ANIMAL BEHAVIOUR, 2006, 72, 951–958
doi:10.1016/j.anbehav.2006.03.008

Daytime naps in night-migrating birds: behavioural adaptation to seasonal sleep deprivation in the Swainson's thrush, *Catharus ustulatus*

T. FUCHS*, A. HANEY*, T. J. JECHURA†, F. R. MOORE‡ & V. P. BINGMAN*
*J. P. Scott Center for Neuroscience Mind and Behavior and Department of Psychology, Bowling Green State University
†Albion College, Albion, Michigan, U.S.A.
‡University of Southern Mississippi, Hattiesburg, Mississippi, U.S.A.

(Received 2 September 2005; initial acceptance 1 December 2005; final acceptance 16 March 2006; published online 14 August 2006; MS. number: A10238)

Many typically diurnal songbird species are routinely subjected to severe sleep deprivation during their seasonal, nocturnal migrations, yet they seem to suffer few of the negative consequences so obvious in sleep-deprived mammals. Studying the Swainson's thrush, a Nearctic–Neotropical long-distance migrant, we investigated seasonal changes in behaviour as possible adaptations to naturally occurring sleep loss during the migratory season. We found that captive Swainson's thrushes substantially change their daytime behaviour in response to significant loss of night-time sleep during migration, engaging in numerous episodes of daytime sleep, unilateral eye closure and drowsiness. Our observations suggest that brief episodes of sleep and sleep-like behaviour during the day, including lateralized naps in the form of unihemispheric sleep, enable migratory birds to compensate for extended periods of nocturnal sleep loss. Although episodes of daytime sleep and unilateral eye closure rarely exceed 30 s, these brief episodes, considering the short sleep cycle of birds, appear sufficiently long to provide recuperative opportunities without stretching a migrant's time budget. Importantly, the temporal structure of the daytime rest and sleep behaviour would not preclude migrants from foraging and replenishing fat deposits during a large portion of the day.

Twice a year billions of songbirds migrate over thousands of kilometres between their wintering and breeding grounds. The vast majority of these birds are diurnal, except during migration when the flights of most species occur at night. By travelling at night, migrants experience decreased predatory pressure, improved atmospheric conditions for flight and more time to feed during the day (Kerlinger & Moore 1989; Moore 1992). In general, nocturnal migrants begin their flights shortly after sunset and fly for several hours, sometimes the entire night (Kerlinger & Moore 1989). Advantages of nocturnal migration aside, migrants necessarily lose substantial opportunity for night-time sleep during the migratory season. In mammals, sleep deprivation and sleep fragmentation result in substantial deficits in cognition (Horne 1988; Bonnet & Arand 2003), physiology (Everson 1995; Rogers et al. 2001) and vigilance (Horne & Reyner 1999; Bonnet & Arand 2003). If sleep deprivation in birds resulted in similar impairments, sleep-deprived migrants would experience considerable disadvantages at stopover sites where they compete for food with nonmigratory species and are subject to predation. Loss of sleep, in addition to energetic constraints (Jenni-Eiermann & Jenni 2003; Lindström 2003; Wikelski et al. 2003), may constrain migratory behaviour. Migratory birds are known to have evolved physiological (Jenni & Schaub 2003; Munro 2003) and morphological (Leisler & Winkler 2003) adaptations in response to the energetic demands of migration. If sleep deprivation were to limit migratory efficiency, it would not be surprising if migrants have also evolved adaptations in response to the negative consequences of sleep loss. For example, migrants might change their daily activity patterns and compensate for lost sleep at night by sleeping/resting during the day. However, daytime sleep would be associated with an increased risk of predation

Correspondence: T. Fuchs, 255 Psychology, Bowling Green State University, Bowling Green 43402, Ohio, U.S.A. (email: fuchs@bgnet.bgsu.edu).

0003–3472/06/$30.00/0

and limit the time available to replenish depleted energy stores. Hence, natural selection may have also promoted complementary/alternative mechanisms for sleep-loss compensation such as unihemispheric sleep (Rattenborg et al. 2000), sleep during migratory flight, a physiological resilience to sleep deprivation, or increased sleep quality during the little time that remains for nocturnal sleep. The hypothesis that unihemispheric sleep (Mukhametov 1985; Rattenborg et al. 2000), a phenomenon during which one hemisphere of the brain engages in slow wave sleep while the other hemisphere displays the electrophysiological correlates of wakefulness, could have a compensatory function during avian migration has been entertained for some time (Rattenborg et al. 2000, 2004), but to date, no scientific evidence is available.

