SYMPOSIUM

Sleep Posture Influences Metabolic Rate and Vigilance in the Common Whitethroat (*Curruca Communis*)

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Synopsis   Migration is an important life-history strategy that is adopted by a significant proportion of bird species from temperate areas. Birds initiate migration after accumulating considerable energy reserves, primarily in the form of fat and muscle. Sustained exercise, such as during the crossing of ecological barriers, leads to the depletion of energy reservesand increased physiological stress. Stopover sites, where birds rest and restore energy, play a fundamental role in mitigating these challenges. The duration of resting at stopover sites is influenced by environmental and physiological conditions upon arrival, and the amount of body fat reserves plays an important role. While sleep is recognized as essential for all organisms, its importance is accentuated during migration, where energy management becomes a survival constraint. Previous research indicated that individuals with larger fat reserves tend to sleep less and favor an untucked sleep posture, influencing energy recovery and anti-predatory vigilance. We explored the relationship between sleep behavior and posture, metabolic state, and energy conservation strategies during migration in the common whitethroat (*Curruca communis*). We were able to confirm that sleeping in a tucked position results in metabolic energy savings, at the cost of reduced vigilance. However, whitethroats did not show alterations of their sleep patterns as a response to the amount of stored reserves. This suggests that they may not be taking full advantage of the metabolic gains of sleeping in a tucked posture, at least at this stage of their migratory journey. We suggest that, to achieve optimal fuel accumulation and maximize stopover efficiency, whitethroats prioritize increased foraging over modulating their sleep patterns.

Introduction

Every year, numerous bird species engage in migratory flights during spring and autumn, to reach the most suitable places to breed or to survive adverse winter conditions. During spring, migrants should minimize total migration duration to arrive at the breeding areas in the shortest possible time, which results in increased reproductive success (Smith and Moore 2005). In preparation for migratory flights, birds accumulate a large amount of energy reserves, mostly in the form of fat and, to a lesser extent, protein (Odum 1960; King and Farner 1966; McWilliams and Karasov 2005). However, the presence of ecological barriers such as seas and deserts forces many species to undertake endurance flights lasting several hours, resulting in rapid energy depletion. As a consequence, individuals need to seek areas where they can rest and refuel, the so-called stopover sites (Bairlein 1985; Biebach et al. 1986; Schmaljohann et al. 2007; Schmaljohann and Eikenaar 2017; Ferretti et al. 2021). The time spent at these sites can vary according to the physiological condition upon arrival, particularly the remaining amount of fat reserves (Dierschke

and Delingat 2001; Fusani et al. 2009; Goymann et al. 2010; Cohen et al. 2014; Smith and McWilliams 2014; Dossman et al. 2018), but also to environmental conditions such as adverse weather (Packmor et al. 2020) and migratory strategy (time- vs. energy-minimizing species, Alerstam et al. 2003).

In addition to rapid variations in the energy reserves stored by the individuals, various additional physiological and behavioral changes characterize the migratory period. One of the most remarkable is the switch in activity patterns observed in many species, particularly passerines, whereby typically diurnal species undertake nocturnal migratory flights (Berthold 1973, 1996; Gwinner 1996). Flying at night is thought to be energetically advantageous due to more favorable atmospheric conditions, including reduced turbulences (Kerlinger and Moore 1989; Schmaljohann et al. 2012) and lower ambient temperatures that facilitate thermoregulation during physical activity (Piersma and Gutiérrez 2021). Moreover, engaging in nocturnal flights may enable migrants to invest their daytime in recovering and restoring energy and water reserves depleted during the night (Lindström 2003; Fuchs et al. 2006; Gómez et al. 2017). However, this restricts the time that a migrant can allocate to sleep, potentially posing a physiological constraint. This appears to be taken to the extreme during spring migration when individuals seek to optimize the time spent at stopover sites to minimize the overall duration of their migratory journey (Hedenström and Alerstam 1997).

