universität wien

MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Analysis of the relationship between physiological condition and rest pattern during spring migration in the garden warbler (*Sylvia borin*) using video recording"

verfasst von / submitted by

Frederik Amann, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2018 / Vienna 2018

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	A 066 878
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie
Betreut von / Supervisor:	Univ.-Prof. Dott. Leonida Fusani, MPhil PhD

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I conducted the study as part of a bigger team which was collecting data for different studies during field season of 2015 on Ponza. My colleague Katharina Schabl was doing a similar study with whitethroats *(Sylvia communis)* and spent the season of 2016 at the island. I would like to thank Professor Leonida Fusani for the opportunity to conduct research in his team and the supervision of my master thesis. I thank Andrea Ferretti, Katharina Schabl, Clara Leutgeb, Marta Trez and Sara Lupi for the good working atmosphere and for helping each other out so greatly during the whole time of the project. Special thanks go to Massimiliano Cardinale and the whole team of the ringing station on Ponza for the support of the research team.

ABSTRACT

The effect of physiological body condition on the activity of birds is often studied using infrared sensors. I used the different technique of continuous video observation, to investigate whether there is a relationship of activity, food uptake and sleep pattern with body condition during stopover in a small migratory passerine in Europe. During spring migration 2015 and 2016, 63 garden warblers were captured on an island near Naples, Italy. They were held from migration for 16 hours in soundproof boxes, while being video-recorded. Water ad libitum and three grams of mealworms were provided. Physiological body condition was calculated using measures of subcutaneous fat stores, pectoral muscle score and body weight. Overall resting behaviour and overall active behaviour were coded. Two sub-states each were relevant: 'Rest Back' and 'Rest Front' for resting behaviour, 'Stationary' and 'Moving' for active behaviour. Active and resting behaviour are mutually exclusive, as are the two sub-states: a relative increase in Rest Back behaviour means a relative decrease of Rest Front behaviour. Birds in a better physiological state generally showed high amounts of resting behaviours during light, while Moving behaviour was low. Birds in low condition showed increased amounts of activity and Moving during day. The birds amount of food intake during their stay in the cages followed a clear all-or-nothing scheme, with birds in lower condition having a significantly higher likelihood of taking up all the food available. During night, birds in good condition showed slightly lower amounts of total resting behaviours as compared to birds in bad condition; while the amount of Rest Back behaviour (beak facing backwards) was substantially lower, and the

amount of Rest Front behaviour (beak facing forwards) substantially higher. My results support previous findings of birds at stopover during migration to exhibit greater activity during day to search for food in dependency of a low body condition; while the differences are not pronounced and might be influenced by other factors. I further suggest, that nightly Rest Back behaviour in garden warblers during migration can be used as an indicator for deeper states of recovery and sleep, whereas the amount of nightly Rest Front behaviour might reflect the physiological readiness of the birds to continue migration, similar to migratory restlessness exhibited during night. I conclude that infrared sensor methods are to be favoured to search for differences in migratory restlessness or plain activity. If a finer distinction of behaviours is needed, video recording should be considered.

INTRODUCTION

Bird migration is a fascinating event and known to humanity since long, early records were already made by ancient Greek writers (Lincoln et al., *Migration of Birds)*. Increased food availability and favourable weather conditions in their wintering grounds drive migratory birds twice a year to undertake tremendous efforts. Having to optimize time and energy-costs, navigate and find feasible stopover-sites to refuel and recover; while also reducing risk of predation and disease and taking changing weather conditions into account, individuals are confronted with huge cognitive and physiological challenges. A variety of behavioural and physiological adaptations to meet these demanding requirements have been observed and studied.

Bird migration consists of two main parts: Actual flight, and stopover at sites that are used to recover. Migration theory predicts birds to spend only one seventh of their time in migration with actual flight, the rest of the time being used to rest at stopover sites (Hedenström & Alerstam 1997). So even though flight is calculated to be roughly three to four times costlier than stopover, total energy spent at stopover sites along the migratory route of a bird is twice as big as the energy spent to fly (Hedenström & Alerstam 1997) - the authors therefore expect “strong selection pressures to optimize fuel accumulation strategies during stopover episodes”.

An important part of research on bird migration focuses on stopover-behaviour, and more specifically on the external and internal factors guiding the decision to leave or to stay. Factors known to influence migration are reviewed in Jenni & Schaub 2003 and include environmental factors such as weather, wind, topography, predation, food availability and competition, and internal factors such as endogenous time programmes, moult, body mass and energy stores as well as other physiological factors.

At stopover sites, if applicable, birds search for food to restore fat depots (refuel), and they also recover from and prepare for oxidative stress that long fasting flights inevitably cause (Skrip et al. 2015). Birds that have sufficiently recovered are expected to continue migration as soon as possible. The criterion for when a state of being "sufficiently recovered" is reached, and whether the weather conditions are considered to be favourable enough to continue migration, depends on the migratory strategy the bird is using. Field data suggests that most birds use a strategy of minimizing total duration of migration (reviewed in Hedenström 2008) - especially during spring, where selection favours an early arrival at the breeding grounds (Kokko 1999). Even though, as a simple rule of thumb for birds to decide when to continue migration, staying for a constant number of days has been shown to work in theory (Erni et al. 2002), some minimum fuel load is considered to be indispensable to trigger departure, which is then likely fine-tuned by present weather at the site and geographical factors (Hedenström 2008, Fusani et al. 2009).

Fuel load of birds can be approximated by visually assessing their subcutaneous fat deposits and rank them in fat-classes, for example increasing from 0 to 8 as introduced by Kaiser 1993. Looking at the influence of fat deposits on stopover duration, a telemetry-study during spring migration was performed on a stopover and refuelling site in western Italy, where garden warblers with low subcutaneous fat stores were shown to stay four times as long as conspecifics with higher fat stores (Goymann et al. 2010). This supported former studies with less sophisticated methods but similar results on other small passerine birds during autumn migration at stopover sites in northern Africa (Bairlein 1985, Biebach 1985).

Another study (Fusani et al. 2009) looked at the link between body condition of long-distance migrants and the amount of migratory restlessness, a behaviour signalling the birds disposition to continue migration. The study was conducted during spring migration on a similar stopover

site as in Goymann et al. 2010. All tested species - garden warblers, whinchats *(Saxicola rubetra)* and whitethroats *(Sylvia communis)* - showed a positive correlation of migratory restlessness during night with body condition (Fusani et al. 2009). Body condition in this study was defined by a single component extracted from the measures of fat score, muscle score and body weight of the birds; and the amount of migratory restlessness was assessed by automatized counts of light barrier crossings during an overnight stay in cages. A follow-up study showed similar results also for short-distance migrants (Lupi et al. 2016). Overall, these findings strongly support the idea about the importance of fuel load on stopover duration.

The listed studies do not look at the actual behaviours the birds exhibit during their stay. Mainly, they distinguish between activity and non-activity (crossing of light barriers or capture/recapture): Activity during day was shown to be higher in lean garden warblers than in fat garden warblers (Fusani et al. 2009, Bairlein 1985), and it was proposed that this reflects food-searching behaviour. However, in other long- and short-distance migratory birds, this pattern could not be detected (Fusani et al. 2009, Lupi et al. 2016), which again shows the numerous factors stopover behaviour of migratory birds depends on: not only fuel load, but also physiological factors (Jenni-Eiermann et al. 2014, Goymann et al. 2017) and constraints (Gannes 2002), predation or other risk aversion (Sillett & Holmes 2002), the availability and quality of food (Fusani et al. 2011, Lindström 2003), as well as the frequency and distribution of stopover sites along the birds migratory route. Therefore, different species might behave differently, also depending on the relative position on their own migratory route (Lupi et al. 2016).

What are the actual behaviours of migratory birds during their stopover period? Studying behaviours in the wild is limited due to the hard accessibility of the birds, especially during night. Video recordings of wild-caught birds during an overnight stay at a stopover site should be better suited to draw more detailed conclusions about stopover behaviour. The relationship between activity patterns and body condition has been studied before (Bairlein 1985, Fusani et al. 2009, Lupi et al 2016), as has been the influence of body condition and food availability on stopover duration (Goymann et al. 2010, Fusani et al 2011). Being part of that research group, I wanted to study the influence of physiological condition on activity patterns, but using a different method allowing for finer distinction of behaviours. I used video-recording to code behaviours associated with activity and with recovery/sleep. My goal was to find out the

influence of body condition on different behavioural indicators of activity, as well as on total activity during night and day, and on food uptake of garden warblers at a stopover site during spring migration.

