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RESEARCH ARTICLE

Seasonal variation in rest–activity patterns in barnacle geese: are measurements of activity a good indicator of sleep–wake patterns?

Sjoerd J. van Hasselt[1,*], Theunis Piersma[1,2] and Peter Meerlo[1]

ABSTRACT

Sleep is a widely spread phenomenon in the animal kingdom and is thought to serve important functions. Yet, the function of sleep remains an enigma. Studies in non-model animal species in their natural habitat might provide more insight into the evolution and function of sleep. However, polysomnography in the wild may not always be an option or first choice and some studies may need to rely on rest–activity recordings as a proxy for sleep and wakefulness. In the current paper, we analyzed how accelerometry-based activity data correlate with electroencephalogram (EEG)-based sleep–wake patterns in barnacle geese under seminatural conditions across different seasons. In winter, the geese had pronounced daily rhythms in rest and activity, with most activity occurring during the daytime. In summer, activity was more spread out over the 24 h cycle. Hourly activity scores strongly correlated with EEG-determined time awake, but the strength of the correlation varied with phase of the day and season. In winter, the correlations between activity and waking time were weaker for daytime than for night-time. Furthermore, the correlations between activity and waking during daytime were weaker in winter than in summer. During daytime in winter, there were many instances where the birds were awake but not moving. Experimental sleep deprivation had no effect on the strength of the correlation between activity scores and EEG-based wake time. Overall, hourly activity scores also showed significant inverse correlation with the time spent in non-rapid eye movement (NREM) sleep. However, correlation between activity scores and time spent in REM sleep was weak. In conclusion, accelerometry-based activity scores can serve as a good estimate for time awake or even the specific time spent in NREM sleep. However, activity scores cannot reliably predict REM sleep and sleep architecture.

KEY WORDS: Activity, Sleep, EEG, Bird, Geese, Seasonality

INTRODUCTION

All mammals and birds appear to spend a large part of their life asleep. It is widely accepted that sleep is homeostatically regulated and that a need for sleep builds up during wakefulness (Benington,

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2000; Deboer, 2013). Yet, despite many theories, the exact function of sleep remains an enigma (Siegel, 2005). However, much of what is currently being learned about sleep is based on experimentation in a handful of mammalian species and almost exclusively in tightly controlled laboratory settings. Indeed, field studies to examine sleep under the natural conditions where it evolved are rare (Rattenborg et al., 2017). In fact, in most ecological studies that assess behavior in the wild, sleep episodes are often little more than blanks in the activity recordings. However, if sleep indeed serves important functions, then the time available for sleep or any restrictions herein may very well be a determining factor in the fitness of an individual.

Recent technological developments allow for detailed studies of sleep–wake patterns and sleep architecture based on recordings of brain activity even in freely moving animals (Vyssotski et al., 2006; Rattenborg et al., 2017; Massot et al., 2019). However, the datalogger methodology and necessary surgical procedures for implantation of brain electrodes required for this approach may not be the first or preferred choice for every study. In many cases, researchers may still choose the simpler approach of inferring sleep–wake patterns from some kind of measurement of movement activity (Stuber et al., 2015; Rattenborg et al., 2017). This has been done in a wide range of species, from small birds that may be too small to carry dataloggers without affecting their natural behavior (Steinmeyer et al., 2010; Stuber et al., 2015), to large mammals in which it is difficult to carry out the necessary surgical procedures (Miller et al., 2008; Mitani et al., 2010; Bäckman et al., 2017; Gravett et al., 2017).

This approach is based on the assumption that a lack of movement indicates that an animal is asleep. However, to date it is unknown how reliable rest–activity recordings are as a proxy for sleep–wake patterns in freely moving animals under (semi)natural conditions. Wakefulness can occur when animals are motionless; for example, in the three-toed sloth (*Bradypus variegatus*) (Voirin et al., 2014). Also, animals might be considered awake as a result of movements registrations, while actually being (partially) asleep; for example, flying birds (Rattenborg et al., 2016), swimming dolphins (Lyamin et al., 2008) or ruminants that continue chewing while asleep (Ruckebusch, 1972).

In a previously reported study in barnacle geese, we used a miniature datalogger system for a detailed electroencephalogram (EEG)-based assessment of sleep and sleep homeostasis under semi-natural conditions in winter and summer (van Hasselt et al., 2021). These dataloggers also contained an onboard accelerometer, and in the present study we analyzed how reliable accelerometry-based activity scores are as a proxy for sleep–wake patterns at different phases of the day and in different seasons. We hypothesized that accelerometry could serve as an adequate proxy for assessing wakefulness and sleep; however,

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assessing detailed aspects of sleep architecture and the distribution of different sleep states probably requires measurements of cortical activity.

MATERIALS AND METHODS

Animals and housing

Twelve barnacle geese, *Branta leucopsis* (Bechstein 1803) (7 males, 5 females), were used in this study to measure sleep and activity. The geese were group-housed in a semi-natural enclosure with access to water and food *ad libitum* (food item numbers 615220 and 384020; Kasper Faunafood, Woerden, The Netherlands). The winter recordings took place between February and March (10 h:14 h average light:dark cycle). The summer recordings took place in June (17 h:7 h light: dark cycle). In between these seasonal recording sessions, the geese were all together in a large outdoor meadow (length×width 68 m×60 m) with a water pond (25 m×15 m) and had food *ad libitum*.