Sleep is an essential component of the biology of all animals investigated so far (Amlaner and Ball 1994; Hendricks et al. 2000; Rattenborg and Amlaner 2002; Shaw et al. 2002; Sauer et al. 2003; Mendoza-Angeles et al. 2007; Hartse 2011; Zhdanova 2011; Trojanowski and Raizen 2016; Nath et al. 2017; Leung et al. 2019). The pivotal role of sleep for the organism is easily understood by considering the consequences of sleep deprivation, which can range from serious physical and cognitive impairment (Karni et al. 1994; Stickgold et al. 2001; Van Dongen et al. 2003) to death (Rechtschaffen 1983; Rechtschaffen and Bergmann 2002; Shaw et al. 2002), in the most extreme cases. Despite being a widespread phenomenon among taxa, there are still significant gaps in our understanding of the functions of sleep. Currently, the main view poses the central nervous system as the primary beneficiary of sleep (Hobson 2005), thanks to specific physiological processes such as the clearance of metabolic waste products from the brain (Reimund 1994; Xie et al. 2013; Zhang et al. 2018; Hill et al. 2020) or neuronal network reorganization (Diekelmann and Born 2010; Chauvette et al. 2012; Tononi and Cirelli 2014). Nevertheless, some theories suggest that sleep may also benefit the periphery of the body. One predominant theory predicts a role of sleep in energy management (Berger and Philips 1993). This theory is mainly based on the 15–20% reduction in metabolic rate occurring during sleep compared to quiet wakefulness in humans (White et al. 1985; Fontvieille et al. 1994; Jung et al. 2011; Markwald et al. 2013) and up to 45% in birds (Ferretti et al. 2019). A more recent version of this theory proposes that sleep efficiently allocates energy resources to the most essential physiological processes at any given time (Schmidt 2014). This theory implies that sleep could be adjusted in response to changes in an individual's energetic, physiological, and ecological requirements (Danguir and Nicolaidis 1979; Lesku et al. 2012; Stuber et al. 2014; Ferretti et al. 2019, 2020). This was supported by a recent study on garden warblers (*Sylvia borin*) that aimed to investigate sleep ecology during spring migration (Ferretti et al. 2019). During stopover, sleep patterns, and postures of this species were closely linked to the need to save energy. Upon arrival at the stopover site, individuals with sufficient energy reserves to continue migration tended to sleep during the day and became active at night. Moreover, they preferred sleeping with the head pulled toward the body, facing forward, a position to which we will hereafter refer as "untucked" (Amlaner and Ball 1994). In contrast, individuals with low energy reserves used the daylight hours for refueling and slept during the night, preferring to sleep with the head turned backward and tucked in the feathers (hereafter referred to as "tucked"; Amlaner and Ball 1994). The preference toward this posture was associated with the need to optimize energy consumption. Indeed, the tucked posture minimizes metabolic rates at the expense of vigilance toward potential predators, which was increased when the birds chose to sleep in an untucked posture (Ferretti et al. 2019). While physiological processes may vary across sleep postures, a substantial proportion of the metabolic advantage associated with the tucked position comes from the reduced heat dissipation resulting from positioning the head between the feathers (Ferretti et al. 2020). Feathers' insulating properties minimize heat loss, making tucked sleep posture an effective thermoregulatory strategy (Scholander et al. 1950; Veghte and Herreid 1965; Fortin and Gauthier 2000; Bouchard and Anderson 2011; Pavlovic et al. 2019). For this reason, this behavior is commonly used by bird species with significant featherless body parts (Pavlovic et al. 2019), as well as in those individuals exposed to adverse environmental conditions and low ambient temperatures (Midtgård 1978; Reebs 1986; Wellmann and Downs 2009). This thermoregulatory advantage of the tucked posture compared to the untucked posture appears to have a significant impact on refueling, and

consequently the duration of the stay on-site, in migratory songbirds during stopover as it appears to provide energy savings of ~9% of daily energy expenditure (Ferretti et al. 2020).

The common whitethroat (*Curruca communis*) is a long-distance migrant that is commonly found at Mediterranean stopover sites. In this species, the foraging effort and the amount of time spent sleeping are independent from the amount of stored fuel reserves (Ferretti et al. 2020). We investigated the possibility that the lack of condition dependence is related to a low metabolic payoff of choosing to sleep tucked. To test this hypothesis, we measured metabolic rates during sleep in different postures in birds carrying different amounts of fat. In addition, we measured vigilance to confirm that the trade-off between energy consumption and predation avoidance is the basis of the preference for a specific sleep posture in migrants during stopover.

Material and methods

Study site

Fieldwork was carried out during April and May 2017, 2018, and 2023 on the island of Ponza (40°54′N; 12°58′E), the largest of the Pontine islands in the Tyrrhenian Sea. Ponza is ~50 km off the Western coast of Italy, along one of the main migratory routes for Palearctic passerine migrants. It is used as a stopover site by thousands of migratory birds crossing the Mediterranean Sea during spring migration (Maggini et al. 2020). The strategic position of Ponza allowed us to catch birds that were likely freshly landed after an endurance nocturnal migratory flight over the Mediterranean Sea (Maggini et al. 2020).