In birds, two main resting positions can be distinguished: Rest Front (RF), where the head of the bird is retracted towards the body while facing forward, and Rest Back (RB), where the head is pointing backward, resting on the bird's back and the beak is under the scapula feathers (figure 2). The latter has been found to be tightly correlated with electrographic sleep in the blackbird *(Turdus merula)*, while the former also contained bigger bouts of quiet wakefulness (QW), a state where the bird was immobile and seemingly asleep but electrographically not in a sleeping state (Szymczak et al. 1993). These two positions therefore are associated with recovery and sleep - and might also tell something about the depth of rest the bird is likely to be in. In a similar manner, two different states of activity can be distinguished: Stationary, where the bird stays at one place, but is clearly awake and active. And Moving, where the bird also moves physically through the cage, being very active and spending more energy. I used these four different states as basis for a detailed examination of the influence of physiological body condition on stopover behaviour of garden warblers during their spring migration. I took video recordings of 63 wild-caught individuals held overnight in cages on a small island in Italy, which is frequently used as stopover site after the birds crossed an ecological barrier on the way to their breeding grounds in northern and central Europe. During 16 hours of stay for each of the birds, I used continuous focal sampling to code for activity and resting patterns during light and dark hours. I expected differences in the activity patterns of birds during night and day - with birds in better condition being more active during night, and birds in worse condition being more active during day. Additionally, I expected differences in food uptake of birds with different physiological condition - with birds in worse condition taking up more food.

MATERIAL & METHODS

Species

Our study species was the garden warbler (*Sylvia borin*), a small European passerine and long-distance migrant. Birds from central Europe leave during the second half of July for their wintering areas south of the Sahara and come back around beginning of May (Südbeck et al. 2005). On Ponza, an island close to Naples and place of our study, first birds arrived in the second half of April. Number of birds for this study were: $n_1 = 35$ (2015) and $n_2 = 28$ (2016).

Study site and method

The study was conducted on Ponza (Italy), a small island around 80 Kilometres west of Naples in the Tyrrhenian Sea (40°55' N, 12°58' E). Ponza is located along one of the main Mediterranean migratory routes. A ringing station is operating on the island during spring migration since 2002. The ringing season usually starts in early March and lasts until end of May. All times given refer to Coordinated Universal Time (UTC) + 1 hours, which is the standard (winter) time for central Europe.

I used 63 (unsexed) garden warblers, caught with mist-nets during ringing operations between 20th of April and 20th of May 2015 and between 17th of April and 13th of May 2016. Birds were caught between one hour after sunrise and 12:00, for this is the time of day with the highest likelihood of new arrivals. Taking birds from very early in the morning could mean that they already slept on the island, taking birds from the afternoon increases the possibility of them already having arrived in the morning.

Immediately after entering the net, the bird was bled from the wing vein (three microcapillaries of blood (210 µl) which was used for another study), put in a small transport bag and carried to the ringing station. A single observer scored subcutaneous fat on a 0 – 8 scale (Kaiser 1993), the size of the pectoral muscles on a 0 – 3 scale and measured the body mass to 0.1 g.

By 12:30, birds were placed in one of three individual fabric cages equipped with 3 grams of mealworms, water ad libitum, three infrared cameras and two mounts/perches (see figure 1 for setup). Each fabric cage was placed inside a soundproof box, so that the animals were

visually and acoustically isolated. The infrared cameras from each cage were connected with a surveillance system storing video material on a hard drive for later analysis. The cages inside the soundproof boxes did receive some natural illumination through a side window, which is important during night, so that the bird is not located in total darkness and can perform moving behaviours such as migratory restlessness (personal observation). Additionally, the fabric cages were illuminated by a daylight lamp built into the roof of each soundproof box (figure 1). Light hours (= hours when the lamp was operating) were set with civil twilight hours at Ponza and adjusted every week. Light hours were from 5:00 to 19:20 during middle of April, and from 4:15 to 20:00 during end of May (detailed Civil Twilight hours for Ponza can be found in the appendix).

Behaviour was recorded from 13:00 until sunrise next morning - approximately 16 hours after observation had started. So, birds had around six/seven hours of daylight, and between eight and ten hours of darkness to be spent inside the cage. Soon after sunrise, each bird's weight, muscle and fat score was recorded once more, the remaining food in the cage was weighted, and the bird was released.

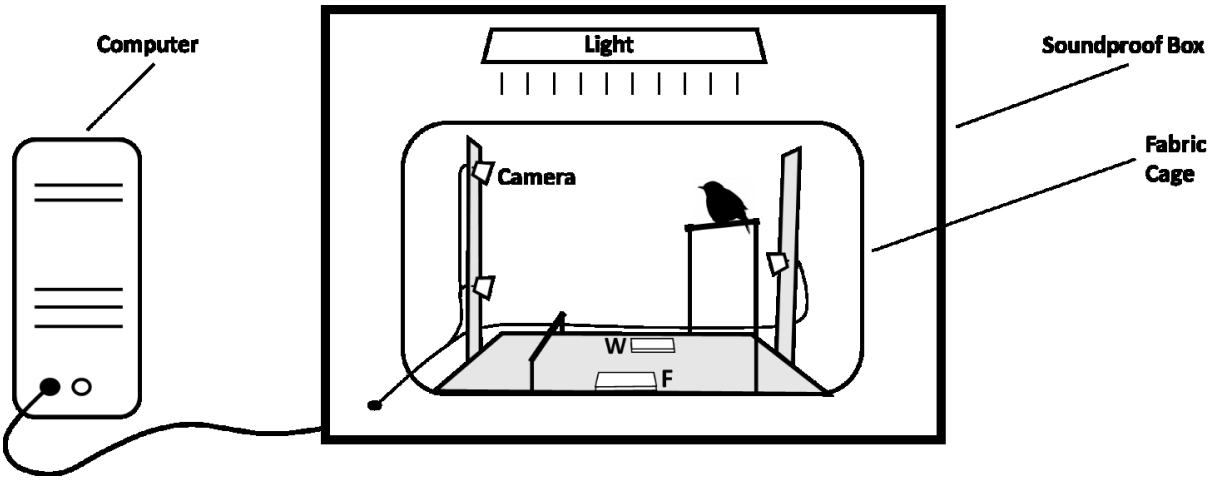


Figure 1: Setup of the observation system for the overnight stay. Soundproof box with a fabric cage inside. It contained the bird, water, food, two perches and three infrared cameras. Three of these observation systems were in use simultaneously. Light = Daylight lamp built into the roof of the soundproof box, W = Water, F = Food.

File preparation

Video files of the three cameras in each cage were automatically saved as .avi - files lasting around 5 minutes each. To concatenate, I used the “append”-command in Virtual Dub (Version 1.10.4, process partly automatized using a self-written script). The resulting three video-files for each cage now covered the whole observation-time for that bird. Using AviSynth, a powerful tool for script-based video post-production, they were then emulated into a single video file containing three synchronized video-streams aligned next to each other. This virtual video file could be read by Solomon Coder (version 15.03.15), which was used to code behaviours of the birds.

Coding behaviour

The videos were coded using the behaviours explained in the ethogram (appendix). The first minute of each five-minute interval was coded, the remaining four minutes were skipped. Test-codings using different protocols (5 min out of 20 min, 15/60, full observation) showed that the 1/5-protocol was best suited for my purpose and allowed realistic derivations of what the bird was doing and in which frequency.

The behavioural repertoire of the garden warblers was similar to the one shown by blackbirds (*Turdus merula*) studied in Szymczak et al 1993. I adapted categories to fit the purpose. ‘Stationary’, ‘Preening’ and ‘Moving’ formed the category of active behaviour; ‘Rest Front’ and ‘Rest Back’ were the two main parts of resting behaviour. Only when indistinguishable between back and front, the state was coded as ‘Rest undefined’. When the bird was not visible (i.e. sitting on the most upper camera), it was labelled as ‘Out of sight’. Dark hours and light hours were indicated by a marker, and the event ‘Wingflap’ was coded (table 1).

Wingflap was defined as when during night, the bird repeatedly flaps its wings as if starting to fly, but its feet stay on the ground or perch - a behaviour performed during migratory restlessness (Rattenborg et al 2004). The bird was considered ‘Stationary’ when visibly awake and from time to time moving some body parts, but not changing position in the cage. When changing position in the cage, jumping and flying around, the bird was considered ‘Moving’.

The last of the active states, sub-state 'Preening', was used when the bird was using the beak to stroke through the feathers and clean itself.

When the bird was inactive and only showing reflex-like movements like breathing or short opening of the eyes, it was coded as in a resting state. When the bird was in a resting state and the beak was facing forward, head mostly retracted towards the body and occasionally dropping to the feet, this was marked as sub-state 'Rest Front' (figure 2). Occasional short scans of the environment with one eye were normal in this state. When the beak was facing backwards, usually tucked under the scapula feathers, and the bird sat almost completely motionless, often for a long time and just on one leg, this was coded as 'Rest Back' (figure 2).

