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Studies on sleep patterns and sleep homeostasis in birds

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CHAPTER 10

General discussion and conclusions

This dissertation contains a collection of studies assessing sleep patterns and sleep homeostasis in three different bird species under both controlled and semi-natural conditions. The knowledge gained from these studies provides new insights into not only the flexibility of sleep time but also the flexibility of sleep homeostasis. The conceptualization of this dissertation started with the idea that some birds experience phases over the year where ecological demands require extended periods of wakefulness (Lesku *et al.*, 2012; Rattenborg *et al.*, 2016). Yet, there remains a gap in our understanding of how these birds can cope with the apparent sleep loss during such times and whether there is a need for any (partial) recovery. Even when birds are capable of temporal changes in physiology that enable them to suppress the need for sleep and cope with sleep loss, there might still be a need for recovery later on. An alternative explanation might be that birds that go without sleep ultimately pay a price for that in terms of lower survival in the long run.

To understand the basic mechanism of sleep and sleep homeostasis, we started with determining the presence and magnitude of sleep homeostatic response to sleep deprivation under controlled laboratory conditions in jackdaws (*Coloeus monedula*) and starlings (*Sturnus vulgaris*). Sleep under a controlled laboratory setting might be different compared to that in the wild. Therefore, to understand what environmental factors can influence sleep, we measured sleep in starlings across the year in a seminatural enclosure. We found strong variation in NREM sleep time across seasons, as well as a strong sleep reducing effect of moonlight. These findings led us to the question of whether sleep homeostasis undergoes similar flexibility across the seasons. For that we measured sleep in the migratory barnacle goose (*Branta leucopsis*) in captivity, housed under seminatural conditions where we deprived them of sleep in winter and summer.

Sleep architecture

In all three bird species that we studied, sleep consisted of NREM and REM sleep that appears similar to mammalian sleep (Gassel, Marchifava and Pompeiano, 1965; Borbély and Neuhaus, 1979; Tobler and Borbély, 1986; Lyamin *et al.*, 2008; Voirin *et al.*, 2014) and earlier reported bird species (Szymczak, 1985; Szymczak, 1986b; Tobler and Borbély, 1988; Szymczak *et al.*, 1996; Rattenborg, Lima and Amlaner, 1999; Martinez-Gonzalez, Lesku and Rattenborg, 2008; Lesku, Meyer, *et al.*, 2011; Lesku and Rattenborg, 2014; Rattenborg *et al.*, 2016; Tisdale *et al.*, 2017). Yet, there is a large variation in the amount of sleep they had per light phase (Table 1). Under controlled baseline conditions, NREM sleep slowly decreases overnight as

shown in **chapter 2** and **chapter 3**. Yet, with light onset, the animals strictly shift to almost complete wakefulness, which might indicate a direct effect of light and/or a strong circadian drive for wakefulness in the early morning. This tightly controlled circadian regulation becomes less clear when the animals were group-housed in a semi-natural enclosure as has been described in **chapter 4** and **chapter 5**. This can be explained by the fact that under seminatural conditions, the onset of the light phase occurs less abrupt due to the occurrence of twilight. Another explanation might be that the animals keep each other more awake to protect themselves from potential danger, threats or disturbances from conspecifics.

NREM sleep homeostasis

Sleep homeostasis is a phenomenon that is reflected by a recovery rebound in both the quantity and quality of sleep following a period of sleep loss (see Figure 1A in **chapter 1**). We tested whether the three bird species have a sleep rebound following sleep deprivation for 4 or 8 h during the dark phase/night time in **chapter 2** (jackdaws), **chapter 3** (starlings) and **chapter 5** (barnacle geese) (see Table 2 for an overview of the outcomes). A sleep homeostatic response can be reflected by the number of NREM sleep epochs and the intensity of NREM sleep. We reported a clear NREM sleep homeostatic response in the jackdaws that was stronger after 8 h of sleep deprivation than after 4 h of sleep deprivation, which was reflected in a larger increase in NREM sleep time and cumulative EEG power (**chapter 2**). Starlings showed a partial NREM sleep homeostasis in NREM sleep time and EEG power with largely similar responses after 4 and 8 h of sleep deprivation (**chapter 3**). Barnacle geese showed predominantly NREM sleep homeostasis in NREM sleep time and very limited in EEG power in summer where the maximum response is reached after 4 hours of sleep deprivation (**chapter 5**). Interestingly, in geese, this compensatory NREM sleep response to sleep deprivation was completely absent in winter.

