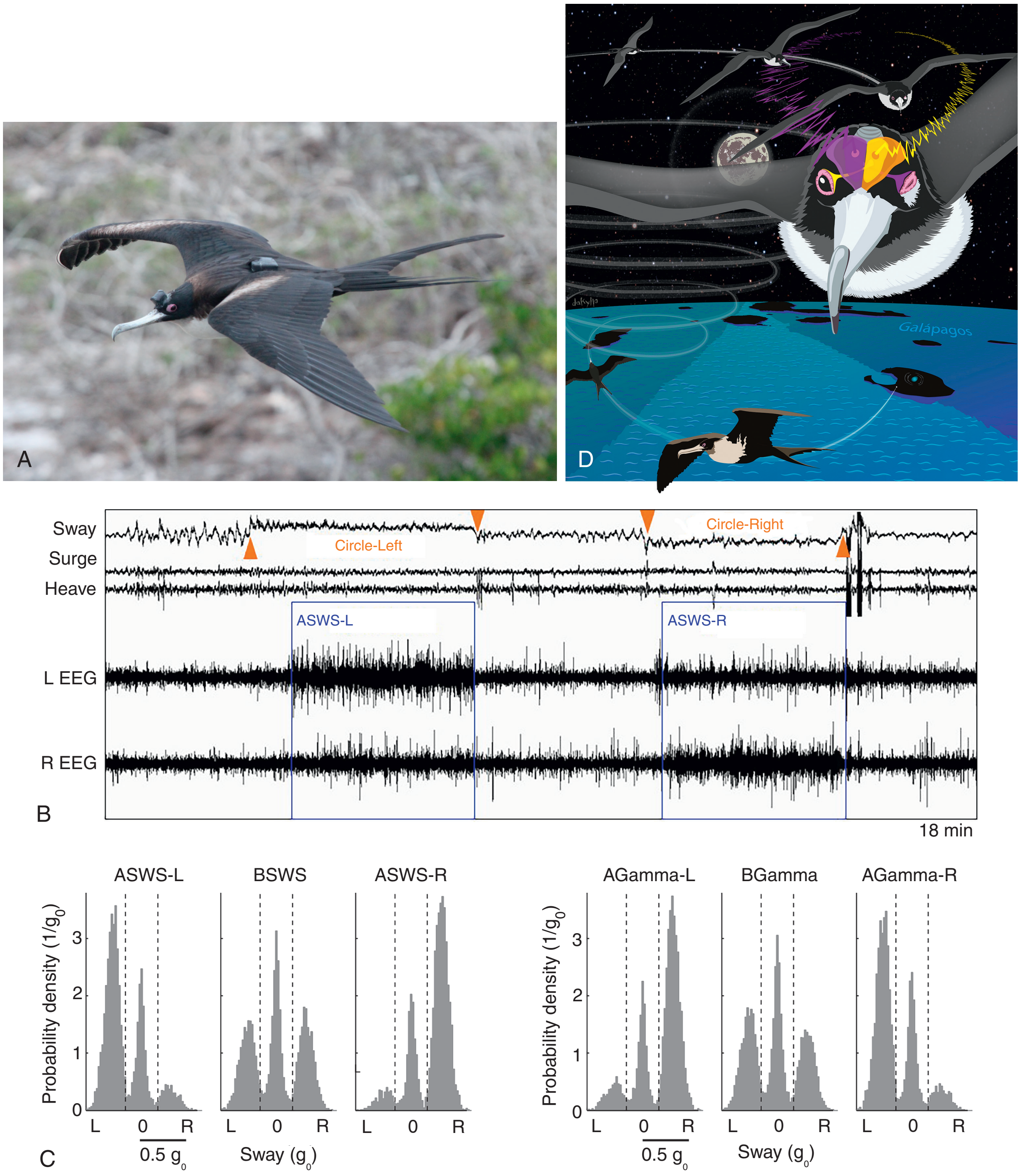

Figure 11.7 Sleep in flight. **(A)** Female great frigatebird with a head-mounted data logger for recording the electroencephalogram (EEG) from both cerebral hemispheres and triaxial acceleration. A GPS logger mounted on the back recorded position and altitude. **(B)** EEG and accelerometry (sway, surge, and heave) recordings from a frigatebird sleeping while circling in rising air currents. When the bird circled to the left (as indicated by centripetal acceleration detected in the sway axis), it showed asymmetric slow wave sleep (ASWS) with the left hemisphere sleeping deeper (larger slow waves) than the right (asymmetric slow wave sleep, left; ASWS-L), and when the bird circled to the right, the right hemisphere slept deeper than the left (asymmetric slow wave sleep, right; ASWS-R); during the other recording segments the bird was awake. **(C)** The relationship between interhemispheric asymmetries in slow wave activity (SWA; 0.75–4.5 Hz) and gamma activity (30–80 Hz) during slow wave sleep (SWS) for all birds combined. During ASWS, the birds usually circled toward the side with greater SWA and lower gamma activity. By contrast, during bihemispheric SWS (BSWS) without asymmetries in SWA or gamma (bihemispheric gamma; BGamma), the birds showed no preference for circling in one particular direction. SWS with greater gamma in the left (asymmetric gamma, left; AGamma-L) or right (asymmetric gamma, right; AGamma-R) hemisphere. **(D)** Illustration showing a bird circling to the right while sleeping with the right hemisphere. Although the birds' eye state is not known, based on studies from other