For a change between (sub)states to be coded as such, the new state had to last longer than three seconds. The full and more detailed ethogram can be found in the appendix.

Measures for activity were on the one hand the total of either active or resting behaviour, or the sub-states Moving, Stationary, Rest Front, Rest Back. According to the definition of the sub-states, Moving was the most active behaviour, followed by Stationary, Rest Front, Rest Back.

Table 1: Coded behaviours. Moving, Stationary, Rest Front and Rest Back were of main interest. States and Sub-states were continuously recorded. Wingflap was an event, therefore recorded every time the behaviour was observed. Beginning of light hours as well as of dark hours were indicated by single event-markers called Light and Dark.

State	Active	Resting	Out of sight
Sub-state	Stationary (ST)	Rest Front (RF)	
	Preening (P)	Rest Back (RB)	
	Moving (M)	Rest undefined (RR)	
Event	Wingflap, Light, Dark		

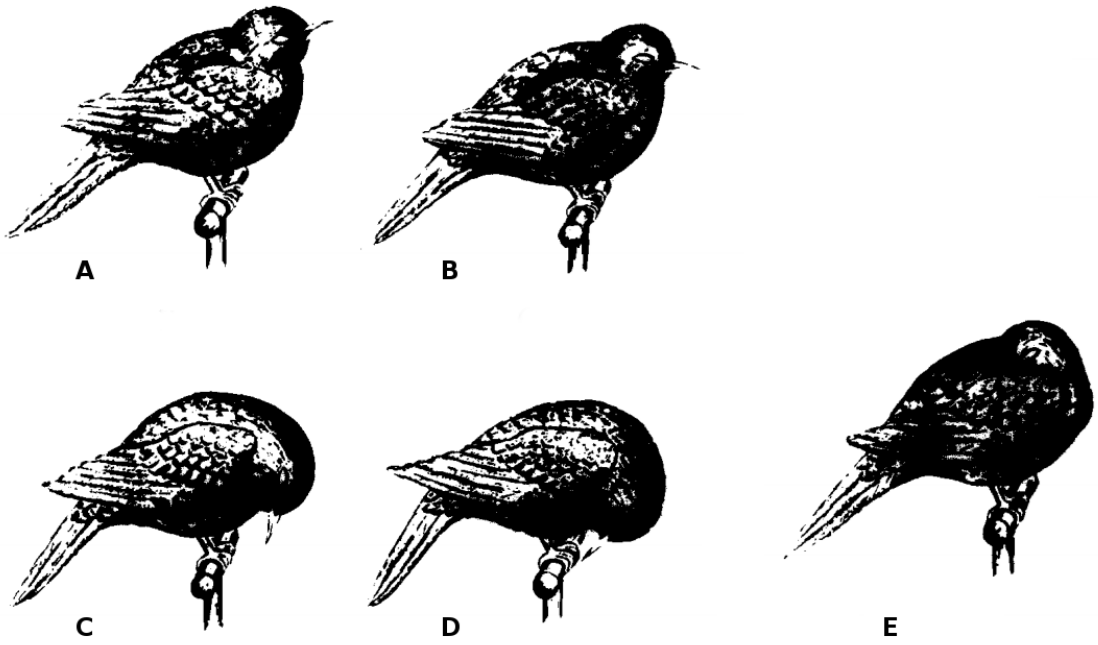


Figure 2: Different resting positions of birds. A-D: Rest Front (RF) with increasing inclination of the beak, E: Rest Back (RB). Modified after Szymczak et al. 1993.

Statistical analysis

I used non-parametric tests, since most of the variables were not following normal distribution or not meeting other assumptions of parametric alternatives. To answer my research questions, I calculated correlations between different activity measures and an index of physiological body condition of birds. I applied simple linear models to check for a linear relationship between body condition and these variables. I checked for an influence of year on the data using Wilcoxon rank sum test. I also searched for behavioural differences between light and dark hours for birds in a similar body condition by means of the same test. I performed a logistic regression to check for the influence of body condition on the amount of food that was taken in by the birds during their overnight stay.

As condition-index (CI), I used a single variable consisting of three physiological measurements: body weight, fat score and pectoral muscle score. Like Fusani et al. 2009, I ran a principal component analysis (PCA) on these measures. From the resulting principal components, PC1

was used as CI for analysis, hereafter called 'Condition'. PC1 explained 71.2% of total variance of the three measures. The loadings (correlation with the variables used to run the PCA) of PC1 were as follows: body weight: 0.615, fat: 0.622, muscle 0.485.

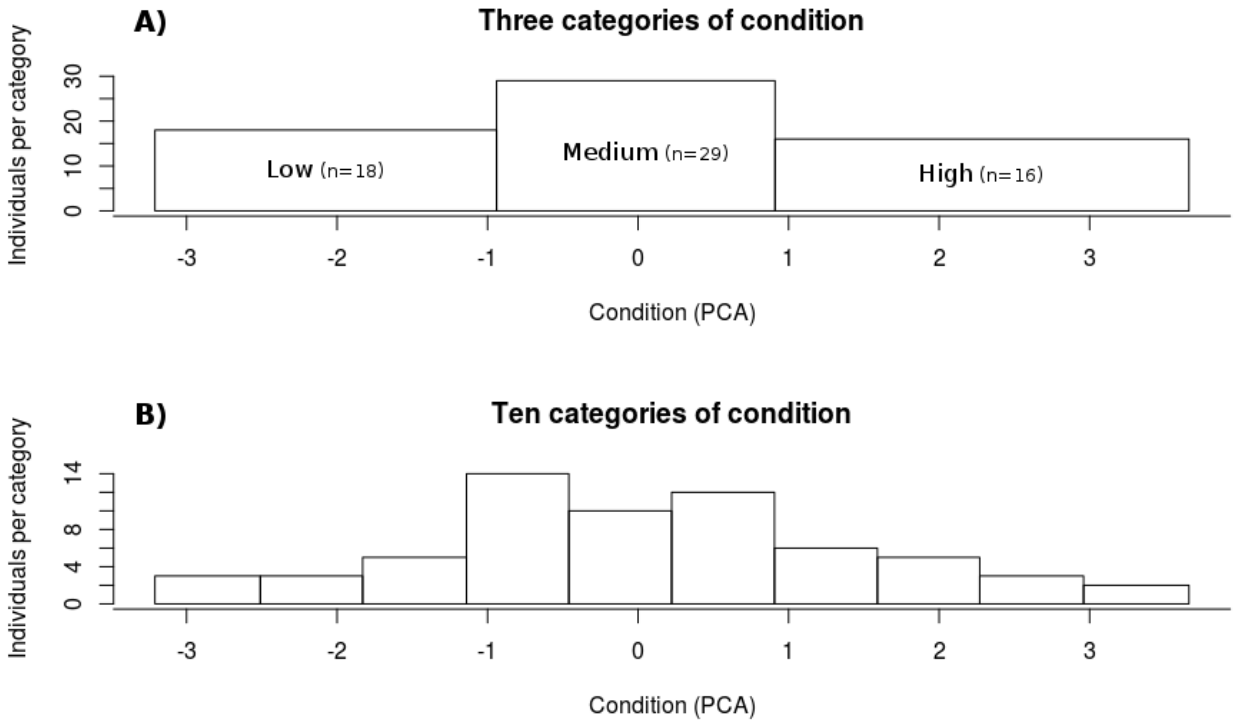


Figure 3: Birds clustered in different categories in dependence of their body condition (as calculated by PCA of the measures body weight, fat and pectoral muscle). Total number of birds: n = 63. A) Division into three Condition-categories using quartiles: 'Low' (n = 18), 'Medium' (n = 29) and 'High' (n = 16). These were used for statistical tests. B) Division into ten even-spaced categories. These were used to illustrate the data (figures 6A and 6B), but not for statistical tests.

For some statistical analysis, birds were clustered in Condition-categories: Lower quartile of birds was put in the category 'Low' (Condition ≤ - 0.99, n = 18). Due to three birds having the same value of Condition exactly at the threshold, these birds were included in the 'Low' Condition class, resulting in an increased number in this class as compared to class 'High'. Upper quartile of birds was put in the category 'High' (Condition > 0.91, n = 16). Intermediate half of

the birds were labelled as ‘Medium’ (n = 29), see Figure 3 A. The chosen categorization reflects a good balance between amount of birds in each category (18, 29, 16) and size/length of category on the x-axis. Be aware that the categories used are not absolute, i.e. the category ‘High’ just represents the quartile of birds in this study with the relatively highest Condition, similarly ‘Low’ represents the lower quartile of birds regarding Condition. Birds in migration are subject to a lot of physiological challenges, therefore are very unlikely to be in “high” physiological condition on an absolute scale.