Surgery

The barnacle geese underwent surgery for implantation of epidural EEG electrodes and subcutaneous electromyogram (EMG) electrodes as previously described (van Hasselt et al., 2021). Surgery was performed under isoflurane anesthesia (1.5–2%). Before surgery, diazepam (0.68 ml; 2 mg kg^{-1}) and meloxicam (0.17 ml; 0.5 mg kg^{-1}) were injected to alleviate stress and pain,

respectively. Five holes (0.5 mm in diameter) were drilled through the crania for the insertion of electrodes (with round gold-plated tips, 0.5 mm diameter; BKL Electronic 10120538, Lüdenscheid, Germany) to the level of the dura mater: two frontal EEG electrodes, one per hemisphere covering the hyperpallium (4 mm lateral of the midline), and three electrodes in a left-to-right line over the caudal part of the telencephalon consisting of one EEG reference electrode (4 mm lateral of the midline), one caudal EMG reference electrode (on the midline) and one ground electrode (4 mm lateral of the midline). Two flexible wires were placed on the neck muscle to record an EMG (PlasticsOne, Roanoke, VA, USA). All electrodes were soldered to a connector (BKL Electronic 10120302, Lüdenscheid, Germany). The connector was subsequently secured to the skull using Paladur dental cement (Heraeus Kulzer, Hanau, Germany) and a 0.6 mm screw served as an anchor point for the implant. A small plastic cap was used to cover the plug and protect it from wear and tear.

Sleep and activity recordings

After a minimum of 2 weeks of post-surgical recovery, activity and sleep–wake patterns in the barnacle geese were measured using a miniature datalogger (Neurologger 2A, Evolocus, Tarrytown, NY, USA). This datalogger records EEG and EMG activity as well as movement acceleration in 3-axes using an accelerometer (LIS302DLH, STMicroelectronics, Geneva, Switzerland). The data were recorded with a sample rate of 100 Hz. With a 3.6 V
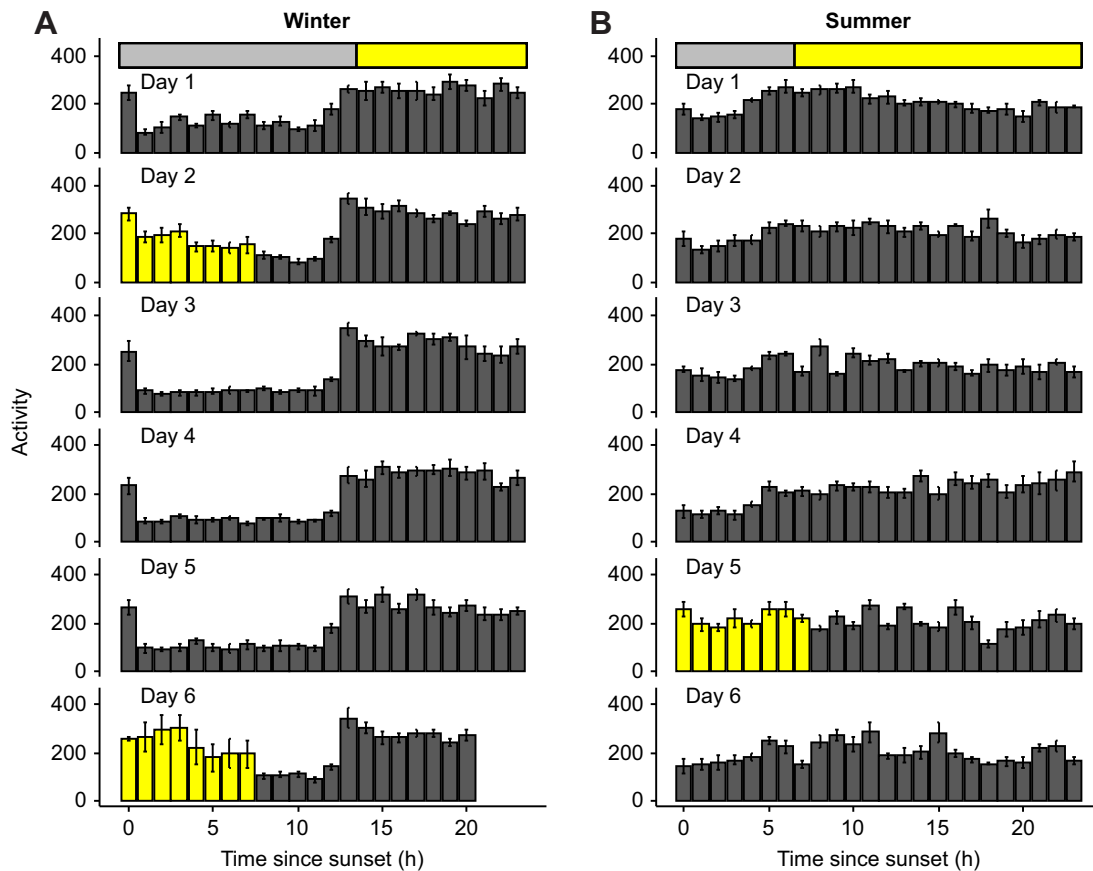
Fig. 1. Average actograms for six consecutive recording days in barnacle geese during winter and summer. (A) In winter (*n*=8), there was a clear daily rhythm in activity, with most activity occurring during daytime. (B) In summer (*n*=8), activity was more spread out over the 24 h cycle. The horizontal gray/yellow bar at the top represents the night–day cycle. The yellow data bars in the graphs represent the hours during which the geese were subjected to sleep deprivation. Data are means±s.e.m.

battery (LS 14250, Saft, Levallois-Perret, France), the loggers could run for approximately 15 days and the data were stored on the datalogger memory chip.

All EEG recordings had a minimum length of 8 days and were collected as previously described (van Hasselt et al., 2021). In short, barnacle geese were housed in two aviaries and underwent two periods of sleep deprivation of 4 and 8 h, starting from sunset in winter and summer in a cross-over design. The loggers were attached to the implants right before noon to have an undisturbed baseline night. After one undisturbed baseline night, a sleep deprivation period was induced by two experimenters, one in each aviary, starting from sunset to last either 4 or 8 h by means of mild stimulation. Standing and walking in the aviary was largely sufficient to keep the animals awake. Whenever animals showed signs of inactivity and eye closure, they were gently tapped on the back. One week later, the sleep deprivation procedure was repeated so that all the geese in both aviaries received both sleep deprivation treatments. In total, every recording yielded a minimum of 3.5 undisturbed days.