birds, the EEG asymmetries suggest that the frigatebirds kept the eye connected to the more awake (lower SWA and higher gamma) hemisphere open and facing the direction of the turn. (**A** photo by Bryson Voirin. **D** illustration by Damond Kyllo. Panels [A to C] reproduced from Rattenborg NC, Voirin B, Cruz SM, et al. Evidence that birds sleep in mid-flight. *Nat Commun*. 2016;7:12468.)

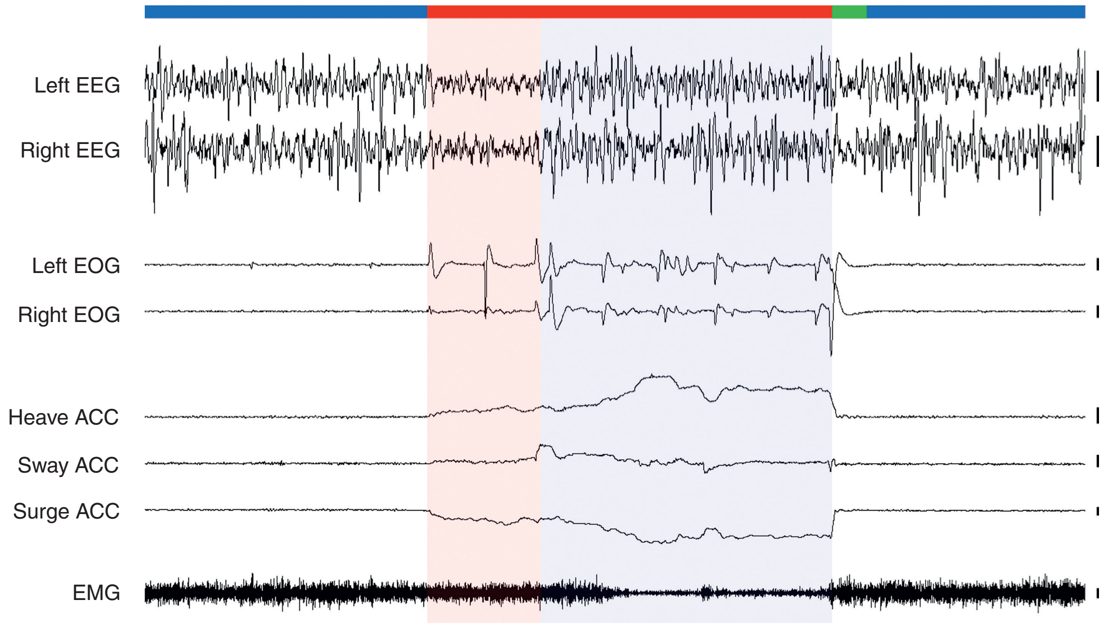

Figure 11.8 Mixed sleep state in an ostrich. The recording begins and ends with periods of non-rapid eye movement (NREM) sleep (*blue bar*) characterized by high amplitude, slow waves in the electroencephalogram (EEG), absence of rapid eye movements (measured via electrooculogram [EOG]), absence of head movements (accelerometer [ACC]), and moderate neck muscle tone (electromyogram [EMG]). NREM sleep is interrupted by a period of rapid eye movement (REM) sleep (*red bar*) with either EEG activation (*red shading*) or slow waves (*blue shading*). Irrespective of the type of EEG activity, rapid eye movements, a forward falling and swaying head with moderate-to-low muscle tone occurred invariably during REM sleep in the ostrich. *Heave ACC*, Movement along the dorsoventral axis with an upward slope denoting downward movement. *Sway ACC,* Lateral axis with up denoting movement to the right. *Surge ACC,* Anterior-posterior axis with down denoting movement forward. Vertical bars to the right of each EEG, EOG, and EMG trace denote 100 mV and 100 mg-forces to the right of each ACC trace. Trace duration: 60 s. (Reproduced from Lesku JA, Meyer LC, Fuller A, et al. Ostriches sleep like platypuses. *PLoS One.* 2011;6:e23203.)