Sleep pattern and metabolic rate

A total of 23 whitethroats were captured in the morning, between 10:30 CET and 12:30 CET, using mist nets. We selected one bird per day between April and May 2023. An experienced ringer (MC) scored the energy reserves of each individual using a standardized scoring of fat from 0 (no fat visible) to 8 (breast muscle fully covered with fat), and muscle from 0 (muscle concave around the sternum) to 3 (muscle bulging from the sternum) (Kaiser 1993; Bairlein 1995). We selected only individuals with a fat score equal to or higher than 1, and muscle score equal to or higher than 2. After these measurements, the bird was placed in a custom fabric cage (50 × 25 × 30 cm) equipped with two perches placed at different heights. The bird was provided with food (mealworms, *Tenebrio molitor*) and water *ad libitum*. Food was removed 1 h before the beginning of the experiment to ensure that metabolic rates were mea-

sured in a postabsorptive state. The experiment started at 16:00 CET when the bird was transferred into a custom-made respirometry chamber, a plexiglass box (15 × 15 × 15 cm, volume = 3.4 L) equipped with a perch. The chamber was fitted into a soundproof box to isolate the animals from external sound stimuli. The box was 65 × 44 × 57 cm and was made soundproof with a 5 cm thick "sandwich" panel (aluminium-foam-aluminium) and an ~2 cm thick acoustic mat. The front door was sealed with triple-layer glass. An LED light system (three bulbs LED STAR CLASSIC A100,1521lm, OSRAM) was mounted above the box, the light of which was diffused through a 5 mm thick acrylic glass and a 4 mm thick white PVC pane. The light in the soundproof box was switched off at sunset (around 19:30 CET). In the night, the interior of the soundproof box received light only through the large window mounted on the front door, reaching a light intensity of <0.1 lux (measured with ScreenMaster lux meter, Hagner, Sweden).

We measured the rate of oxygen consumption ($\dot{V}O_2$) using an open flow-through system. Incoming air was dried through a Drierite® column and supplied to the chamber at a constant flow rate of 600 mL/min. The flow was generated by a mass flow system (MFS, Sable Systems Europe GmbH, Berlin, Germany). After passing through the chamber, the outcoming air was subsampled at a rate of 250 mL/min and measured using a portable gas analyzer (Field Metabolic System—FMS, Sable Systems Europe GmbH, Berlin, Germany), which measured the fraction of H_2O, CO_2, and O_2 in the exhaled air. Every 20 min of measuring air coming from the bird, we took a 5-min reference sample to correct for drift. We calculated $\dot{V}O_2$ using formulas from Lighton (2018). We recorded the behavior of the bird during the whole metabolic measurement using two infrared-sensitive cameras placed inside the soundproof box and connected to a recording system (700-line ccd camera; 16 fm/s HANDIKAM, Redruth, Cornwall, England). Ambient temperature during the metabolic measurement was continuously monitored using a custom-made sensor (Research Institute of Wildlife Ecology, University of Veterinary Medicine Vienna; Resolution 0.0625°C; Accuracy ± 0.1°C). The measurement was stopped at sunrise and the birds were released.

Video analysis

Sleep was scored behaviorally using the software Solomon Coder (version 19.08.02) (Ferretti et al. 2019). A single observer encoded continuous video recordings. The experimental period was divided into two periods: day (from 16:00 CET until sunset) and night (from sunset until sunrise). We categorized five distinct behaviors: "moving", "stationary", "rest", "untucked", and

"tucked". Birds were coded as "moving" when they moved regularly on the perch or floor, jumping and exploring the chamber, and "stationary," when the feet were kept on the ground (or perch) and the legs were not moved except for turning or stretching, but the eyes were open. A bird was considered asleep when it was motionless for >5 s, showing piloerection, and with at least one eye closed. The 5-s criterion is based on the EEG signs of slow-wave sleep measured in different bird species, including songbirds, within seconds after closing the eyes (see figures in Rattenborg et al. 2004; Lesku et al. 2012; Scriba et al. 2013; Tisdale et al. 2017, 2018). Asleep birds were classified into two sub-states: "untucked" when the neck was retracted, the eye was closed and the head pulled toward the body but facing forward, and "tucked" when the neck was turned backward and the head tucked into the scapular feathers (Amlaner and Ball 1994; Ferretti et al. 2019). Finally, we categorized "rest" when it was not possible to determine whether the eyes were open or not, but the bird was motionless with ruffled feathers.