Table 2. The presence of a sleep homeostatic response in the 3 bird species for NREM and REM sleep. The symbols indicate a complete homeostatic response that is dependent on the duration of sleep deprivation (+), a partial homeostatic response that has yet to be confirmed if it is dependent on the duration of previous wakefulness (+/-), no evidence for a homeostatic response to sleep deprivation (-).

| Species | Season | NREM sleep | REM sleep |
|-------------------------|--------|------------|-----------|
| <i>Coloeus monedula</i> | | + | + |
| <i>Sturnus vulgaris</i> | | +/- | - |
| <i>Branta leucopsis</i> | Winter | - | + |
| | Summer | + | +/- |

In mammals, the homeostatic response to sleep deprivation is often mostly reflected by an increased NREM sleep EEG power in the slow-wave range or delta range (1 – 5 Hz) (Franken, Tobler and Borbély, 1991; Huber, Deboer and Tobler, 2000; Deboer, 2013). For all the bird species studied in this thesis, sleep deprivation induced an increase in NREM sleep EEG power in a broad frequency range from 1.5 to 25 Hz (**chapter 2, chapter 3** and **chapter 5**). Interestingly, in both songbird species, there was an opposite response in sleep intensity between 0.4 – 1,5 Hz where NREM sleep EEG spectral power significantly decreased compared to baseline. This indicates that the gold standard of slow wave activity (SWA) in the delta range (1 – 4 Hz) as a response to sleep deprivation does not apply to birds. Therefore, these findings strongly caution against extrapolating mammalian-based sleep homeostatic definitions to different taxonomic groups.

REM sleep homeostasis

Among the three bird species that were investigated, there was much variation in the occurrence of REM sleep during baseline sleep with less than 1% per TST in starlings, 11.5% in barnacle geese and 19% in jackdaws where the two extremes are among the same order of songbirds (Table 1). Additionally, the occurrence of a homeostatic REM sleep rebound was similarly variable (Table 2). Among these songbird species, jackdaws showed mammalian-like sleep homeostasis reflected by an increase in REM sleep time that was only observed after 8 hours of sleep deprivation but not after 4 hours of sleep deprivation (**chapter 2**). On the other hand, starlings show a complete lack of REM sleep homeostasis (**chapter 3**). Since jackdaws and starlings belong to the same order of songbirds, there must be a more complex explanation than taxonomy alone for the differences in REM sleep.

Table 1. Overview of sleep characteristics for NREM and REM sleep as a proportion of TST, nighttime and daytime. Abbreviations: TST: total sleep time, REM: rapid-eye-movement, NREM: non-REM.

| Nighttime (%) | | | | | |
|-------------------------|--------|------------|-----|-----------|-----|
| Species | Season | NREM sleep | SEM | REM sleep | SEM |
| <i>Coloeus monedula</i> | | 75.3 | 2.1 | 17.2 | 2.3 |
| <i>Sturnus vulgaris</i> | | 82.8 | 1.7 | 1.3 | 0.4 |
| <i>Branta leucopsis</i> | Winter | 55.6 | 2.2 | 8.1 | 1.0 |
| | Summer | 40.4 | 1.9 | 6.6 | 0.7 |
| Daytime (%) | | | | | |
| Species | Season | NREM sleep | SEM | REM sleep | SEM |
| <i>Coloeus monedula</i> | | 4.3 | 1.0 | 0.1 | 0.0 |
| <i>Sturnus vulgaris</i> | | 6.7 | 1.9 | 0.0 | 0.0 |
| <i>Branta leucopsis</i> | Winter | 16.8 | 1.0 | 1.6 | 0.5 |
| | Summer | 29.1 | 1.8 | 3.3 | 0.4 |

Barnacle geese showed on average 11.5% REM sleep of TST which is close to the average of 8% of REM sleep per TST of all recently examined bird species (Roth *et al.*, 2006). Barnacle geese showed a REM sleep homeostasis response to sleep deprivation in both seasons except after 8 hours of sleep deprivation in winter (**chapter 5**).

Taking the results from the three species together, it appears that the amount of baseline REM sleep to some degree predicts the magnitude of the response to sleep deprivation. The starling had very little REM sleep under baseline conditions and also did not show a REM sleep response to sleep deprivation. Instead, the jackdaws had the highest amount of REM sleep under baseline conditions and also had the strongest rebound after sleep deprivation. The geese were in the middle and showed a partial REM sleep rebound depending on season. The strong variation that we found among these species may be relevant information in our search for the functions of REM sleep.