was higher on land. In addition, during the first 10 hours after landing, a gradual decline in SWA occurred, suggesting that the birds were compensating (at least in part) for sleep lost in flight.

The small amount of sleep exhibited by female great frigatebirds in flight and some male pectoral sandpipers is difficult to reconcile with the extensive body of research demonstrating that waking performance rapidly declines in response to far shorter periods of sleep loss in animals ranging from insects to humans. Understanding how these birds seemingly circumvent large amounts of sleep may lead to new perspectives on the mechanisms and functions of sleep.

Sleep in Palaeognathic Birds

The presence of two sleep states in birds that are remarkably similar to mammalian NREM and REM sleep raises the question as to how these similarities arose. Although the fossilization of hard anatomical structures allows paleontologists to trace how bones have changed over evolutionary time, scientists can only infer the evolution of sleep states by studying living animals as proxies for extinct ones. Notably, modern-day monotremes are mammals yet lay eggs like reptiles. Because these animals retain some "primitive" traits thought to be present in the common ancestor to all mammals, including egg-laying, monotremes are often viewed as a window into the biology of early mammals.[98] Studies of sleeping monotremes, such as the platypus (*Ornithorhynchus anatinus*), may therefore provide clues to the evolutionary origins of mammalian NREM and REM sleep. Siegel and colleagues recorded eye movements and twitches of the head and bill in sleeping platypus, similar to brainstem-generated REM sleep phenomena in marsupial and eutherian mammals; however, the EEG did not show REM sleep-like activation but instead showed NREM sleep-like slow waves.[99] The presence of this mixed state in monotremes suggests that with the appearance of the lineage giving rise to marsupial and eutherian mammals, REM sleep incorporated the neocortex and NREM and REM sleep became temporally segregated.[100]

As with the monotremes and their retention of ancestral features, so too do Palaeognathae (Box 11.1).[98,101] Although it had been known for a half century that invariably species of Neognathae engaged in NREM and REM sleep, it remained unclear whether these states were shared by all living birds and therefore likely an ancestral condition for all birds. Despite an initial description of platypus-like sleep in a Palaeognath, the ostrich (*Struthio camelus*) (Figure 11.8),[39] a more recent study on another Palaeognath, the elegant crested tinamou (*Eudromia elegans*), showed behavioral and electrophysiologic sleep states typical of Neognathae.[40] Given that the small, flighted tinamous may better represent early birds (Box 11.1), that were also small and flighted, they may also better represent the form of sleep states in the most recent common ancestor to all birds than the large, flightless ostrich. Consequently, the evolutionary pattern proposed for mammals may not apply to birds.[40]

REPTILES, AMPHIBIANS, AND FISH

The similarities between sleep in mammals and birds reflect either inheritance from a common ancestor (stem amniote) with similar states or a case of convergent evolution.[25] Although we cannot tell for certain how the stem amniote slept, in theory, we can infer how it slept through examining sleep in living reptiles, amphibians, and fish. Unfortunately, this seemingly straightforward approach has been confounded by the diversity of findings reported in the few reptiles, amphibians, and fish examined (reviewed in Libourel and Herrel,[64] Eiland and colleagues,[102] Hartse,[103] and Kelly and colleagues[104]). Reports include no behavioral nor electrophysiologic signs of sleep, signs of one NREM sleep-like state, two types of sleep suggestive of NREM and REM sleep, or electrophysiologic states that are not readily relatable to either NREM or REM sleep. Our ability to interpret this diversity is hindered by uncertainty over its source. In addition to interspecific differences in sleep, the animals' age, variation in neural architecture, electrode type and placement, housing conditions and habituation, temperature effects on the poikilotherm EEG, and the method used to assess arousal thresholds (when conducted) may all contribute to the variation across studies. In most cases, the lack of replication by independent laboratories further complicates matters. Without knowing the extent to which this variation reflects true interspecific differences, it is impossible to reconstruct the evolution of sleep states in vertebrates.