We calculated the time needed to reach an equilibrium in the gas composition coming from the chamber based on chamber size and flow rate using the formula $T = (V/\text{FR})\ln\{1-[(100-F)/100]\}$ (Lighton 2018), where V was the volume of the chamber, FR the flow rate, and F the fraction of exchanged volume, which we set to 95%. This yielded $T \sim 15$ min. Therefore, for the analysis of metabolic rates, we considered only behaviors that were expressed continuously for longer than 15 min, to ensure that the signal from the respirometry chamber reached a stable value. We calculated the average rate of O_2 consumption in 5-min intervals through the uninterrupted duration of each behavior, ensuring that these intervals were 15 min apart, beginning after 15 min from the start of each behavior. We also excluded the 5 min preceding the transition to a different behavioral state. For instance, if the interval spanned from minute 15 to minute 25, we would include the values recorded from minute 15 to minute 20.

Reaction time

In spring 2017 and 2018, we tested arousal threshold in 25 whitethroats displaying different sleep postures (sleep untucked: 20 trials from 15 individuals; sleep tucked: 18 trials from 12 individuals; 2 individuals were tested in both postures). Reaction time to an acoustic stimulus was used as an indicator of anti-predator alertness. When the bird displayed one of the two sleep postures for a minimum of 5 min, the operator played back an audio recording of crunched leaves (recorded in a soundproof room at the University of Vienna).

Since terrestrial predators like cats and rats pose the main threat to migratory birds at our stopover site (personal observation), we conducted tests prior to the experiment to simulate this type of predation. We experimented with various sounds, including natural ones like breaking twigs and crunching leaves, as well as artificial sounds like white noise. Among these stimuli, the sound of crunching leaves consistently triggered a reaction. Raw recordings were analyzed using VirtualDub (Version 1.10.4) by counting the number of frames from the onset of the stimulus until the animal first showed a reaction. The start of the reaction was defined as the onset of the transition to alert posture, which was characterized by a visible reduction of the feather volume and open eyes. To measure the reaction time, the total number of frames elapsed between stimulus and response was then converted to seconds. Some birds were tested twice ($N = 13$, minimum 30 min between trials). We controlled for habituation to the noise adding the order of trials as a covariate in the statistical model. See Ferretti et al. (2019) for further details.

Statistical analysis

We defined a condition index (hereafter simply condition) as the first component of a principal component analysis that included fat score, muscle score, and body mass at capture. To investigate sleep patterns, we used beta regression models to investigate the correlation between condition and the ratio of time spent sleeping to total time spent in captivity, separately for day and night. We used two further beta regression models (one for day and one for night) to investigate the correlation between condition and the ratio of untucked sleep and total sleep time.

We tested for differences in rates of O_2 consumption between behaviors using a linear mixed-effects model (LMM). We used the behavioral substates as a categorical fixed effect, while including ambient temperature and body mass as additional, continuous fixed effects. Individual identity was added as a random effect. We then used a Tukey test for pairwise post hoc comparisons between all behaviors.

We used an LMM to test for differences in reaction time between sleep postures, considering the order of sampling as a fixed effect, and controlled for repeated measurements by computing random intercepts for each bird ID.

All analyses were performed using R version 4.3.0 (R Core Team 2023) on the RStudio (2023.06.1 + 524) IDE, using a significance level of $\alpha < 0.05$. All models, functions, and related packages used for statistical analyses are summarized in Supplementary Table S1.

Ethical note

All experimental procedures, including the permission to trap and temporarily hold birds in temporary captivity were authorized by the Regional Government (Determina Regione Lazio N. G02278 of June 6, 2015, N. G03435 of March 20, 2018, and N. G07077 of June 10, 2021) in accordance with EU and Italian laws, and were communicated to, and performed according to the guidelines of, the Ethic and Animal Protection Committee (ETK) of the University of Veterinary Medicine, Vienna.

Results

There was no significant correlation between body condition and the total time they spent asleep both during the day (Table 1, Fig. 1A) and during the night (Table 1, Fig. 1B). When the birds were sleeping, there was no significant correlation between the proportion of time spent sleeping untucked and body condition during the day (Table 1, Fig. 1C). However, birds with better energy reserves tended to spend more time sleeping untucked during the night (Table 1, Fig. 1D).