Data analyses

The accelerometer data from the logger were used to calculate overall dynamic body acceleration (ODBA) according to published procedures (Duriez et al., 2014). All three accelerometer channels were individually smoothed by applying a running mean of 1 s. Furthermore, for all three channels and every time point, the smoothed values were subtracted from the unsmoothed values for the same time point. Then, ODBA was calculated as a vectoral sum by applying the square root of the sum of the squares of the three accelerometer channels (Duriez et al., 2014). ODBA is relative to the gravitational pull of the Earth (g=9.81 m s^{-2}), and the unit of measurement is milli-g (mg). For simplicity and consistency, in results and figures we refer to ODBA as activity as it is a detailed activity measure.

All EEG/EMG recordings were automatically scored every 4 s for wakefulness, non-rapid eye movement (NREM) sleep and rapid eye movement (REM) sleep by using machine learning algorithms (Somnivore Pty Ltd., Parkville, VIC, Australia). The program used all available (electrophysiological)
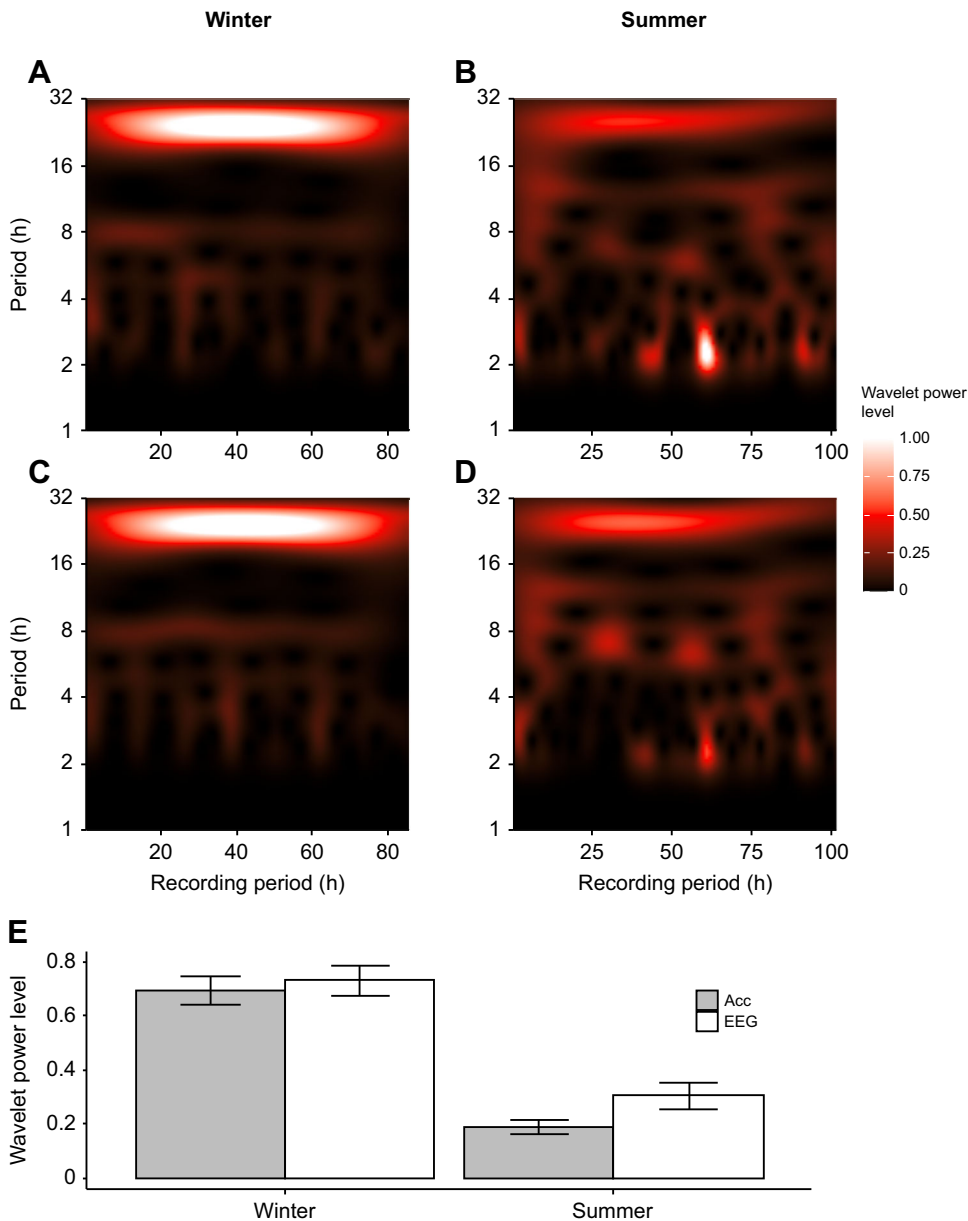