Two recent studies of lizards, using state-of-the-art methods, suggest that some of this variation reflects interspecific differences in the neural correlates of sleep behavior. Shein-Idelson and colleagues recorded the bearded dragon lizard (*Pogona vitticeps*) at night using high-density electrode arrays placed in the dorsal cortex and dorsal ventricular ridge (DVR; Box 11.2).[105] During behavioral sleep, the DVR recordings revealed two electrophysiologic patterns that alternated approximately every 80 seconds with equal time spent in each state. The first was characterized by high-amplitude sharp waves, similar (in part) to those previously reported in some studies of lizards, turtles, and crocodilians.[64,103] The second was characterized by DVR activity similar to that occurring during wakefulness and eye movements occurring more frequently than during the first sleep state. Based on these findings, the authors proposed that these states are homologous to NREM and REM sleep in mammals and birds.

Importantly, Libourel and colleagues replicated these findings in the bearded dragon, but not in another species of lizard, the Argentine tegu (*Salvator merianae*), despite recording from the same brain region (Figure 11.9).[106] Two sleep states, named S1 and S2, were identified in tegus. S1 was also characterized by high-amplitude sharp waves, but the amplitude was lower, the duration was shorter, and they occurred far less often than in dragons. As in earlier reptile studies,[64,103] high-amplitude sharp waves increased in number after sleep deprivation. The second sleep state (S2) was associated with isolated eye movements, but the LFP was characterized by a 15-Hz oscillation not found during wakefulness. Nonetheless, this oscillation was suppressed by a selective serotonin reuptake inhibitor, a category of drugs that suppresses REM sleep in mammals and birds.[107] Interestingly, the sleep architecture of tegus more closely resembled that of birds than dragons, in that short bouts of REM-like S2 occurred hundreds of times a night. Finally, in both species, no twitches occurred during putative REM sleep. Despite the differences in phenotype, these two studies suggest that two sleep states, in some respects, similar to NREM and REM sleep are present in at least some reptiles.

In contrast to the few early electrophysiologic investigations of adult fish (reviewed in Hartse[103] and Kelly and colleagues[104]), a recent study suggests that two sleep states may exist in young zebrafish (*Danio rerio*). Leung and colleagues used larval zebrafish, genetically modified to fluoresce, to image whole brain activity, eye movements, heart rate, and trunk muscle activity.[108] The fish were recorded restrained in agar at night during (I) spontaneous wake and sleep, (II) sleep following sleep deprivation, and (III) after being treated with drugs known to induce NREM and REM sleep in mammals. Two types of sleep called slow bursting sleep (SBS) and propagating wave sleep (PWS) were identified. SBS was characterized by synchronous bursts of activity punctuated by periods of neuronal silence in the dorsal pallium that were most pronounced following sleep deprivation or the administration of hypnotic drugs. During spontaneous sleep, the onset of PWS was characterized by a wave of trunk muscle contraction lasting 10 to 15 seconds and a burst of neural activity lasting 5 minutes that propagated throughout the neuroaxis. After the burst of neural activity, activity across the neuroaxis was suppressed below waking levels for 20 minutes. A similar state was induced by drugs that induce REM sleep in mammals, although the temporal sequence of events differed considerably from that during spontaneous PWS. Finally, although the eyes moved freely during wakefulness, rapid eye movements were not detected during spontaneous PWS.

The synchronous bursts of cortical activity during SBS bear some similarity to the bursts of activity associated with slow waves during mammalian and avian NREM sleep, although the frequency is much slower in zebrafish. And, in general terms, the widespread activation of the neuroaxis during PWS is similar to the activation of the neuroaxis occurring during mammalian REM sleep. However, the long muscle contraction at the onset of PWS is unlike the brief, intermittent twitches that characterize REM sleep in mammals and birds. The absence of eye movements, a finding also reported in a behavioral study of adult zebrafish,[109] is also inconsistent with the proposed relationship between PWS and REM sleep. In addition, the prolonged period of suppressed neural activity following the wave of activity is unexpected if this state is homologous to REM sleep.