We found significant differences in metabolic rate between the five behavioral categories (Supplementary Table S2). Pairwise post hoc tests revealed significant differences between active and all other behavioral states, as well as between tucked sleep and all other behaviors. However, differences among quiet wakefulness, rest, and untucked sleep were not statistically significant (Table 2, Fig. 2). Ambient temperature did not have a significant effect on oxygen consumption, while body weight and light conditions showed significant effects (Supplementary Table S2).

Finally, the analysis of the reaction time showed that the reaction to an acoustic stimulus is slower in birds sleeping tucked than untucked. Birds sleeping untucked (20 trials from 15 individuals) had a faster response than those sleeping tucked (18 trials from 12 individuals) (LMM: estimate $= -0.237$; SE $= 0.081$; $t = -2.927$; 95% CI $= [-0.40, -0.07]$; Cohen's $d = -2.93$; P-value $= 0.006$, Fig. 3).

Discussion

In this study, we found evidence for an energetic gain of sleeping in a tucked posture compared to an untucked posture in the common whitethroat, as we previously observed in a closely related migratory species, the garden warbler (Ferretti et al. 2019). Our findings on energy consumption during different behavioral states mirror the patterns reported for other migratory (Ferretti et al. 2019) and non-migratory bird species (Shankar et al. 2022), confirming a robust distinction
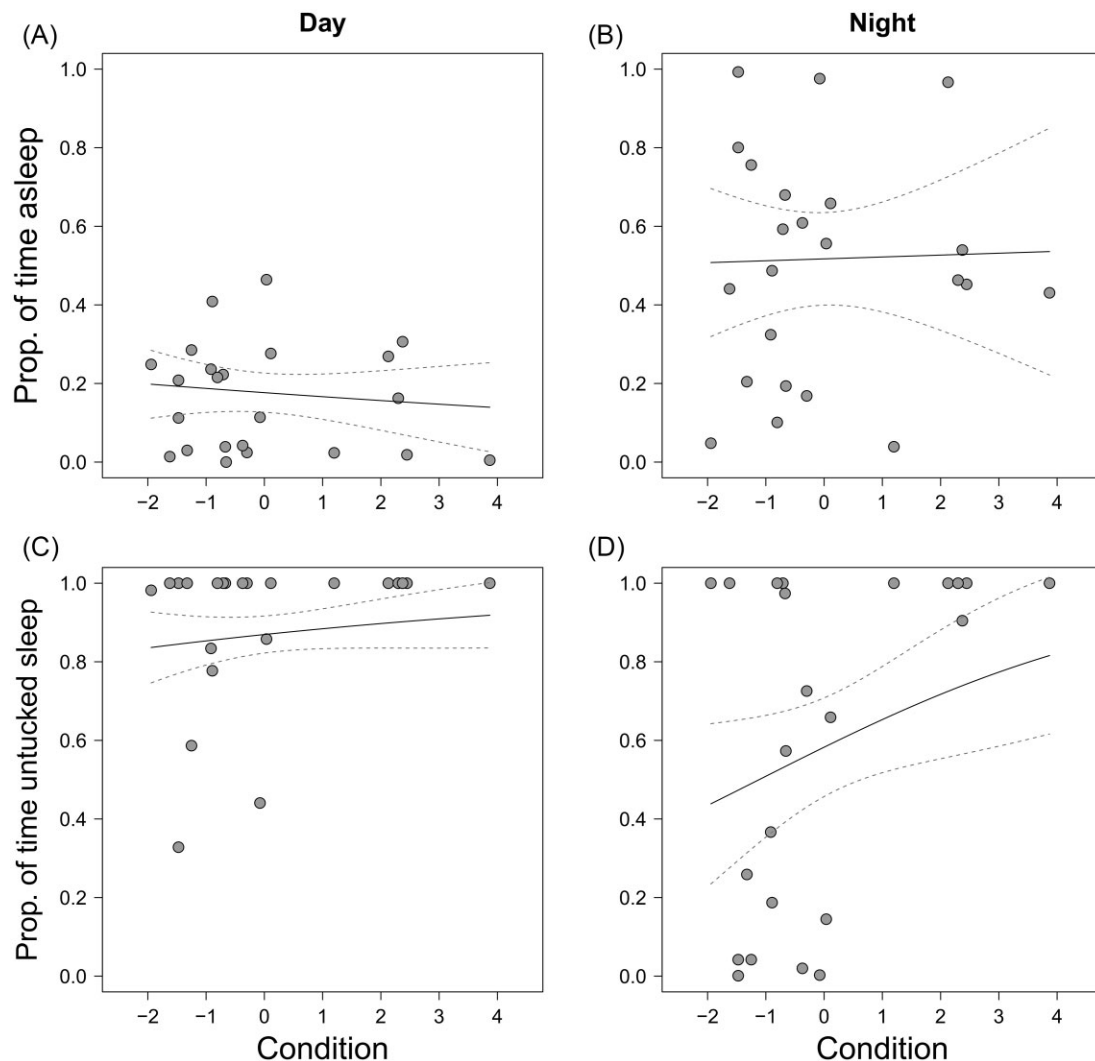
between sleep and awake metabolism. Therefore, we can discard the hypothesis that the lack of condition-dependence in sleep patterns in the whitethroat is due to a lack of substantial energetic gains. Whitethroats seemingly choose to favor shallower, safer untucked sleep, and increased foraging, even when their fuel stores are already large.