Especially during discussion, I use the term ‘lean birds’ and ‘fat birds’ as synonyms for birds in low/bad body condition and high/good body condition.

Statistical analyses were performed using R Studio (RStudio Inc., Version 1.1.423) and R (R foundation for statistical computing, Version 3.2.3). Some Graphs were edited using Gimp (Version 2.8.16).

Since all my final deductions in this work rely on less than five tests, a Bonferroni-correction of the alpha-level (0.05/5) results in a new, conservative measure of 0.01, which the relevant tests pass. However, single test-results with a significance-level at 0.05 are still shown in the results-section, as well as some trends ($\alpha < 0.1$).

RESULTS

The behaviour of garden warblers during their stay showed differences between night and day and between birds in good Condition and birds in bad Condition. One should bear in mind that total resting behaviour and active behaviour were mutually exclusive, and birds were always in either of these states, except when out of sight, which was negligible. Therefore, in the following sections, speaking of an increase in resting behaviour, means at the same time a decrease in active behaviour and vice versa. The same is true for Moving and Stationary, as well as for Rest Back and Rest Front. Wilcoxon rank sum test was performed to compare all dependent variables of interest between years. It was non-significant for all - thus, data of both years was pooled in the analysis.

Difference in behaviours between night and day

A comparison between night and day for the main recorded behaviours of all birds is given in figure 4. Birds moved significantly more during light hours than they did during dark hours (Wilcoxon rank sum test with continuity correction, $W = 1370$, $n = 63$, $p < 0.01$). Also, they showed more Rest Front ($W = 745$, $n = 63$, $p < 0.001$) and less Rest Back ($W = 3215.5$, $n = 63$, $p < 0.001$) behaviour during light hours as compared to dark hours. The amount of Stationary behaviour didn't differ between day and night. Also, the amount of total resting behaviour (constituted of Rest Front, Rest Back and Rest undefined) didn't differ between night and day for all birds together. In reverse conclusion, that also means that active behaviour didn't differ between night and day at the whole-group level.

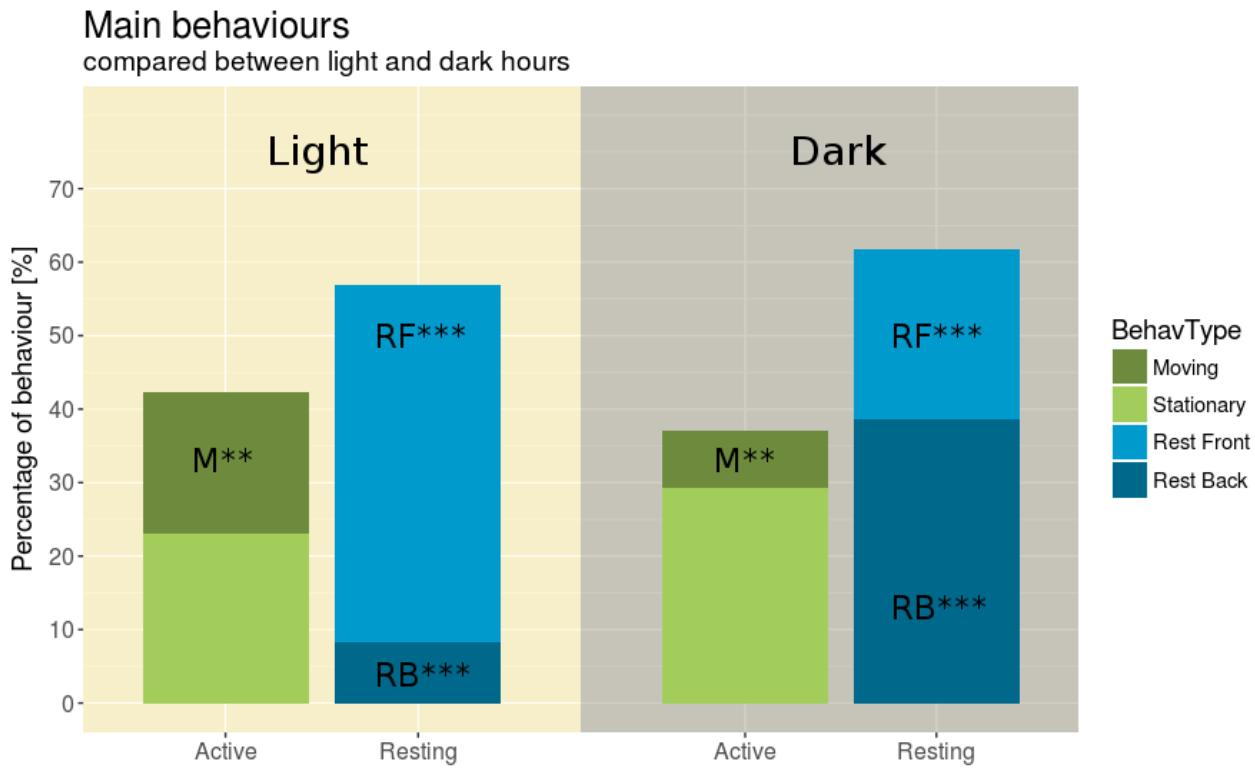


Figure 4: Main behaviours recorded – comparison between light and dark hours. Mean of behaviour as percentage of all behaviours during the respective observation time. Data of all birds, not sorted by Condition, n = 63. Due to negligible size (< 1 %), Rest undefined and Preening are not shown. Birds showed significantly more Moving and Rest Front during light hours; and more Rest Back during dark hours. Amount of total resting behaviour (Rest Front + Rest Back + Rest undefined) didn't differ significantly between light and dark hours. (Wilcoxon rank sum test with continuity correction, Significance levels: *p<0.05, **p<0.01, ***p<0.001)

When the birds were clustered by Condition-categories, total amount of resting behaviour showed differences between night and day (figure 5). Birds in category 'Low' showed significantly more resting behaviour during night than during day (Wilcoxon rank sum test, W = 85, n = 18, $p < 0.05$). Birds in category 'Medium' (n = 29) and 'High' (n = 16) didn't show differences in amount of resting behaviour between night and day. Amount of Rest Back behaviour was higher during night for birds in Low (W = 15, $p < 0.001$) and Medium (W = 152, $p < 0.001$) Condition, but no difference was found for birds in High Condition. The reverse pattern was found for Rest Front behaviour: Birds in category Low (W = 289, $p < 0.001$) and Medium (W = 721, $p < 0.001$) showed more Rest Front during day than during night, while birds

in High Condition didn't show any difference. Moving behaviour differed only for birds in Low Condition: They moved significantly more during day than during night ($W = 263$, $p < 0.001$); birds in Medium Condition showed a trend in the same direction ($W = 527$, $p = 0.099$). Only birds in High Condition showed significantly more Stationary behaviour during night hours as compared to daylight hours ($W = 66$, $p < 0.05$).