Based on mammalian studies, REM sleep is linked to brain plasticity and regulation of neuronal connectivity, which is thought to be important for memory formation and consolidation (Diekelmann and Born, 2010). This leads to the assumption that REM sleep is important in the brain for information processing and storing in animals with high cognitive abilities. This might partly explain why we see more REM sleep in jackdaws (19% of TST) compared to starlings (< 1% of TST) because corvids have cognitive abilities comparable to that of certain primates (Olkowicz *et al.*, 2016; Pika *et al.*,

2020). However, this would imply that starlings are the least cognitively developed species among the ones we studied, because of the extremely low amount of REM sleep. The latter seems unlikely since starlings are capable of performing cognitive tasks (Farrell *et al.*, 2012), have an extensive song learning repertoire (Eens, Pinxten and Verheyen, 1992; Mountjoy and Lemon, 1995) and need sleep for memory consolidation (Brawn, Nusbaum and Margoliash, 2010). These findings suggest that cognitive capacity is unlikely the full explanation for variation in REM sleep between species.

The variability of REM sleep among species may partly be due to the fact that REM sleep is more difficult to detect in birds compared to mammals in their EEG because REM sleep episodes in birds are in general very brief, and REM sleep is not always accompanied by complete loss of EMG muscle tone, even when the head drops. Along this line, one may wonder whether REM sleep in birds is always expressed at the cortical level as it is in mammals. However, this is unlikely the full explanation for the large REM sleep variation we see in our studies, given that our electrode placement and analysis were similar for all species. Also, an underestimation of REM sleep in starlings is not supported by the fact that we did not see clear REM sleep behaviours such as head droppings (unpublished observations). Perhaps further and more detailed studies are needed here that include measurements of muscle tone, eye closure and iris diameter. Indeed, iris diameter in birds appears to be a good indicator for REM sleep estimation and could perhaps confirm or clarify differences in REM sleep among birds (Ungurean *et al.*, 2020).

Flexibility of sleep

One of the most intriguing findings of this dissertation is the fact that sleep is strongly modulated by environmental factors and shows much more flexibility than what has been previously thought based on controlled laboratory studies (Aulsebrook *et al.*, 2016; Rattenborg *et al.*, 2017). One of those environmental processes that strongly modulates sleep patterns and sleep duration is seasonality. In **chapter 4** we showed that starlings have 5 h less NREM sleep in summer compared to winter, which seemed related to the much shorter night length in summer compared to winter. In fact, we provided evidence that starlings may live under a constant high sleep pressure in summer as indicated by a steeper slope in the decline of NREM sleep EEG power during the first three hours of the night and also by the fact that the birds displayed mid-day naps in summer. Similarly, although less pronounced, barnacle geese have

2 h less NREM sleep in summer compared to winter (**chapter 5**). This reduction of sleep time in summer was paralleled by a strongly attenuated daily rhythm in sleep and wakefulness. In summer, sleep was more spread out over the 24-h cycle. The decrease in circadian regulation in barnacle geese can be explained by the fact that during summer, wild migratory barnacle geese breed in the high Arctic under 24 h light conditions (Eichhorn, *et al.*, 2009). The arrhythmic sleep-wake patterns would then facilitate feeding activity across the 24-h day.

In our starlings under semi-natural conditions, we did not observe this suppression in daily rhythmicity during summer, even though starlings can migrate to similar Northern latitudes compared to geese. Starlings are an omnivorous species and may therefore retain their circadian organization in summer as has been reported for Arctic-breeding insectivorous bird species with a circadian activity that coincides with the activity peaks of insects (Silverin *et al.*, 2009) compared to the arrhythmic herbivorous barnacle goose. Therefore, there is still a stronger circadian regulation in the starlings during summer, with most sleep during the shorter nights, which might explain why sleep time in summer is more strongly suppressed in the starlings than in the geese.