During the day, sleeping was rare and occurred almost always in the untucked position. Therefore, it seems that lean whitethroats do not take full advantage of tucked sleep even though it may allow an earlier departure as a consequence of faster energy accumulation. This observation may seem counterintuitive but may be related to different stopover strategies adopted by whitehtroats as opposed to garden warblers. While garden warblers fully rely on internal signals to determine their energy management, thus maximizing energy savings when their reserves are low, and departing from the site when energy reserves are sufficient (Goymann et al. 2010; Ferretti et al. 2019), whitethroats respond to the availability of food and use a more opportunistic strategy (Ferretti et al. 2020). When receiving ad libitum food, whitethroats will increase foraging independently of their condition. Foraging in caged whitethroats was generally higher than in garden warblers irrespective of the amount of available food (Ferretti et al. 2019). In addition to differences in migratory strategy, the decision to minimize tucked sleep during daylight hours, further underscores the importance of the trade-off between alertness and energy conservation. During the day, temperatures are higher compared to nighttime. As a result, birds experience a significantly smaller difference between body and environmental temperatures, leading to lower heat dissipation in the untucked posture compared to nighttime. Considering the lower energetic advantage of the tucked vs. untucked posture in this part of the day, birds may therefore prefer to sleep in a posture that allows for a quicker escape, or not to sleep at all.

Birds adopt specific sleep postures to regulate body insulation, crucial for managing heat dissipation (Ferretti et al. 2019; Pavlovic et al. 2019, 2020). This tucked posture is believed to reduce thermal conductance and diminish heat loss, especially in bird species with relatively large featherless body parts, such as bills and legs (Pavlovic et al. 2019). Recent research, particularly in garden warblers, has quantified the thermoregulatory benefits of the tucked posture, revealing potential energy savings of up to 9% of daily energy expenditure during stopover (Ferretti et al. 2020). Interestingly, the relative amount of energy saved by sleeping tucked instead of untucked, when considering not only the thermoregulatory advantage in terms of heat loss (9%) but the total metabolic advantage, was of 28.6%

Table 1 Outcome of beta regression models testing the effect of condition on the proportion of time spent asleep, and sleep posture preference during the day and the night

Response variable	Predictor	Estimate	Std. Error	95% CI	Cohen's d	z-value	P-value	Pseudo R^2
% Day sleep	Condition	−0.073	0.111	[−0.29, 0.15]	−0.64	−0.661	0.508	0.026
% Night sleep	Condition	0.02	0.15	[−0.28, 0.32]	0.13	0.13	0.896	0.001
% Day untucked sleep	Condition	0.137	0.133	[−0.12, 0.40]	1.02	1.033	0.301	0.113
% Night untucked sleep	Condition	0.302	0.166	[−0.02, 0.61]	1.86	1.819	0.069	0.205