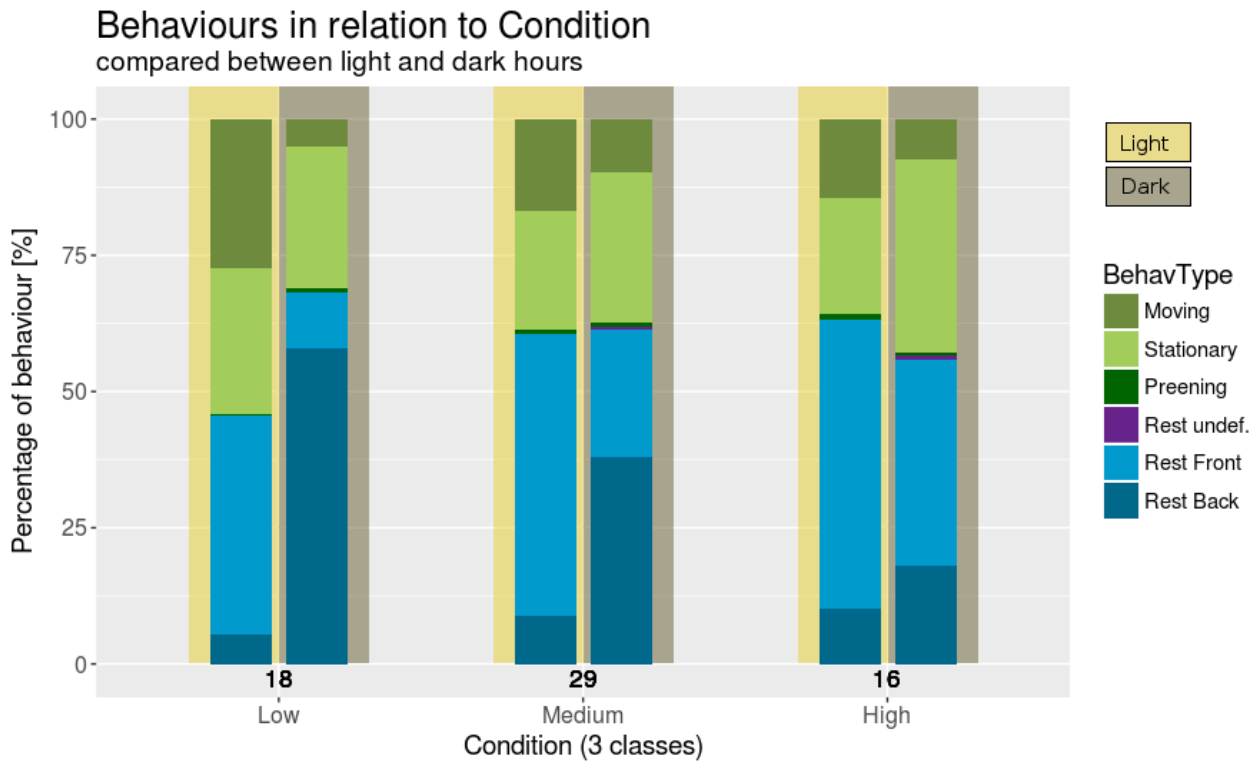
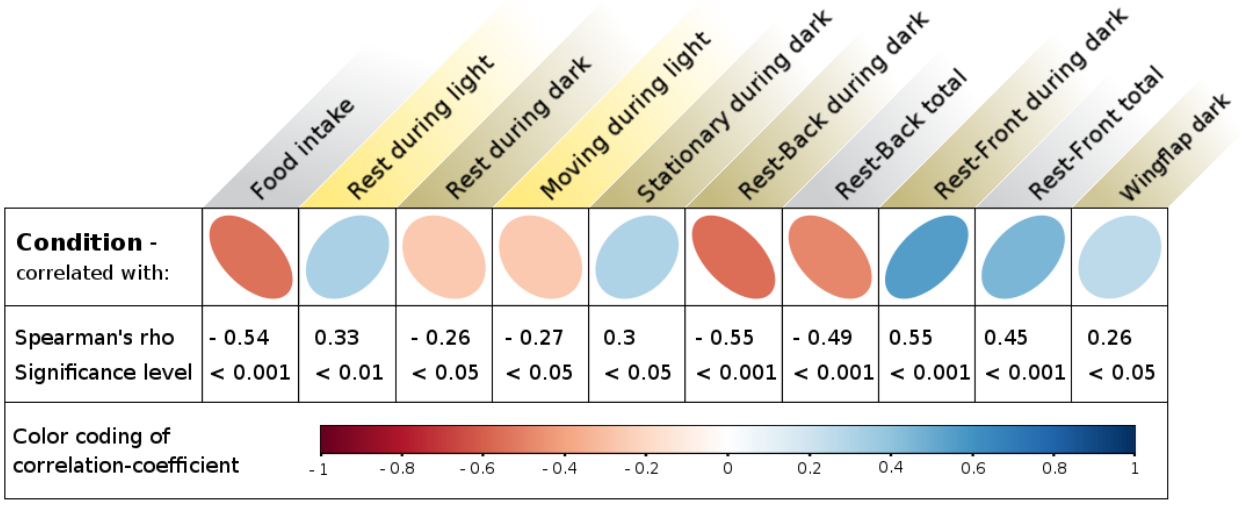


Figure 5: All behaviours of birds in Condition-categories 'Low', 'Medium' and 'High' compared between light and dark hours. Number of birds in each category is printed at the base of the bars. Only birds in Category 'Low' showed significantly more resting behaviour during dark hours than during light hours, while they also differed in amount of Moving, Rest Back and Rest Front. Birds in category 'Medium' differed only in Rest Back and Rest Front between light and day. While birds in 'High' Condition showed a significant difference only in amount of Stationary behaviour. Test statistics see text above.

Difference in behaviours linked to Condition

Different measures of activity and resting, as well as total food intake during stay in the cage correlated with Condition of birds, which is summarized in table 2 and visualized in figure 6A and 6B. Food intake decreased with increasing Condition (r_S = -0.54, p < 0.001). Resting behaviour increased during light (r_S = 0.33, p < 0.01) and decreased during dark (r_S = - 0.26, p < 0.05). Birds with higher Condition showed less Moving during light (r_S = - 0.27, p < 0.05) and more Stationary behaviour during dark (r_S = 0.3, p < 0.05) as birds with a lower CI. Rest Back behaviour during night decreased strongly with increasing Condition (r_S = - 0.55, p < 0.001), as did Rest Back behaviour during total sampling time (r_S = - 0.49, p < 0.001). Rest Front behaviour showed the opposite pattern, namely, with increasing Condition of birds, it increased during dark (r_S = 0.55, p < 0.001) as well as during total sampling time (r_S = 0.49, p < 0.001). There was a significant but weak positive correlation between Condition and scored number of the behaviour Wingflap during dark hours (r_S = 0.26, p < 0.05).

Table 2: Correlation Matrix for the CI 'Condition' - correlated with different measures of activity as well as with Food intake of the birds, n = 63. Colour, width and orientation of ellipses code for strength and direction of correlation (i.e. Spearman's rho). Measures of activity correlated negatively with Condition during light, and positively during dark. Resting behaviour correlated positively with Condition during light and negatively during dark.



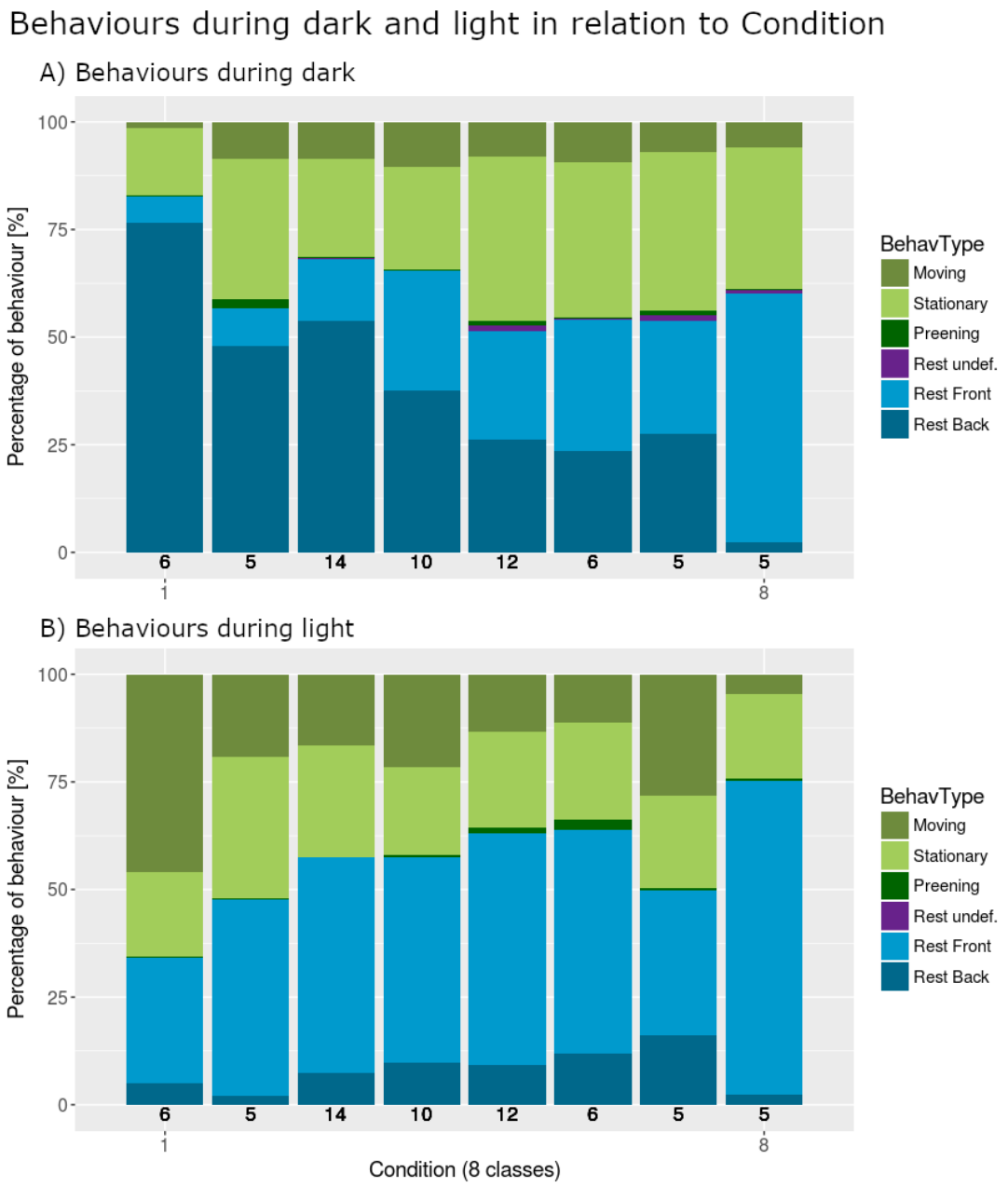


Figure 6: Overview. Amount of different behaviours during dark and light hours plotted against Condition (higher class = better physiological condition). Mean percentage of behaviours in each class stacked on each other. Number of birds in each class is printed at the base of the bars. Classes were made using the ten classes shown in figure 3B, but merging the two lowest and two highest classes, resulting in an increased n in these categories. Graph was made for visual understanding of the data; no statistical tests were performed on grounds of the depicted subdivision of Condition (PCA). **A)** Behaviour during dark: Rest Back behaviour decreased with increasing Condition, while Rest Front behaviour increased. Total resting behaviour decreased slightly with increasing Condition. **B)** Behaviour during light: Moving behaviour decreased with increasing Condition, while Rest Front and total resting behaviour increased.