Fig. 2. Wavelet analysis of the activity scores. (A–D) Heatmap of the Morlet wavelet power levels from the actograms shown in Fig. 1 (excluding the sleep deprivation days) for winter (A,C; n=8) and summer (B,D; n=8) based on activity (accelerometry; A,B) and wakefulness (electroencephalogram, EEG; C,D). In winter, there was a clearer 24 h period in the activity rhythm than in summer. This was true for both activity and wakefulness. (E) Wavelet power levels based on the period between 23 and 25 h for accelerometry (Acc) and EEG data. The wavelet power levels around 24 h decreased significantly during summer compared with winter ($P<0.0001$, linear mixed model). Data are means±s.e.m.
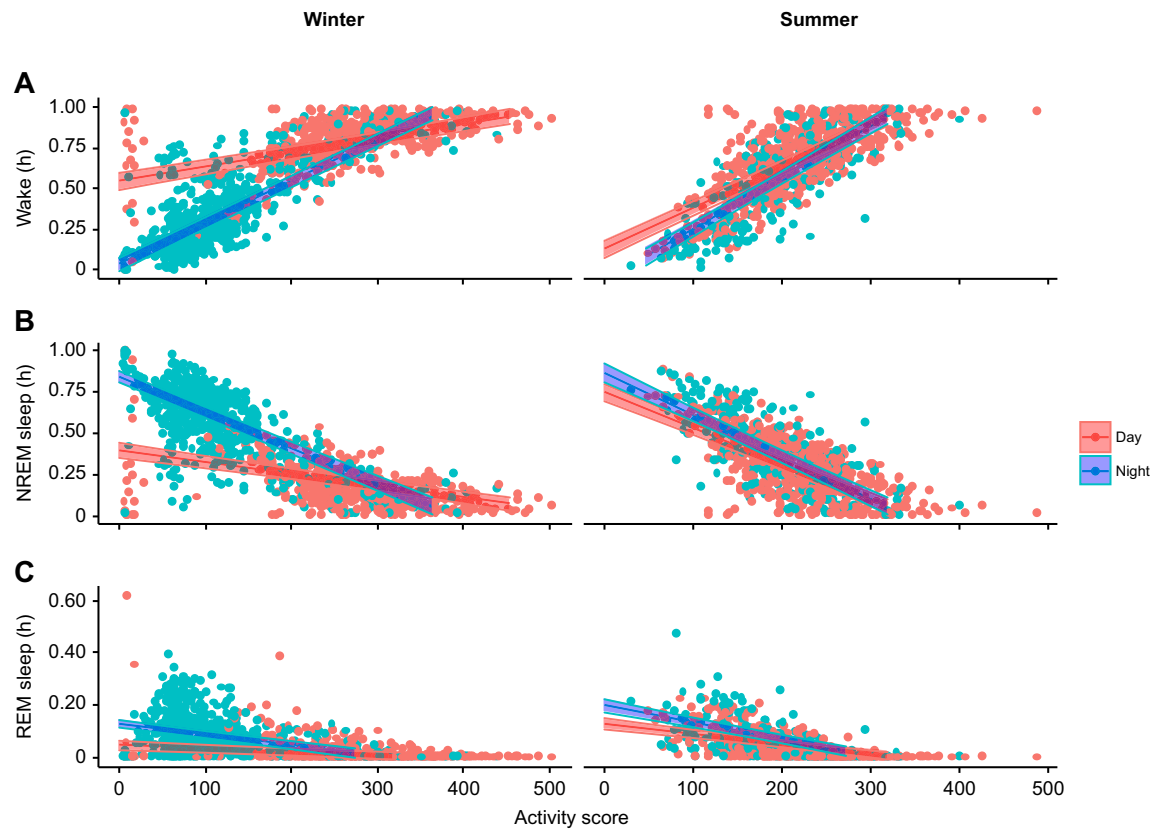
Fig. 3. Correlation between hourly activity scores and the three vigilance states for undisturbed baseline recordings. Data are shown for wakefulness (A), non-rapid eye movement (NREM) sleep (B) and rapid eye movement (REM) sleep (C) during the day and night, for winter (left, n=8) and summer (right, n=8). The regression lines display model predictions based on bootstrap simulations, with the shaded area around the predicted line denoting the 95% confidence interval (CI). In winter, the correlations were significantly steeper during the night compared with the day ($P<0.05$, *post hoc* test after linear mixed model). In summer, the slopes of the regression lines were similar.

channels (EEG+EMG+accelerometer) to determine the vigilance state based on input from a subset of manually scored epochs (±100 epochs per vigilance state). Epochs were scored as wakefulness in the case of high-frequency, low-amplitude EEG activity in combination with high EMG and accelerometer output. NREM sleep was scored when the signal showed high-amplitude, low-frequency EEG activity with reduced EMG activity and a lack of accelerometer output. Epochs were scored as REM sleep when there was high-frequency, low-amplitude EEG activity with low EMG activity and low accelerometer output that sometimes coincided with a slight head drop. This program was initially validated for successfully scoring pigeon EEG (Allocca et al., 2019) and we confirmed it is equally successful in analyzing our goose recordings (van Hasselt et al., 2021). A subset of the recordings performed in winter and summer (three 24 h recordings each) revealed an overall scoring agreement between an experienced sleep scorer and the autoscore of 87.5±0.6% and 85.1±0.9%, respectively. To validate the autoscoring in more detail, F-measures were calculated, which include the precision, sensitivity and specificity of the autoscore compared with the manual score (Allocca et al., 2019). For the winter recordings, the F-values were 0.92±0.0 for wake, 0.85±0.01 for NREM sleep and 0.51±0.04 for REM sleep. For the summer recordings, the values were 0.90±0.01 for wake, 0.85±0.03 for NREM sleep and 0.52±0.06 for REM sleep. The lower F-values for REM sleep presumably are the result of the much shorter episodes and consequently more frequent transitions states, which may affect

the accuracy of both manual and autoscoring. The average amount of REM sleep per day did not differ between manual scoring and autoscoring (3.7±0.4% per day for manual scoring and 6.3±0.3% per day for autoscoring during winter, and 4.8±1.5% per day for manual scoring and 4.5±2.1% per day for autoscoring during summer; P=0.15 and P=0.7, respectively; *post hoc* test after linear model).

All hourly activity scores and EEG-based wake and sleep data were correlated by calculating the Pearson correlation coefficients over all the baseline days where the hours of sleep deprivation and recovery day were omitted from the analysis. Next, we did an analysis to test whether the correlation strength was affected by experimental sleep deprivation by comparing the first 8 h immediately after sleep deprivation with the corresponding hours during the baseline recordings.