Fig. 1 Relationship between condition, proportion of time spent asleep, and sleep posture preference during the day (**A, C**) and the night (**B, D**). Condition is the first principal component of a PCA, including fat score, muscle score, and body mass. Each dot represents an individual and the lines are the regressions calculated using a logistic regression model. The 95% CI are represented with a dashed line.
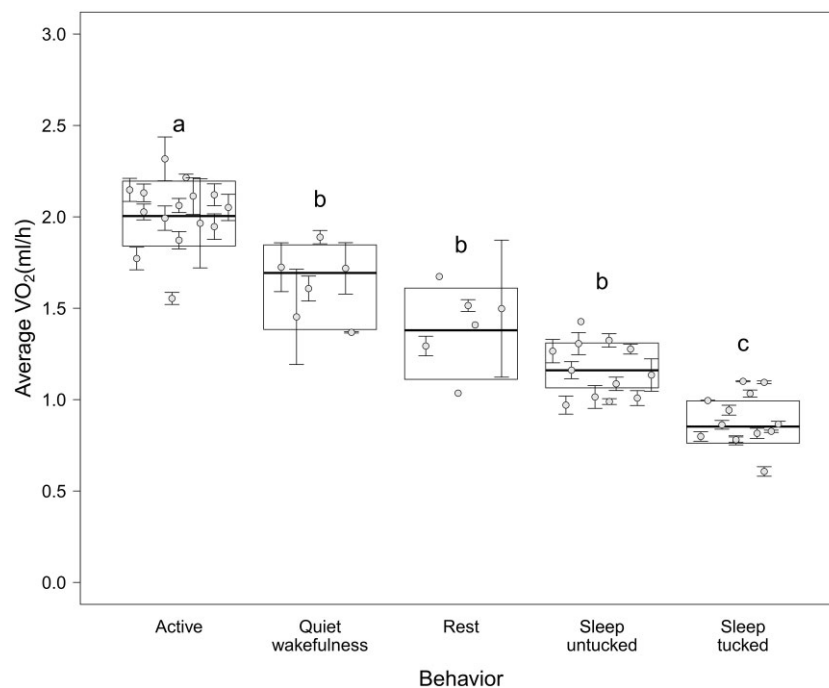
in the whitethroat compared to 18.1% in the garden warbler (Ferretti et al. 2019). This difference can be attributable to the smaller size of the whitethroats—as evidenced from the difference in average body mass of whitethroat (15 g) and garden warbler (22 g)—and, consequently, larger surface area to volume ratio (Schmidt-Nielsen 1984; McNab 2002).

Despite variations in the relative energetic advantage of sleeping tucked, our study confirms that sleep posture preference among songbirds during stopover results from a trade-off between energy gain and the need to be reactive to potential threats. These findings hold particular significance for conservation efforts, as many islands that serve as stopover sites for thousands of migra-

Table 2 Outcome of pairwise post hoc comparisons of metabolic rate in whitethroats displaying different behaviors

Pairwise differences	Estimate	Std. Error	df	t-ratio	P-value
Active—rest	0.751	0.064	396	11.747	**<0.001**
Active—tucked sleep	0.955	0.037	287	25.799	**<0.001**
Active—untucked sleep	0.779	0.034	393	23.041	**<0.001**
Active—stationary	0.638	0.052	396	12.283	**<0.001**
Rest—tucked sleep	0.204	0.07	385	2.915	**0.031**
Rest—untucked sleep	0.028	0.066	397	0.415	0.994
Rest—stationary	−0.113	0.077	397	−1.474	0.58
Tucked sleep—untucked sleep	−0.177	0.045	327	−3.972	**0.001**
Tucked sleep—stationary	−0.317	0.065	363	−4.871	**<0.001**
Stationary—untucked sleep	−0.141	0.058	394	−2.433	0.109

Statistically significant effects are outlined in bold typeface.
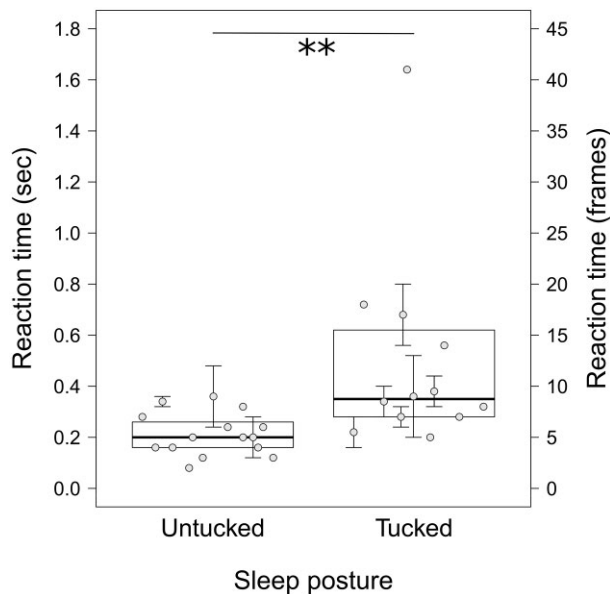