Linear regression models were applied to predict different measures of resting and activity based on body condition of the birds.

Condition had significant influence on resting behaviour during light hours, with birds in better Condition spending more time resting ($F_{1,61}$= 10.59, $p < 0.01$, $R^2 = 0.14$). Influence of Condition on resting behaviour during light is depicted in figure 6B and 7.

Condition had no significant influence on resting behaviour during dark hours, but a trend for birds in better Condition spending less time resting could be observed ($F_{1,61}$= 3.77, $p = 0.06$, $R^2 = 0.06$).

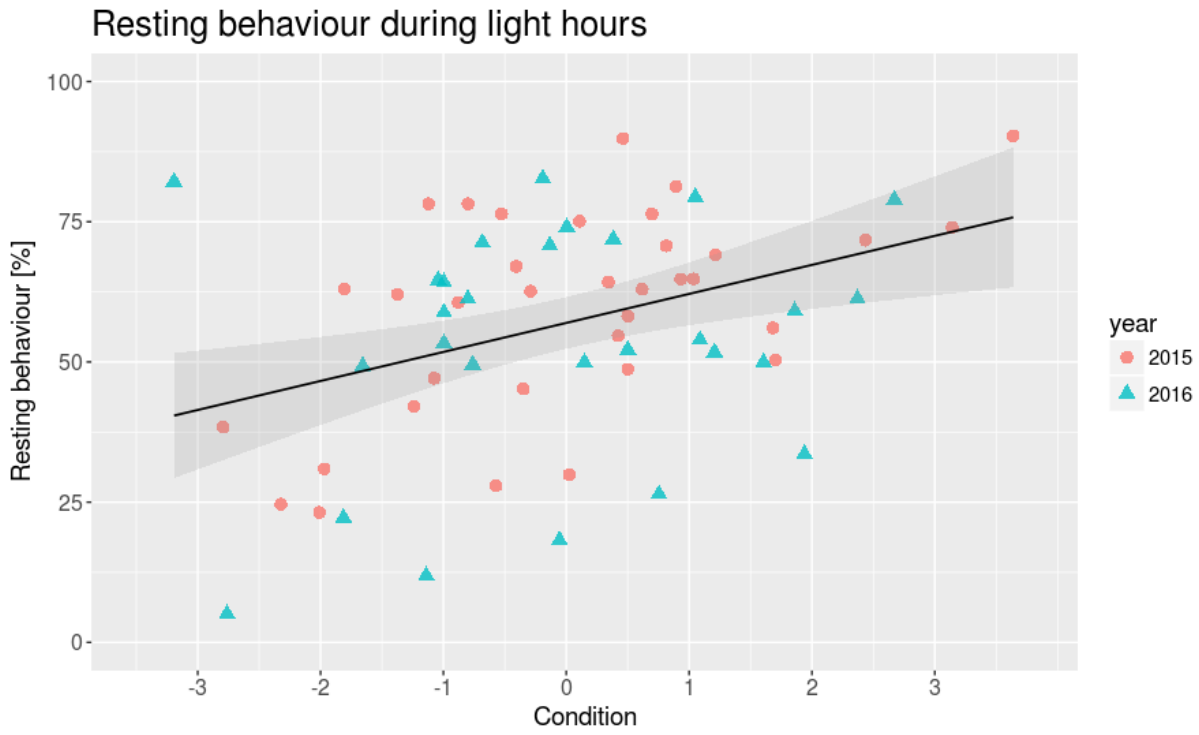


Figure 7: Percentage of total resting behaviour during light hours plotted against Condition of the birds (n = 63). Applied linear model is shown as a black line, with the 95% confidence interval around.

Condition had significant influence on Moving behaviour during light hours, with birds in better Condition spending less time moving ($F_{1,61}$= 5.87, $p < 0.05$, $R^2 = 0.07$) (figure 6B).

Condition had significant influence on Stationary behaviour during dark hours, with birds in better Condition spending more time stationary ($F_{1,61}$= 4.95, $p < 0.05$, $R^2 = 0.08$).

Condition had strong influence on Rest Back behaviour during dark hours, with birds in better Condition spending significantly less time in this state ($F_{1,61}$= 28.03, $p < 0.001$, $R^2 = 0.31$, see figure 8, or 6A). During light hours, no effect of Condition on amount of Rest Back behaviour was observed. A linear regression performed for total observation time, states a significant influence of Condition on Rest Back behaviour, with birds in better Condition spending less time in this state ($F_{1,61}$= 22.85, $p < 0.001$, $R^2 = 0.27$).

Rest Front behaviour during dark hours was strongly influenced by Condition, with birds in better Condition spending significantly more time in that state ($F_{1,61}$= 31.30, $p < 0.001$, $R^2 = 0.34$) (figure 6A). During light hours too, birds in better Condition spent more time in Rest Front behaviour as compared to birds in worse Condition ($F_{1,61}$= 6.29, $p < 0.05$, $R^2 = 0.09$), (figure 6B). So, naturally, also for total observation time, this effect remained ($F_{1,61}$= 24.86, $p < 0.001$, $R^2 = 0.29$).

No linear influence of Condition on the amount of the behaviour Wingflap was found.

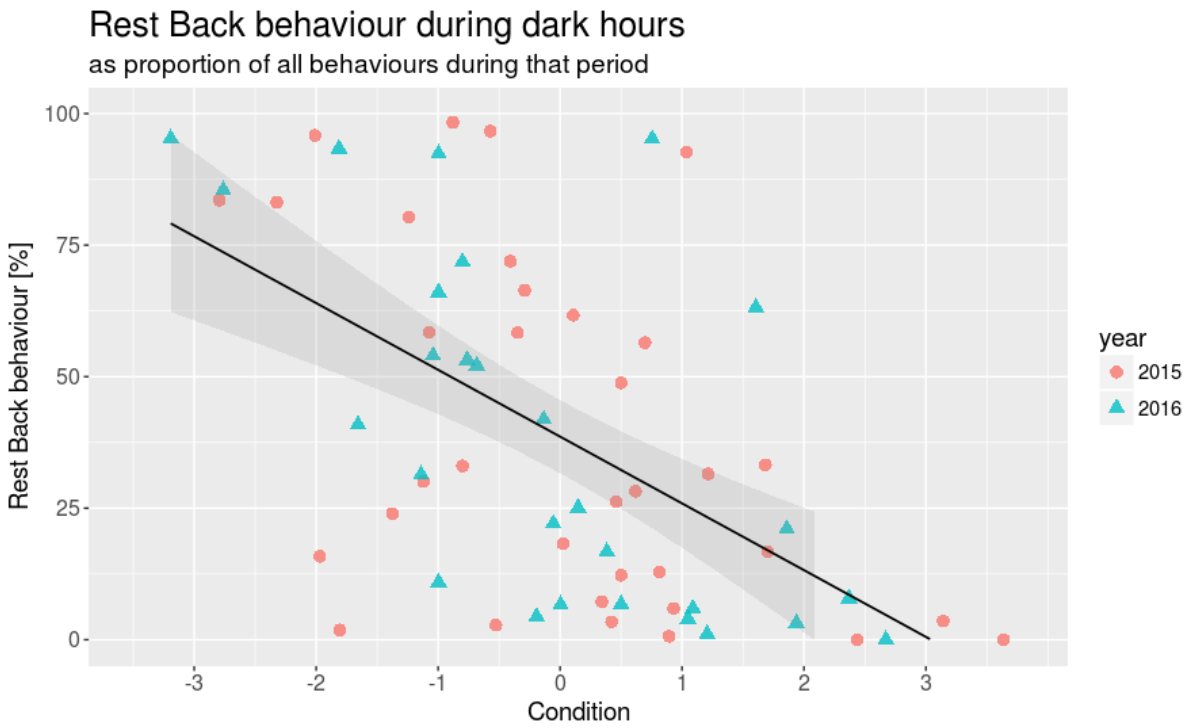


Figure 8: Percentage of Rest Back behaviour during dark hours plotted against Condition of the birds (n = 63). Applied linear model is shown as a black line, with the 95% confidence interval around.