Statistics
Data were analyzed in the statistical program R and were modeled according to linear mixed effect models by taking animal ID as a random effect, using the lme4 package (v.3.0.1., http://www.R-project.org/; Bates et al., 2015). A linear model was computed when the model performed better without a random component. From the lme4 package the BootMer function was used for bootstrapping. This yielded accurate model estimates based on 10,000 simulations including 95% confidence intervals (CI) (Buckland et al., 1998; Morris, 2002). *Post hoc* analysis was done using the lsmeans
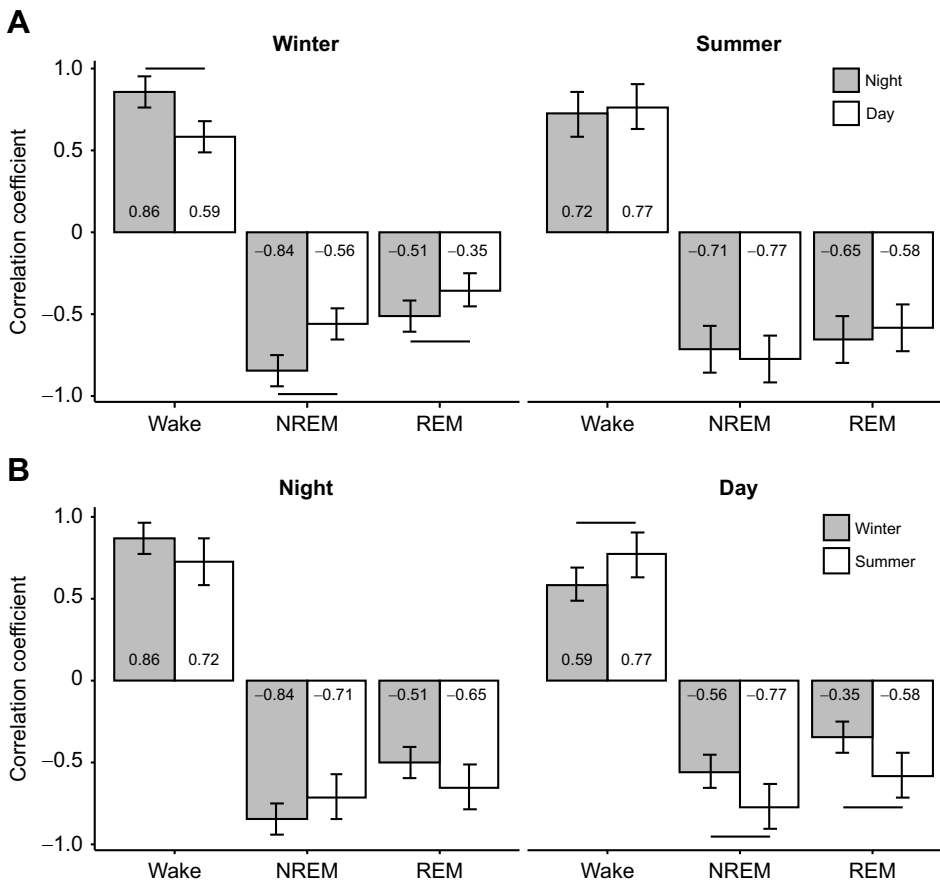
Fig. 4. Correlation of hourly activity scores and the EEG stages (wakefulness, NREM sleep and REM sleep) during day/night and season. (A) Correlation between night and day within season. In winter, all correlations during the night were significantly better than those during the day. This was not the case for the summer recordings. (B) Correlation between seasons within night and day. The correlations between activity and all sleep stages were significantly better during the day in summer compared with the day in winter. This effect was not observed for the night-time correlations between the seasons. Horizontal bars indicate significant differences ($P<0.05$, *post hoc* test after linear model). Data are means±95% CI ($n=8$ in winter, $n=8$ in summer).

package (Lenth, 2016). Time–frequency analysis was computed on the activity and EEG datasets by using a Morlet wavelet power analysis (Morlet et al., 1982a,b; Roesch and Schmidbauer, 2018). All correlation statistics were done using Pearson correlation coefficients. Acquired *P*-values <0.05 were considered statistically significant.

RESULTS

In winter, the geese displayed a clear day–night rhythm in their activity, with most of it occurring during daytime (Fig. 1A). In summer, activity was more spread out over the 24 h cycle (Fig. 1B). Morlet wavelet analysis performed on the activity scores (without the sleep deprivation days) showed that during winter, barnacle geese had a clear 24 h period in their activity rhythm (Fig. 2A). In summer, this periodicity was much weaker (Fig. 2B). The same Morlet wavelet analysis on the hourly EEG-based wake time scores similarly showed a clear 24 h rhythm in wakefulness during winter and a strongly reduced daily rhythm in summer (Fig. 2C,D). After averaging all wavelet power levels computed between the periods of 23 and 25 h, the average wavelet power level was significantly lower in summer than in winter for both activity- and EEG-based waking scores (*P*<0.001, linear mixed model; Fig. 2E). The wavelet power analysis showed there were no significant differences between activity- and EEG-based waking, independent of season.

We computed a linear mixed effect model to assess the relationship between hourly activity scores and the time spent in each of the three vigilance states for daytime and night-time only for the undisturbed baseline recordings (Fig. 3). The hourly activity scores significantly predicted EEG-based time spent in wakefulness

(Fig. 3A), NREM sleep (Fig. 3B) and REM sleep (Fig. 3C), both in winter and in summer. Overall, the more movement the geese displayed, the more time they spent awake and the less time they spent in NREM and REM sleep.