Fig. 2 Rate of O_2 consumption in common whitethroats exhibiting different behaviors (active: 110 measures from 15 individuals; quiet wakefulness: 13 measures from 6 individuals; rest: 8 measures from 6 individuals) and sleep postures (sleep untucked: 58 measures from 12 individuals; sleep tucked: 75 measures from 13 individuals), averaged over 5-min periods. Different letters (**a–c**) indicate behavioral states that differed significantly from each other. Boxplots show the median and inter-quartiles calculated on the entire sample. Circles indicate the individual mean values from 5-min intervals for each behavioral state and the error bars represent the Standard Error of the mean from multiple measurements of the same individual.

tory birds annually grapple with managing small mammal populations, like stray cats and rats. These mammals, which have a substantial portion of their diet consisting of birds (Dierschke 2003; Harper and Bunbury 2015; Loss et al. 2022), pose a significant threat to migratory bird populations. Furthermore, these species are often found to hunt migratory birds even during daylight hours (personal observation) at our stopover site, despite being typically nocturnal. There is urgent need of studies that reveal vulnerabilities of migratory

songbirds, as such knowledge is critical for enhancing conditions at stopover sites and, consequently, improving the prospects for the recovery of declining migratory species.

Because sleeping in a tucked posture may bring larger advantages for the whitethroat compared to the garden warbler, one could predict that in the former this posture would be adopted to a higher extent by individuals with low fat reserves, and in general for a higher proportion of time. However, this was not the case, since

Fig. 3 Response latency between the activation of the trigger and the change of the posture from sleeping to alert. Boxplots show the median and inter-quartiles calculated on the entire sample, and circles show the individual mean values for each sleep posture (untucked: 20 trials from 15 individuals; tucked: 18 trials from 12 individuals). We represent error bars for individuals in which the reaction test was performed more than once.

the proportion of birds sleeping untucked during the night was not lower than in garden warblers, but rather slightly higher (whitethroat in the current study = 60%; garden warbler in Ferretti et al. 2019 = 46%).

During the night, the choice of a tucked posture was more likely when reserves were low; however the relationship was not as strong as is the case of garden warblers (Ferretti et al. 2019). Though not statistically significant, the findings of the current study align with those of our earlier investigation comparing this aspect in the two species (Ferretti et al. 2020). This concordance is evident when comparing the trend lines of the two studies. Our results altogether strongly suggest that whitethroats choose opportunistically to maximize fuel deposition when food is available, independently of their fuel reserves, in line with the predictions of a time-minimizing strategy (Alerstam et al. 2003). Along with this, they seem to prioritize safety when sleeping by choosing an untucked position more frequently.

In summary, this study showed that while postural choices during sleep can have important energetic benefits in migratory passerine birds during stopover, some species may choose not to take advantage of such benefits and resort more to foraging. The ecological causes of these intraspecific differences require further attention and a comparative approach. Irrespective of interspecific differences in stopover strategy, we confirmed that the choice of a specific sleep posture balances the

needs to minimize metabolic consumption and to remain vigilant. The preference for prioritizing either energy conservation or vigilance appears to be influenced by the interplay between available energy reserves and the time of day. So far, this type of investigation has been performed only on long-distance migrants, thus we have no knowledge on how species performing shorter migrations deal with sleep. Hence, additional investigations are necessary to determine whether this utilization of sleep for managing energy reserves extends to short-distance migrants, which may employ distinct energy management strategies. Finally, our studies on sleep hold particular significance for conservation efforts, emphasizing the need for a comprehensive understanding of how migratory birds utilize various stopover sites. Such insight is imperative for enhancing the management conditions of these critical areas, upon which the survival of numerous bird species depends.

Author contributions

A.F., I.M., and L.F. conceived the study; M.P., A.F., and M.C. conducted the experimental work; M.P., A.F., and I.M. analyzed the data; A.F., I.M., M.P., and L.F. wrote the paper.

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Supplementary data

Supplementary Data available at *ICB* online.

Conflict of interest

The author declares no conflict of interest.

Data availability

Datasets and codes used in this study are available at https://phaidra.vetmeduni.ac.at/o:2921, or available from the corresponding author upon reasonable request.

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