The recent studies on dragons, tegus, and zebrafish have important implications for interpreting the confusing research on sleep in poikilothermic vertebrates. Notably, the differences between two species of lizards recorded using the same methodology in the same laboratory suggest that at least some of the variability reported in the earlier literature reflects real interspecific differences in sleep. Further research on poikilothermic vertebrates, using modern methods, is clearly needed to characterize the ancestral sleep state(s) present in the stem amniote, as well as the functional implications of sleep's diverse expression in poikilotherms.

FUNCTIONAL IMPLICATIONS

Relatively few studies have examined the functional aspects of sleep in nonmammalian vertebrates. Early on, the fact that unequivocal NREM and REM sleep had been found only in mammals and birds, both homeotherms, led to the proposal that NREM sleep, in particular, evolved to conserve energy.[110] The lower metabolic rate during NREM sleep[111] and its continuity with hypometabolic states, such as torpor and

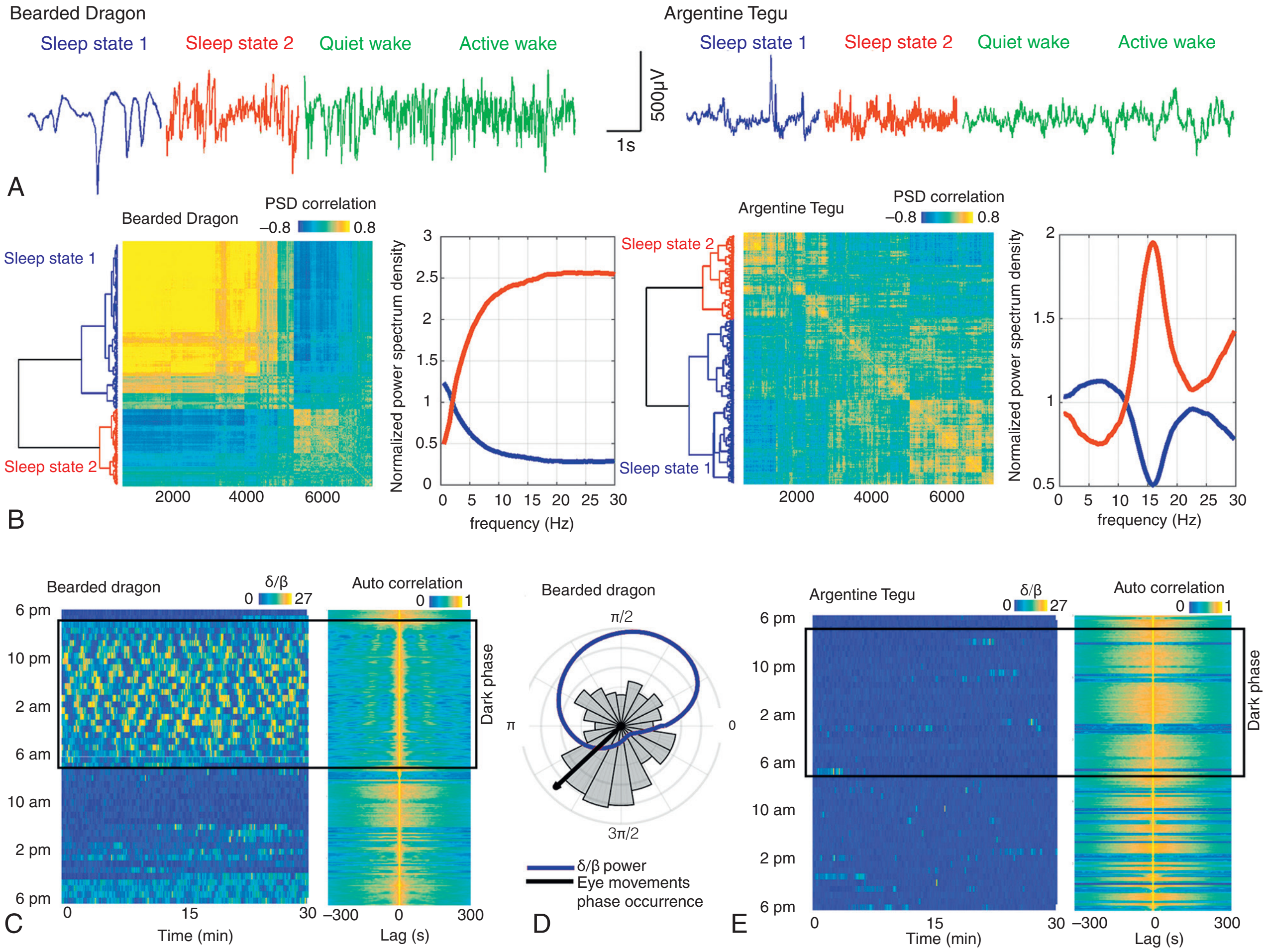

Figure 11.9 Sleep states in lizards. **(A)** Local field potential (LFP) recorded from the dorsal ventricular ridge of a bearded dragon (*left*) and Argentine tegu (*right*) during sleep state 1 (S1, sharing similarities with mammalian non-rapid eye movement sleep) in *blue*, sleep state 2 (S2, sharing similarities with mammalian rapid eye movement sleep) in *red*, and quiet and active wake in *green*. **(B)** Plots for each species (dragon, *left*; tegu, *right*), show a dendrogram (*left*) and correlation map (*middle*) obtained from the hierarchic clustering of the distance between the correlation of each LFP 3-second window power spectrum density (*PSD*). To the right of each correlation map are the normalized mean power spectra of the two clusters computed for one animal representing the two distinct sleep states identified, S1 in *blue* and S2 in *red*. The comparison of the normalized power spectra of each state reveals a frequency profile that is clearly different between the two species, with desynchronized activity (composed of all the frequencies higher than 5 Hz) for the bearded dragon during S2 and a power spectrum mainly composed of 15-Hz oscillations for S2 in the tegu. **(C)** The band power ratio (δ [0.5–4 Hz]/β [11–30 Hz]) computed as in Shein-Idelson and colleagues[105] for the bearded dragon. Each horizontal segment represents 30 minutes of the computed ratio. The value of the ratio is color coded from 0 (*blue*) to 27 (*yellow*). The figure from the *top* to the *bottom* represents the evolution of the ratio over 24 hours, with the *dark rectangle* indicating the dark phase. On the right, the normalized autocorrelation map of the ratio is illustrated. Both figures reveal a