In summer, the activity scores correlated with vigilance states similarly for night-time and daytime. In winter, however, the correlations between activity and vigilance states were lower for daytime (*P*<0.05, *post hoc* test after linear model; Fig. 4A). Also, these daytime correlations between activity and vigilance states were significantly lower in winter than during summer (*P*<0.05, *post hoc* test after linear model; Fig. 4B). In general, the correlation between activity scores and time spent in REM sleep was significantly lower than between activity scores and NREM sleep (*P*<0.001, *post hoc* test after linear model).

The 4 h and 8 h periods of sleep deprivation not only increased wakefulness but also increased activity, but more so in winter than in summer (Fig. 5). The correlation between accelerometry-based hourly activity scores and EEG-based hourly waking and sleep time persisted during the first 8 h after sleep deprivation (Fig. 6). In fact, for the 8 h window immediately following sleep deprivation, the correlations between activity and the three vigilance states were not different from the correlations for the same time window during the preceding baseline day, either in winter or in summer (Fig. 7).

DISCUSSION

The barnacle geese displayed a more pronounced day–night rhythm in activity in winter than in summer. A possible explanation for this reduction may lie in the fact that barnacle
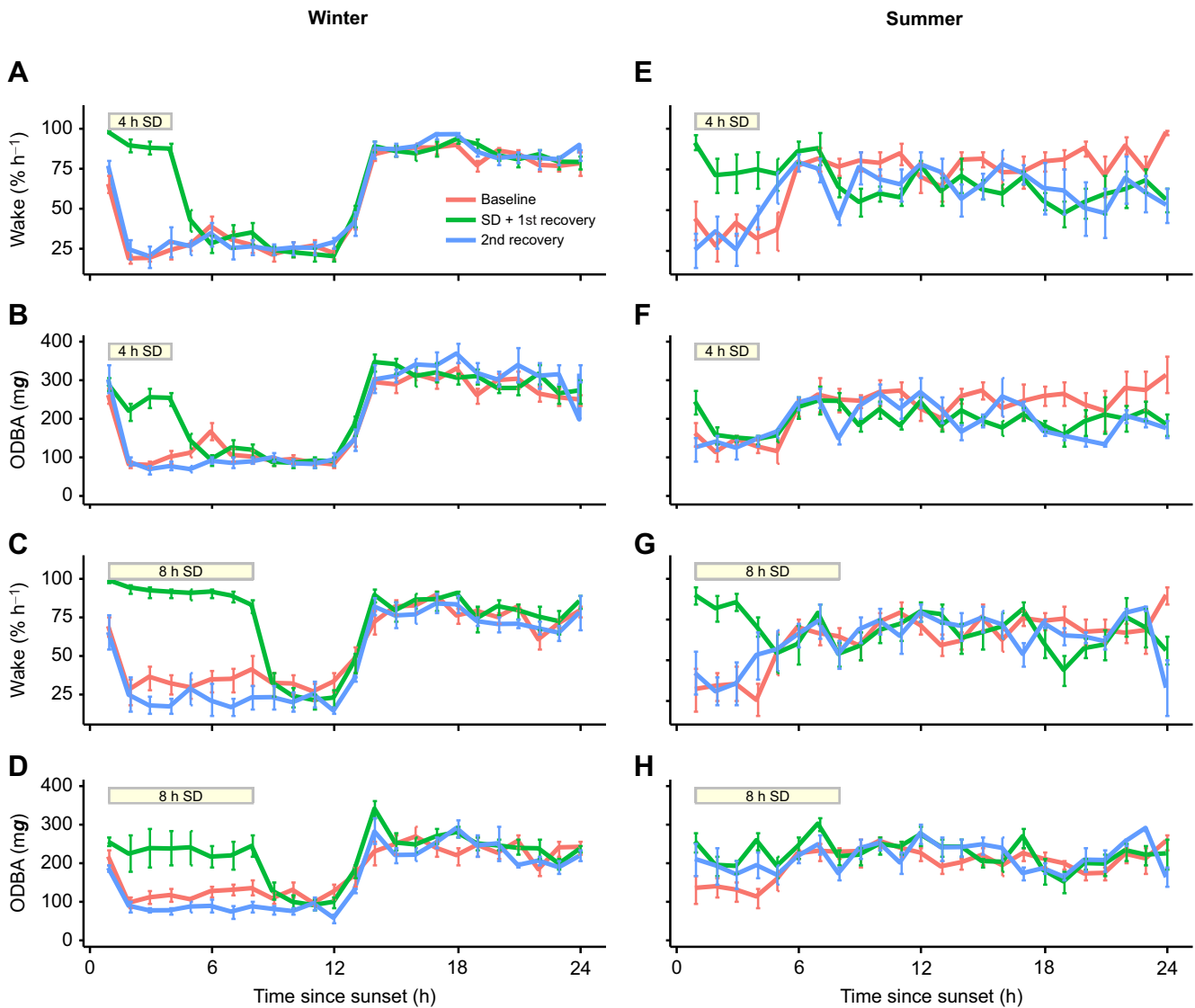
Fig. 5. Comparison between EEG and accelerometry data for baseline, sleep deprivation and recovery. EEG (A,C,E,G) and accelerometry (overall dynamic body acceleration, ODBA; B,D,F,H) data are shown for winter (left) and summer (right) following 4 h (top two rows; n=8 for winter; n=7 for summer) and 8 h (bottom two rows; n=6 for winter; n=8 for summer) of sleep deprivation (SD), as indicated by the yellow bar. In winter, activity was more strongly correlated with wakefulness than in summer. Data are means±s.e.m.

geese are a migratory bird species and the northerly breeding source populations spend a large part of the summer under constant light conditions above the Arctic Circle (Eichhorn et al., 2009). Under these conditions, a strong rhythm may not have any specific advantage (Steiger et al., 2013). In fact, the lack of rhythmicity in this herbivorous goose species might facilitate feeding at any time of day. This is reflected in a faster growth rate for goslings in the Arctic compared with goslings in temperate regions (Boom et al., 2022). Besides barnacle geese, other Arctic bird species show a similar reduction in circadian rhythmicity (e.g. ptarmigan, *Lagopus muta*; Stokkan et al., 1986), as well as mammals (e.g. reindeer, *Rangifer rangifer*; van Oort et al., 2005). However, insectivorous bird species still retain strong 24 h circadian rhythms in the Arctic that coincide with the activity peaks of insects (Silverin et al., 2009).