In our study, we observed the behaviour of 12 Swainson's thrushes during the migratory and nonmigratory seasons. The Swainson's thrush, a Nearctic–Neotropical long-distance migrant, travels up to 5000 km from its breeding grounds in northern Canada and Alaska to its wintering grounds in Central and South America. It is also one of the few species whose migratory behaviour has been studied during migration by radiotelemetry (Cochran 1987). However, it is prohibitively difficult to study sleep in free-flying migrants. Fortunately, captive migratory birds readily display the behavioural changes associated with the migratory season in the form of appropriately oriented nocturnal restlessness or 'Zugunruhe' (Berthold et al. 2000). In our study, the sleep and other behaviour of the experimental Swainson's thrushes were videotaped and analysed over the course of more than 12 months to behaviourally characterize sleep in this species and to detect behavioural adaptations to sleep loss as the birds transitioned between migratory and nonmigratory states.

METHODS

Adult Swainson's thrushes of mixed gender were mist-netted on the Mississippi gulf coast in the autumn of 2002 and 2003. All necessary federal (F. R. Moore) and state (V. P. Bingman) permits were obtained. Birds were temporarily housed at the University of Southern Mississippi, and then transported to Bowling Green State University (BGSU). Transport and housing conditions were in accordance with BGSU animal care and use regulations. The thrushes were individually placed in cages (60 × 40 × 40 cm) and housed in the BGSU animal facility. Birds were maintained on an ad libitum diet of mealworms (*Tenebrio molitor*), mixed fruit, moistened monkey biscuits (Mazuri, St Louis, Missouri, U.S.A.) and a vitamin supplement (Eight in One Pet Products, Hauppauge, New York, U.S.A.). Water was available at all times.

Behaviour

We operationally defined seven behavioural states: active wakefulness, alert wakefulness, drowsiness (D), front sleep (FS), back sleep (BS), unilateral eye closure (UEC) and wing whirring.

Behavioural states

Active wakefulness. Active wakefulness is characterized by ongoing locomotor activity (perch hopping). In experiment 1 (see below), we used the additional operational distinction of specific and 'nonspecific' behaviours. Goal-directed behaviours (grooming, singing and feeding), which serve a definable purpose, were subcategorized as specific behaviours. General activity, mostly in the form of perch hopping, does not serve any observable purpose, but can consume large amounts of time, and was therefore categorized as nonspecific behaviour.

Alert wakefulness. Round eyes, quick and frequent head movements and an absence of locomotor activity characterize this behavioural state. In addition, the posture of alert wakefulness is more erect than during drowsiness or front sleep, and feathers are not ruffled (Fig. 1d).

Drowsiness. A bird is perched in a sitting position with oval or partially closed eyes. Feathers are ruffled; head movements are either slow or absent (Fig. 1c).

Front sleep. The front sleep position resembles that of drowsiness. The state is further characterized by ruffled feathers, a lack of head movements and closed eyes (Fig. 1b).

Back sleep. A bird is perched in a sitting position. The head is facing backwards and is partially buried in the scapula feathers. The bird's eyes are usually not visible in this posture (Fig. 1a).

Unilateral eye closure. Unilateral eye closure (UEC) is the most reliable behavioural indicator of unihemispheric sleep in birds (Kavanau 1998; Rattenborg et al. 2000). Therefore, we were particularly interested in possible changes in the quantities of UEC as the experimental Swainson's thrushes transitioned between a migratory and nonmigratory state. UEC was solely defined by eye state. One eye had to be completely closed and the other eye had to be fully visible and open. Behaviours shorter than 2 s were not included in the analysis.

Wing whirring. A flight substitute, characterized by wing flapping, in an erect perched position. Birds occasionally lose contact with the perch, but usually return to a perched position immediately and resume flapping activity.

Data Collection and Analysis

To determine seasonal behavioural state (migratory/nonmigratory), activity was recorded continually with infrared motion detectors, mounted on the ceilings of the holding cages during the entire observation period (12 months). A bird was classified as migratory if it showed nocturnal activity on every night for at least 1 week, and as nonmigratory if it did not show nocturnal activity for at least 7 days. Observations were made during both spring and autumn migratory seasons, as well as during summer