Food intake

Food intake decreased with increasing Condition (r_S = -0.54, $p < 0.001$) as seen in table 2. Furthermore, a logistic regression was performed, to predict the influence of Condition on Food intake of the birds. Data followed a clear binomial distribution as one can see in figure 9. Therefore, depending on the amount of food intake in grams, birds were put in one of the two categories: "High food intake" (intake > 1.5 g) and "Low food intake" (intake ≤ 1.5 g). With these two classes as dependent variable, the regression model was performed. The model found a highly significant influence of Condition on Food intake ($p < 0.001$, Residual deviance = 68.3 on 61 degrees of freedom, Odds ratio = 0.38). The odds ratio indicates the prediction that, when Condition is raised by one unit, the odds ratio is 0.38 times as large – therefore, birds are 2.63 times less likely to be in class "High food intake". The predicted probabilities, which are easier to interpret visually, are plotted in figure 9. Both, the odds ratio and the probabilities, are predicted values based on the model that was calculated by the data collected. Therefore, they intrinsically fit the data plotted in figure 9, and still need to be tested with independent data. Food was exclusively taken up during light hours.

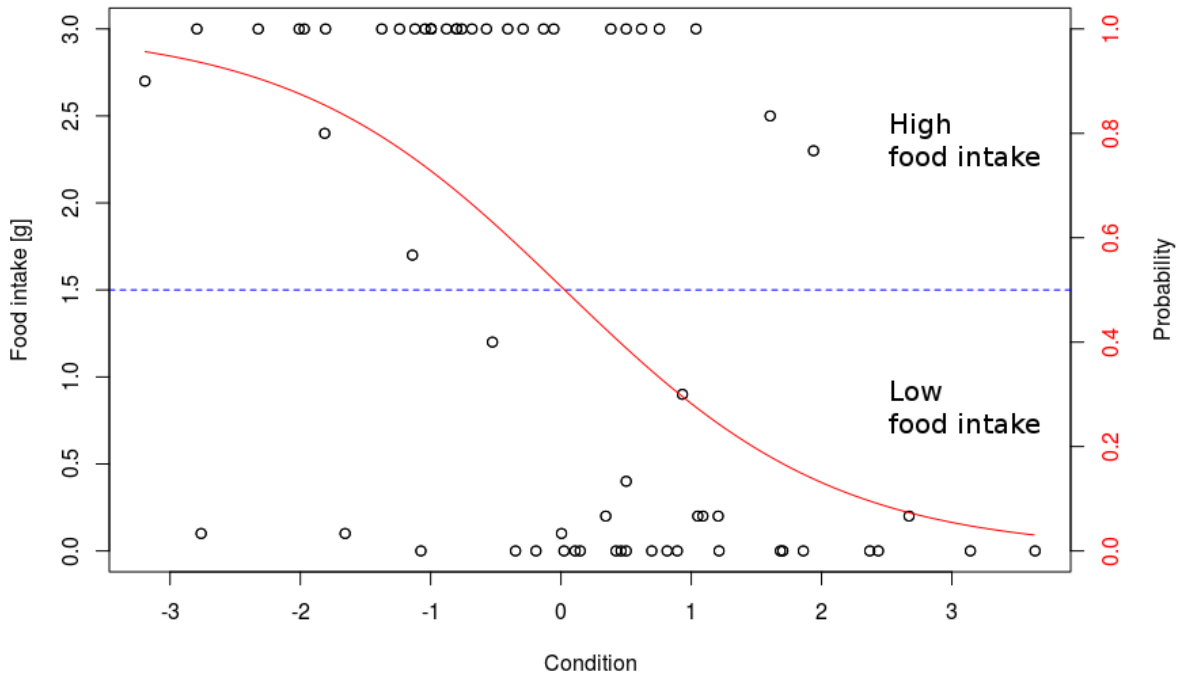


Figure 9: Food intake in grams plotted against Condition of the birds. Blue dashed line marks the threshold above which birds were classified as having "High food intake" (n = 32), and below which as having "Low food intake" (n = 31). These categories were used for calculating a logistic regression model.

Red curve plots the predicted probabilities of the performed model, so the probability for a bird with a given Condition to be in the category “High food intake”.

Summary

During night, the behaviours of birds in low physiological condition were constituted to a greater degree of general resting behaviour and deeper states of resting as they were during daylight - which was therefore filled more with active states, other active behaviours such as Moving, and lighter states of resting. This whole pattern became less pronounced with increasing Condition of the birds (figure 5, 6A and 6B). So, birds in a better physiological state generally showed high amounts of resting behaviours during light, while Moving behaviour was low. During night, these birds showed slightly lower amounts of total resting behaviours as compared to lean birds, while the deeper states of resting were substantially lower and the slighter forms of resting substantially higher (table 2, figure 6A and 6B). The birds amount of food intake during their stay in the cages followed a clear all-or-nothing scheme (figure 9). Birds in lower Condition had a significantly higher likelihood of taking up all the food available (table 2, figure 9).

DISCUSSION

My results show that the amount of active behaviour of garden warblers during spring migration correlates with their physiological condition - negatively during light, and positively during dark hours - as recorded by video-observation of an overnight-stay in soundproof cages (see table 2). Additionally, during dark hours, the amount of resting behaviour with the head facing backwards and the beak tucked under the scapula feathers, is significantly higher in birds having a low Condition; while these birds also take up more food during their time in the cage.

The higher active and moving behaviour of lean birds during daylight, combined with a higher food intake (which was also just happening during day), strongly supports the idea that these birds use the light hours on stopover sites to actively search for food. This has been proposed by previous studies which have also found higher activity of lean garden warblers during light hours (Bairlein 1985, Fusani et al. 2009); a similar pattern was found in different thrushes after crossing the Gulf of Mexico (Young & Moore 1993). An endogenous factor determining food-uptake behaviour and migratory restlessness in migratory birds has recently been identified: The hormone ghrelin. Garden warblers with high fat score had higher levels of ghrelin and took up less food. When birds were injected with unacetylated ghrelin, food intake, especially of lean birds, decreased and migratory restlessness increased (Goymann et al. 2017). This goes together with my findings of lean birds having a higher likelihood of taking up food, suggesting lower levels of ghrelin. But refuelling in terms of increasing fat deposits is not the only important factor. Since migratory birds at stopover sites not only recover from, but also prepare for, oxidative challenges posed by long fasting-flights (Skrip et al. 2015), they are expected to rebuild antioxidant capacity during their stay – by endogenously building up enzymatic antioxidant capacity, and by taking up dietary antioxidants. It has been shown that birds at stopover during autumn migration are trying to find and take up food that is high in antioxidants (Alan et al. 2013, Bolser et al. 2013). In newly arrived garden warblers at a stopover site during spring migration, antioxidant capacity didn't show a correlation with measures of body condition, and oxidative damage increased with increasing absolute fat mass (Skrip et al. 2015) - so not only lean but also fat birds should have a need to rebuild antioxidant capacity. The search for antioxidants, beneath refuelling, might therefore be an additional driver of daylight activity that makes also birds with high fat score/body condition to have increased activity

during day. However, when tested in 2012 on Ponza, antioxidant capacity remained unchanged with stopover duration in garden warblers, which was argued to be caused by the scarcity of antioxidant-rich food resources in spring on the island (Skrip et al. 2015). In autumn, when birds are supposedly less urged to use a time-minimization strategy (Hedenström 2008), and food supply at the island is richer in antioxidants (i.e. berries), stopover-behaviour of garden warblers on Ponza might look different.

Still, it is plausible to assume that birds which can afford it are spending less time and energy on food searching behaviour – it might be more rewarding for them to save energy during day and limit exposure to threats (Hedenström 2008). Birds in migratory disposition have been shown to become more risk averse in their food-uptake behaviour when already having gained enough fuel to continue migration (Moore & Simm 1986). Risk-aversion must be an important factor: 85% of annual mortality in a small North American long-distance migrant were shown to happen during migration (Sillett & Holmes 2002). Even though, naturally, a lot of other factors (unfavourable weather, physical exhaustion, etc.) are playing a role in the increased mortality during migration, predation and the exposure to parasites and disease are without question very important. But even with the above-mentioned risks, what prevents lean birds of spending all possible time with taking up food, thus being able to continue migration earlier? Since especially when using a time minimization strategy during spring migration, rewards of early arrival (Kokko 1999) could make up for the increased risks and costs.