rhythmic alternance with a period of around 90 seconds across episodes, with δ frequencies (*yellow*) and episodes with β (*blue*) during the dark phase, when the animal is lying on the floor with the eyes closed. **(D)** The distribution of the eye movements within each δ–β cycle; the mean phase is represented with a *black arrow*. The *red line* is the mean δ/β power ratio across the δ–β cycle. **(E)** Same as **(C),** but for the Argentine tegu. The figure reveals no clear cycle in the δ/β power ratio over 24 hours. (Reproduced from Libourel PA, Barrillot B, Arthaud S, et al. Partial homologies between sleep states in lizards, mammals, and birds suggest a complex evolution of sleep states in amniotes. *PLoS Biol.* 2018;16:e2005982.)

hibernation,[112] contributed to this hypothesis. More recently, Schmidt proposed that the primary energy savings resulting from sleep is not simply due to the reduction in metabolic rate, but rather arises from the more efficient allocation of energy to specific processes during specific states.[113] In mammals and birds, REM sleep with its suppressed thermoregulatory responses, may allow energy usually allocated to thermoregulation to be reallocated toward other processes without incurring additional energetic costs.[82,113] Although the presence of NREM and REM sleep-like states in some poikilothermic reptiles suggests that these states may not be exclusively linked to homeothermic animals, engaging in two sleep states may still conserve energy in poikilothermic animals if performing the associated functions during temporally segregated states is more efficient.[113]

Along with many other lines of evidence, the fact that some marine mammals and birds sleep unihemispherically during continuous activity (rather than dispensing with sleep altogether)[96,97] suggests that sleep performs functions that specifically benefit the brain. Research on sleep's role in maintaining adaptive brain performance has primarily focused on mammals. Brain-related functions fall into two general categories: (1) maintenance and restoration and (2) synaptic dynamics involved in memory consolidation.[114] As in the mammalian neocortex, transcripts that encode proteins involved in cellular maintenance are expressed in the forebrain of sleeping birds.[115] Also, the local, use-dependent regulation of NREM sleep SWA suggests that SWA is involved in, or correlated with, restorative processes occurring in the brain in response to prior waking activation.[70] In addition, as in mammals,[116] sleep has been implicated in various forms of memory processing, including imprinting in chicken chicks,[117,118] song learning in zebra finches,[119,120] and memory consolidation in starlings.[121] However, little work has linked sleep-dependent memory processing to specific sleep states or brain oscillations in birds.