Perhaps another reason for the weak daily rhythms in summer might be that the geese during this time are molting and breeding.

The reduction in circadian amplitude may imply an increase in vigilance around the clock, which could aid them in protecting their offspring and themselves against predators during this vulnerable period. In contrast to waterfowl, songbirds maintain the ability to fly during molt, which could be one reason why songbirds do not show a similar reduction in circadian rhythmicity during this time (Steinmeyer et al., 2010; Stuber et al., 2015; van Hasselt et al., 2020).

Overall, there was a highly significant correlation between the hourly activity scores and the time spent in EEG-based wakefulness: the more animals were awake, the more they moved. This correlation between activity and waking varied somewhat with the phase of the day and season. In winter, the correlation between activity and waking time was lower for daytime than for night-time. Furthermore, the correlation between activity and waking during daytime was lower in winter than in summer. These findings imply that during daytime in winter, there were many instances where the birds were awake but not moving.
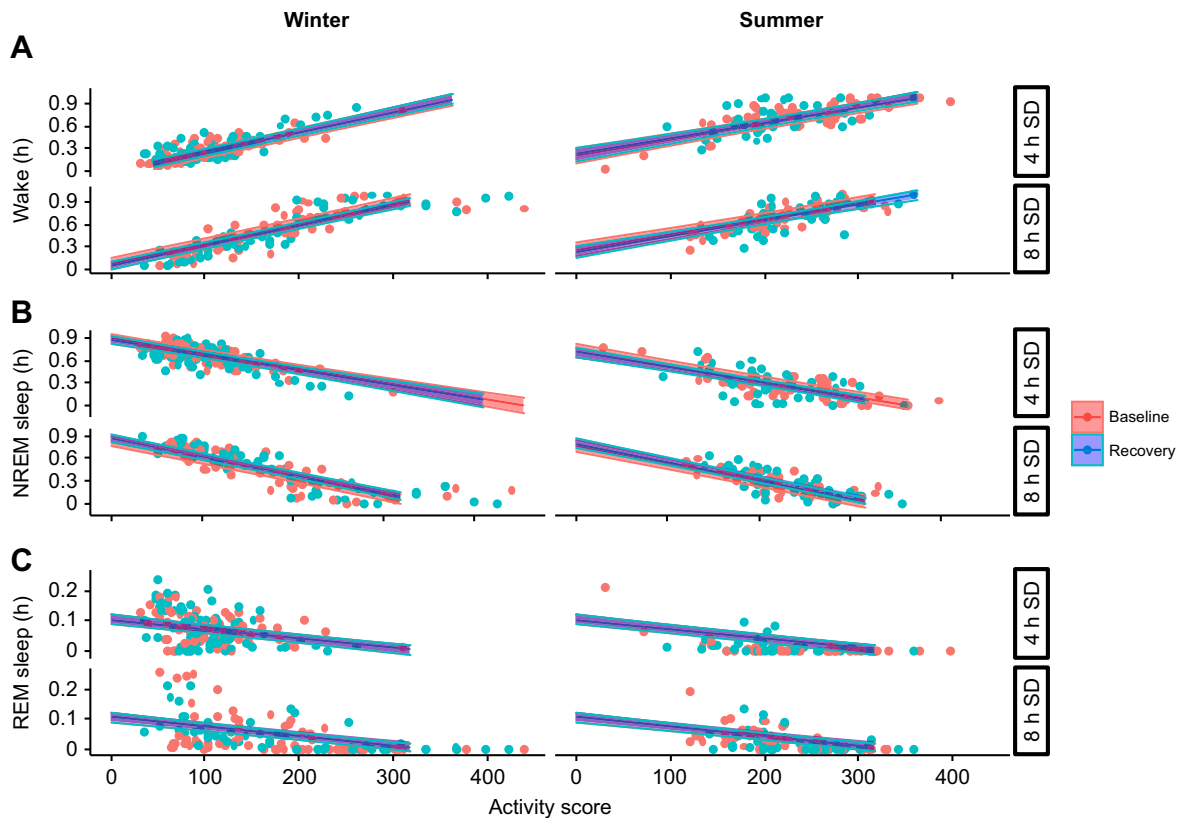
Fig. 6. Correlation between hourly activity scores and vigilance states for baseline and recovery from sleep deprivation. Data are shown for wakefulness (A), NREM sleep (B) and REM sleep (C), during the day and night, for winter (left; n=8 for 4 h SD; n=6 for 8 h SD) and summer (right; n=7 for 4 h SD; n=8 for 8 h SD). The regression lines display model predictions based on bootstrap simulations with the shaded area around the predicted line denoting the 95% CI. There were no differences between the baseline and recovery day for all sleep stages in both 4 and 8 h SD groups.

In barnacle geese, sleep consists of mostly NREM sleep (88.5%), which makes it nearly the inverse of waking time. It is therefore not surprising that we also found strong, yet negative, correlations between hourly activity scores and time spent in NREM sleep. In contrast, REM sleep only makes up 11.5% of total sleep time, which may be one of the reasons that it showed weaker correlation with activity scores. While REM sleep episodes are characterized by low activity scores, this is true for NREM sleep as well. Therefore, most episodes with little to no activity will represent NREM sleep and will only poorly predict REM sleep.

The correlation between activity scores and EEG-based waking time and NREM sleep was unaffected by experimental sleep deprivation. After 4 or 8 h of sleep deprivation in summer, the slope of the regression between activity scores was similar. The finding that sleep deprivation did not affect the relationship between activity scores and sleep–wake patterns coincides with our earlier finding that barnacle geese show no compensation in sleep time after sleep deprivation in winter and only a modest response in summer (van Hasselt et al., 2021).