Another factor that strongly influenced sleep under seminatural conditions in our studies was the phase of the moon. In both starlings and barnacle geese, NREM sleep was suppressed by 2 h during nights with full moon compared to nights with new moon (**chapter 4, chapter 5 and chapter 6**). The most obvious explanation for this finding is a direct sleep-suppressing effect of light reflected from the moon, particularly during the full moon phase. This idea of a sleep-suppressing effect of moonlight is supported by the further finding in geese that sleep could also be suppressed by low-level artificial light at night (ALAN), particularly on overcast nights with an increase in ALAN levels due to its reflection from the clouds (**chapter 6**). With highest cloud cover level, observed light levels were similar to those measured during full moon at our study site. In fact, when ALAN reaches similar light levels to full moon, the reduction in NREM sleep time is also similar to the the reduction of NREM sleep time of nights with full moon (**chapter 6**). Therefore, light seems to be the most likely explanation as to why birds decrease NREM sleep time under the full moon. Barnacle geese might have adapted to promote wakefulness during moonlit nights because this is a relatively safe time for foraging since predators are easily detected (Tinkler, Montgomery and Elwood, 2009; Portugal *et al.*, 2019). Nevertheless, while light is a likely explanation for the reduction in sleep time during full moon, other factors may play a role as well. During full moon, barnacle geese showed a strong

tendency for reduced daytime sleep as well, which is not easily explained by an effect of moonlight. It might be that birds can respond to changes they sense in the magnetic field since the full moon can cause fluctuations in Earth's magnetic field by its gravitational pull (Chapman, 1913).

Measuring sleep in a more natural context yields surprising findings and shows an enormous magnitude of flexibility that is not observed in controlled laboratory conditions. However, it may not always be possible or desirable to measure EEG in wild bird species because they are too small to carry the necessary equipment (see Figure 2 **chapter 1**) or because it is difficult to re-capture them. Accelerometry-based activity measurements may then be the next-best alternative. In **chapter 7** we tested in barnacle geese how reliable accelerometer-based activity is as a proxy for sleep-wake determination since we collected EEG and accelerometer data simultaneously. We found that accelerometer data serves as a good proxy for sleep, yet the data should be interpreted with caution. The correlation strength between activity and EEG varies with season and daytime/nighttime. More importantly, the correlation between activity and REM sleep is substantially weaker compared to NREM sleep. This might be a species-specific feature where activity might correlate better in species with higher amounts of REM sleep.

Prospects

The studies described in this thesis clearly demonstrate the importance of studying sleep in a more ecological context for understanding the true flexibility of sleep and its functions. One important step is to study more species to allow for detailed phylogenetic comparisons. Another exciting challenge will be to continue our studies on sleep in birds under truly wild conditions. Many important questions lie ahead, including how geese organize their sleep during the arctic breeding season under conditions of continuous day light, when they are constantly busy guarding their young.

Another question is if or when geese sleep during their migrations. Do they stop over to sleep or are they capable of sleeping in mid-air, even though they mostly use a continuous wing-flapping technique and do not have long gliding flights like some other birds? This is important since the only bird species so far that has been reported to sleep during flight based on EEG recordings is the frigate bird, which only sleeps during soaring and gliding techniques (Rattenborg *et al.*, 2016). In **chapter 9**, we described our explorative expeditions to prepare for EEG studies in wild geese

in the future. These expeditions allowed us to build experience with fieldwork in wild geese, with the potential field sites and with the recording technologies that enable us to execute the EEG experiments in the future. During these expeditions, we collected GPS data of 4 geese with high-resolution accelerometer data which provide us with clues on how active barnacle geese are during migration but also during their stop-over sites to see if there is time for rest and recovery. In addition, the recorded accelerometer data can give us some details in the animals' motion during flight to see what flight techniques they use. For measuring sleep in the wild across different seasons, including the breeding phase and the migration phase, battery life and memory capacity are still limiting factors. We have now gathered information on how reliable intermittent EEG recording schedules are (**chapter 8**). During future experiments on tracking sleep in migratory barnacle geese, we might be able to extend the total recording time by using these EEG recording schedules and at the same time obtain the same explanatory value as a continuous recording. Our analysis showed that even with intermittent recordings up to 1 min per half hour, the data yields the same explanatory value as compared to a continuous recording.

In conclusion, the results presented in this thesis show that birds are an interesting group for studying sleep, both under controlled and (semi)natural conditions. The variation and flexibility of sleep under seminatural conditions is much larger than expected based on laboratory studies, which cries for more research aimed to understand how birds can cope with the consequences of this enormous flexibility in sleep. One aspect of this is REM sleep. As clearly demonstrated in this thesis, there is a substantial amount of variation in REM sleep time in birds, even among the same order. More research is needed that is aimed at understanding the function of REM sleep in birds and whether this is similar to what we call REM sleep in mammals.