In mammals, several studies suggest that the brain oscillations occurring during sleep are actively involved in processing information.[16,90,116,122-125] In particular, a prominent model suggests that neocortical slow waves, thalamocortical spindles, and hippocampal SWRs form a system of interacting oscillations involved in gradually integrating information initially stored in the hippocampus into existing information in the neocortex for long-term storage, via a process of memory reactivation during sleep.[116] Direct connections from the hippocampus to the medial prefrontal cortex (PFC) play an important role in this systems-level memory consolidation.[126,127] However, unlike the mammalian hippocampus, which receives input from most high-order neocortical association areas contributing to a memory via the entorhinal cortex, most comparable regions in the avian DVR do not provide input to the hippocampus.[22,128] Moreover, anatomic or functional connections between the hippocampus and nidopallium caudolateral (NCL)—the avian analogue of the mammalian PFC—have not been found in birds.[22,128,129] Furthermore, although the avian hippocampus is involved in storing spatial memories, there is no evidence of hippocampal memories transferring to other brain regions in birds.[22] Consequently, it is perhaps not surprising that some of the oscillations (spindles and SWRs) implicated in transferring hippocampal memories during mammalian NREM sleep have not been found in birds.[13,22]

Even though there is reason to think that hippocampal memories are not processed at a systems level during avian sleep, propagating slow waves could be involved in transferring memories between other brain regions.[13,16,117,130] In addition, the local, use-dependent regulation of slow waves may also be involved in processing information locally in avian and mammalian brains.[70,71] Local slow waves might strengthen synapses and thereby memories stored in the respective region, while weakening unimportant synapses that would otherwise introduce noise into the system and increase its energetic demands.[90]

In contrast to its role in mammals and birds, sleep's potential role in processing information in reptiles has not been examined. Attempts to infer how the reptilian brain may process information are complicated by the fact that the electrophysiologic correlates of sleep vary across studies and species. Nonetheless, the high-amplitude sharp wave, an electrophysiologic correlate of sleep in several reptilian species, has recently received attention with regard to memory processing. Recordings from the dorsal cortex and DVR revealed high-amplitude sharp waves in a variety of reptiles; although their incidence, duration, and morphology vary across studies and species.[64,106] Hartse[103] noted the similarity between reptilian sharp waves and sharp waves recorded from the mammalian hippocampus during NREM sleep. More recently, Shein-Idelson and colleagues[105] also noted this similarity between these electrophysiologic events. In addition, they also detected high-frequency (>70 Hz) oscillations during sharp waves that they relate to the ripple component of mammalian hippocampal SWRs. However, it is unclear whether these sharp waves reflect the same phenomenon as mammalian hippocampal SWRs or a variant of the slow oscillation that gives rise to slow waves in mammals and birds,[13,15,131] as fast (80–200 Hz) ripple-like activity also occurs during the up state of the neocortical slow oscillation.[132] Regardless of which interpretation is correct, reptilian sharp waves are likely to be involved in memory reactivation, as it is thought to occur during both mammalian SWRs *and* slow oscillation up states.[132]

The function of avian REM sleep and REM sleep-like states in reptiles remains unclear. As in mammals, the high amount of REM sleep in developing owls suggests a common role in brain development. However, the apparent absence of a hippocampal theta oscillation suggests that processes linked to this oscillation in mammals[122] occur either via different mechanisms or not at all in birds. In reptiles, the various ways in which REM sleep-like states manifest (or do not) makes it difficult to generalize about the functional implications of these findings. Even within lizards, the reptilian group with the most reports of REM sleep-like states, the neural signatures, vary widely.[106] Further research is clearly needed to understand the mechanisms and functional implications of this unexpected, yet potentially informative, diversity. Additional research is also needed to understand why REM sleep has not been demonstrated in several studies of reptiles. Was REM sleep missed in some species? If not, was it evolutionarily lost, or did REM sleep evolve independently multiple times in mammals, birds, and some reptiles? If REM sleep is really only present in some reptiles, further comparisons of reptilian species with and without REM sleep may provide clues to its functions. Hints of a REM sleep-like state in cuttlefish (*Sepia officinalis*),[133] members of an invertebrate group (cephalopod molluscs) renowned for their complex cognitive abilities, but not in sea slugs (gastropod molluscs),[134] raises the intriguing possibility that REM sleep has evolved many times, even in invertebrates, during the course of evolution.