Overall, the data indicate that in barnacle geese under semi-natural conditions, activity is a good indicator of waking time, with correlation coefficients between 0.59 and 0.86. It also provides a good estimate of NREM sleep time, with correlation coefficients between −0.56 and −0.84. However, activity scores showed a much weaker relationship with REM sleep, with correlation coefficients as low as 0.35. The lower relationship for REM sleep might be due to the fact that small changes in specific accelerometer channels are less pronounced in the overall measure

of activity that we used (ODBA). Additional sensors such as a magnetometer or gyroscope might improve the correlation with REM sleep.

Importantly, activity scores in the present study were based on accelerometry with a head-mounted datalogger that recorded even the most subtle head movements. Obviously, the correlation between movement activity and EEG-based vigilance states depends on how activity is assessed. For example, measuring activity with a device mounted on the back instead of the head presumably would lead to weaker correlations because it would only record gross body movements and not the head movements that may still occur in animals that are otherwise motionless.

Furthermore, notwithstanding the highly significant correlations between behavioral rest–activity patterns and EEG-based sleep–wake patterns, it must be kept in mind that under specific conditions such correlations can deteriorate. For example, various studies have reported that wake-related behaviors such as open eyes, standing position and movements can be associated with slow brain waves that are characteristic of NREM sleep (Berger and Walker, 1972; Ruckebusch, 1972; Rattenborg et al., 2001; Goldshmid et al., 2004; Gnone et al., 2006; Lyamin et al., 2008; Lesku et al., 2011; Pigarev et al., 2011).

In conclusion, this study shows that barnacle geese under semi-natural conditions have strong daily rhythms in activity and sleep during winter but only weak daily rhythms in summer. Additionally, this study provides evidence that the translational strength of activity to EEG states is affected by season and
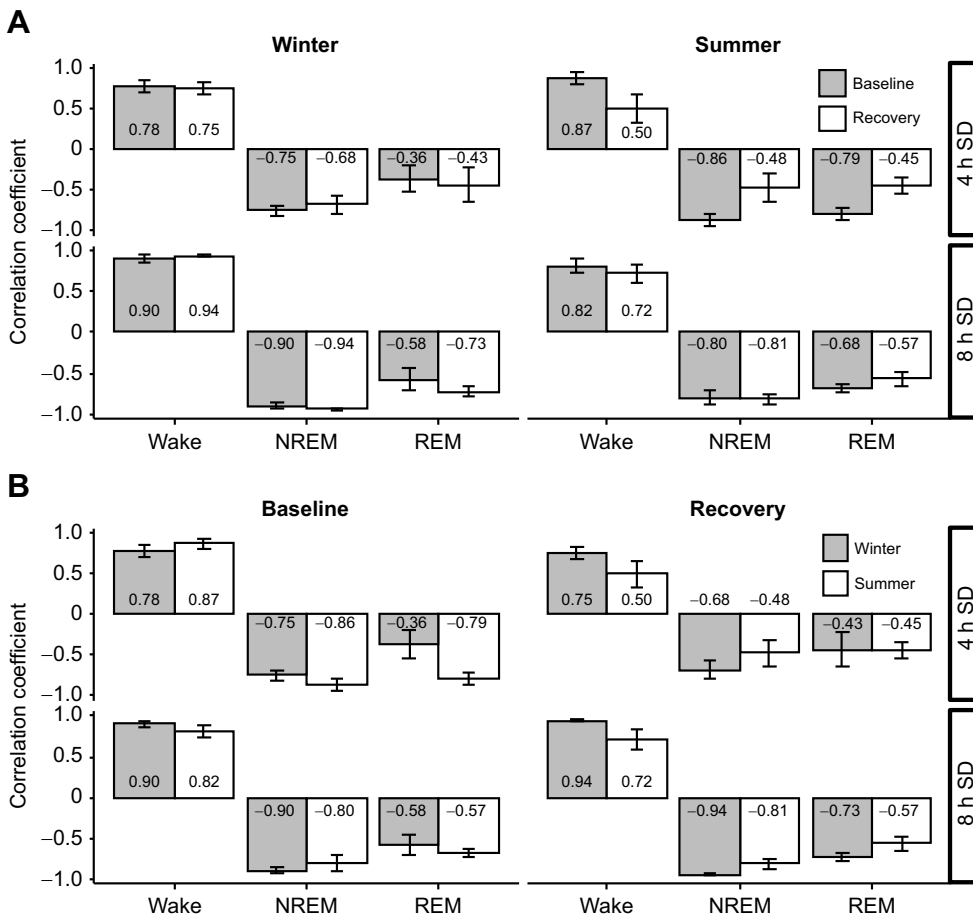
Fig. 7. Correlation between hourly activity scores and the EEG stages (wakefulness, NREM sleep and REM sleep) following sleep deprivation. (A) Correlation between baseline and recovery from sleep deprivation within season (4 h SD: n=8 for winter, n=7 for summer; 8 h SD: n=6 for winter, n=8 for summer). There were no significant differences between baseline and recovery day in both seasons for both sleep deprivation periods (recording day: P=0.79; recording day×EEG stage: P=0.16; *post hoc* test after linear mixed model). (B) Correlation between season within baseline and recovery (4 h SD: n=8 for winter, n=7 for summer; 8 h SD: n=6 for winter, n=8 for summer). There were no overall differences in the calculated correlation coefficients between season for all stages (season: P=0.32; season×EEG stage: P=0.16; *post hoc* test after linear mixed model). Data are means±s.e.m.

day–night phase. Also, the study suggests that activity is a good proxy for overall sleep time but does not provide detailed explanatory value for the two different sleep states.

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