CLINICAL PEARL

Comparative research on animals from diverse taxonomic groups can influence our understanding of sleep in humans. Research on birds can provide new perspectives on the “first night effect,” motor control during sleep, the functions of brain oscillations, and neurobehavioral performance during prolonged wakefulness. The recent discovery of REM sleep-like states in some reptiles provides a new opportunity to investigate the functions of this mysterious state.

SUMMARY

Despite last sharing a common ancestor over 300 million years ago, birds exhibit two states that are in many, but not all, respects similar to mammalian NREM and REM sleep.

Through studying reptiles, amphibians, and fish, researchers have attempted to determine whether these states were present in the last common ancestor to mammals and birds or evolved independently in each lineage via convergent evolution. However, in contrast to mammals and birds, wherein the two states are similar across most of the species examined within each group, the results have been highly variable in poikilothermic vertebrates. These include no behavioral or electrophysiologic signs of sleep, signs of one NREM sleep-like state, two types of sleep suggestive of NREM and REM sleep, or electrophysiologic states that are not readily comparable to either NREM or REM sleep. Recent studies suggest that at least some of this variability reflects true interspecific differences in the electrophysiologic correlates of sleep. This diversity thwarts attempts to draw simple conclusions regarding the evolution of NREM and REM sleep. Nonetheless, it may serve as a rich resource for investigating the mechanisms and functions of sleep-related brain activity.

SELECTED READINGS

Aulsebrook AE, Johnsson RD, Lesku JA. Light, sleep and performance in diurnal birds. *Clocks Sleep*. 2021;3(1):115–131.

Dave AS, Margoliash D. Song replay during sleep and computational rules for sensorimotor vocal learning. *Science*. 2000;290:812–816.

Derégnaucourt S, Mitra PP, Fehér O, et al. How sleep affects the developmental learning of bird song. *Nature*. 2005;433:710–716.

Dewasmes G, Cohen-Adad F, Koubi H, et al. Polygraphic and behavioral study of sleep in geese: existence of nuchal atonia during paradoxical sleep. *Physiol Behav*. 1985;35:67–73.

Jones S, Pfister-Genskow M, Benca RM, et al. Molecular correlates of sleep and wakefulness in the brain of the white-crowned sparrow. *J Neurochem*. 2008;105:46–62.

Lesku JA, Rattenborg NC, Valcu M, et al. Adaptive sleep loss in polygynous pectoral sandpipers. *Science*. 2012;337:1654–1658.

Lesku JA, Vyssotski AL, Martinez-Gonzalez D, et al. Local sleep homeostasis in the avian brain: convergence of sleep function in mammals and birds? *Proc Biol Sci*. 2011;278:2419–2428.

Leung LC, Wang GX, Madelaine R, et al. Neural signatures of sleep in zebrafish. *Nature*. 2019;571:198–204.

Libourel PA, Barrillot B, Arthaud S, et al. Partial homologies between sleep states in lizards, mammals, and birds suggest a complex evolution of sleep states in amniotes. *PLoS Biol*. 2018;16:e2005982.

Lyamin OI, Kibalnikov AS, Siegel JM. Sleep in ostrich chicks *(Struthio camelus). Sleep*. 2021;44(5):zsaa259.

Rattenborg NC, Voirin B, Cruz SM, et al. Evidence that birds sleep in mid-flight. *Nat Commun*. 2016;7:12468.

Scriba MF, Ducrest AL, Henry I, et al. Linking melanism to brain development: expression of a melanism-related gene in barn owl feather follicles covaries with sleep ontogeny. *Front Zool*. 2013;10:42.

Tisdale RK, Lesku JA, Beckers GJL, et al. Bird-like propagating brain activity in anesthetized Nile crocodiles. *Sleep*. 2018;41:zsy105.

van der Meij J, Martinez-Gonzalez D, Beckers GJL, et al. Intra-"cortical" activity during avian non-REM and REM sleep: variant and invariant traits between birds and mammals. *Sleep*. 2019;42:zsy230.

van Hasselt SJ, Mekenkamp GJ, Komdeur J, et al. Seasonal variation in sleep homeostasis in migratory geese: a rebound of NREM sleep following sleep deprivation in summer but not in winter. *Sleep*. 2021;44(4):zsaa244.

Yamazaki R, Toda H, Libourel PA, Hayashi Y, Vogt KE, Sakurai T. Evolutionary origin of distinct NREM and REM sleep. *Front Psychol*. 2020;11:567618.

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