The first part of the answer is, that physiological limits regarding food uptake come to play. Gannes 2002 found evidence that in blackcaps *(Sylvia atricapilla)*, intake rate upon arrival at a stopover site was physiologically limited and prevented large mass gains until assimilation organs were sufficiently recovered. A second part of the answer is likely to be the need to recover from oxidative stress that was posed upon the birds by long endurance and fasting flights. Since the birds just crossed a large ecological barrier (Mediterranean Sea), levels of oxidative damage are high upon arrival at Ponza. Jenni-Eiermann et al. 2014 studied short-distance migrants in the alps during their autumn migration and compared birds caught during stopover and birds caught during nightly endurance flight. They found that oxidative damage and antioxidant capacity was higher for birds in migration, and conclude, that avoiding oxidative stress might be an overlooked factor that shapes bird migration. Skrip et al. 2015 show that birds at stopover not only prepare for endurance flight by upregulating antioxidant capacity

and building fat stores, but that they also recover from oxidative damage. They found that oxidative damage levels of garden warblers decreased with stopover duration, while fat anabolism increased. So, birds during stopover need to recover, they should balance well between needed active engagement in food searching behaviour and physical recovery through rest or sleep. This notion is supported by my data in two ways: First, lean birds spent more of their daylight time active than fat birds, while this difference wasn't extremely pronounced and thus reflects the need to recover physically for all the birds irrespective of body condition. Other studies found the same daylight-activity pattern for garden warblers, also on Ponza, but not for other long- and short-distance migrants (Lupi et al. 2016, Fusani et al. 2009). This can be interpreted in a similar manner, namely that in these species, daylight activity and food searching behaviour might be less influenced by body condition, and stronger influenced by other factors, such as the need to recover from oxidative damage. Secondly, and this is my main point, I found a strong pattern regarding resting position in dependency of body condition, especially during night. Birds in low condition spent profoundly more time in a Rest Back (RB) position as compared to birds in high condition (figure 6A, 8). The total amount of resting during night, again, as during day, didn't change so much with condition (though still showing a decreasing trend, see figure 6A and table 2). The difference was just, that birds in better condition were spending their resting time during night almost exclusively in a Rest Front (RF) position (figure 6A). I argue here, that the difference in amount of RB/RF behaviour in dependency of body condition reflects the migratory disposition of the birds. While these two positions likely also have different up- and downsides regarding recovery and rest.

In a study investigating sleeping behaviour in three different passerine species of South Africa, birds spent significantly more time in RB when temperature was at 5 °C, well below their thermoneutral zone (Wellmann & Downs 2009). This was interpreted as thermoregulatory behaviour, since the RB position reduces heat loss as it decreases volume/surface ratio and thus helps to save energy. However, increased amount of RB behaviour in the current study is unlikely due to saving energy, since temperature in the cages was around or above the thermoneutral zone of garden warblers, which lies at around 20 °C (Klaassen & Biebach 1994). The reason for the difference in resting position must therefore be looked for somewhere else. RB posture has been found to be tightly correlated with electrographic sleep in the blackbird, and around 60 % of REM sleep (rapid eye movement) was spent in RB position (Szymczak et al.

1993). Whereas during RF position, it is quite likely that the birds were not sleeping all the time, since states of quiet wakefulness (QW) can occur also when the bird is immobile and having its eyes closed (Szymczak et al. 1993). The amount of QW in blackbirds varied between different hours of the day (including night), and roughly ranged between $\frac{1}{18}$ and $\frac{1}{7}$ of total time – and it was almost exclusively shown when in a RF position. Looking at my results regarding resting position during night, it is therefore likely that lean garden warblers slept more than fat individuals. It has been shown that a common North American passerine is generally able to deal greatly with reduced amounts of sleep when in a migratory state, i.e. they could maintain adaptive brain functions even though sleeping less than a third of the normal time when not in a migratory state (Rattenborg et al. 2004). Still, this study didn't distinguish between physiological condition of the birds. So, it might be that lean birds in fact do need more sleep than birds in good condition. Alternatively, the lean birds could exhibit the default programme of stopover recovery, while the low amount of RB and high amount of RF in fat birds reflects some sort of 'mental restlessness' - which doesn't show in a physical way like normal migratory restlessness does, but still mirrors the birds mental and physiological readiness to continue migration in an environment where it can't continue migration (i.e. a cage). In such a setting, this could be the best fit alternative behaviour to actual migration and possibly even emulate similar sleep patterns that might be at work during nightly migratory flights, namely unihemispheric and bihemispheric short wave sleep (U+B SWS) interrupted by brief awakenings to scan for predators and other visual stimuli used for navigation (Rattenborg 2006, Rattenborg et al. 2016). Short visual scans of the environment, including slowly turning the head with only one eye open, were repeatedly observed when birds were in RF position, while it was difficult to estimate the eyelid position and finer head movements when birds were in RB position (personal observation). It is possibly more effort for birds in RB position to scan the environment as compared to being in RF position, but this remains to be tested. In an experiment about group-sleeping behaviour in mallard ducks *(Anas platyrhynchos)*, individuals sleeping at the edge of the group were significantly more likely to have the eye open which was directed away from the group, thus being able to detect potential threats (Rattenborg et al. 1999). The authors unfortunately don't state in which position the birds were sleeping and if they performed regular scans of the environment; but the situation in a group differs from our

experimental conditions anyways, since birds sleeping alone can experience threats from different directions, which results in the necessity for regular scans.

So, RF position might provide some advantage regarding alertness and overview, while under circumstances of migration likely reflects the bird's readiness to migrate; whereas RB position, again under circumstances of migration, likely is used for deeper states of rest or sleep and signals the birds need to recuperate before being able to continue migration.

Wingflap-behaviour, which is the common behavioural measure of migratory restlessness, somewhat increased with increasing condition, but didn't show a clear or pronounced pattern. This might be owing to methodological shortcomings during coding: It was very difficult to distinguish between real Wingflap-behaviour that clearly reflected migratory restlessness (coded) on the one hand - and other flapping and jumping behaviour that was more likely to represent attempts to escape the cage (non-coded) on the other hand. The decision to label a flapping event as Wingflap was therefore not satisfyingly consistent across video coding. Setting the ethogram differently could help in future studies using focal observation. Coding both behaviours, 'Wingflap' (WF) as well as 'Flap and Jump' (FJ), or merging them under the term 'physical restlessness', would make coding of these behaviours more explicit and might result in a clearer pattern regarding the relation with body condition.

Since eyelid closure is stated to be the most useful behavioural index of sleep (Szymczak et al. 1993), and other studies also find a tight connection (Rattenborg et al. 1999), it would be interesting for future studies investigating sleep behaviour in birds, to assess eye-closure of both eyes more accurately. Additionally, scans of the environment should be recorded, as they might reveal a connection to resting position. However, for a clear distinction in which state of wakefulness or sleep the bird is in, electroencephalography is inevitable.

Significance and Conclusion

My results show that the amount of active behaviour of garden warblers during spring migration correlates with their physiological condition, negatively during light, and positively during dark hours. Additionally, birds in a low physiological condition are more likely to take up food, and their amount of Rest Back behaviour during dark hours is strongly significantly higher, while the amount of nightly Rest Front behaviour is much higher for birds in good condition.

My results support previous findings of birds at stopover during migration to exhibit greater activity during day to search for food in dependency of a low body condition; while the differences are not pronounced and might be influenced by other factors such as the need to recover from oxidative damage, and also do vary between species. I further suggest, that nightly Rest Back behaviour in garden warblers during migration can be used as an indicator for deeper states of recovery and sleep, whereas the amount of nightly Rest Front behaviour might reflect the physiological readiness of the birds to continue migration, similar to migratory restlessness exhibited during night.

It wouldn't have been possible to detect differences between Rest Back and Rest Front behaviour by using automatized counts of light barrier as has been done in other studies (Fusani et al. 2009, Lupi et al. 2016). Therefore, the methods used in my study can detect finer differences in bird behaviour in comparison to infrared sensor methods. The main findings in the above studies, however, overlap well with my findings regarding activity. So, infrared sensor methods are to be favoured to search for differences in migratory restlessness or plain activity, since they have a lower workload as compared to focal observation. But if a finer distinction of behaviours is needed, as is the case for determining resting position, video recording should be considered.

LITERATURE

Alan, R. R., McWilliams, S. R., & McGraw, K. J. (2013). The importance of antioxidants for avian fruit selection during autumn migration. *The Wilson Journal of Ornithology*, *125*(3), 513-525.

Bairlein, F. (1985). Body weights and fat deposition of Palaearctic passerine migrants in the central Sahara. *Oecologia*, *66*(1), 141-146.

Biebach, H. (1985). Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia*, *41*(5), 695-697.

Bolser, J. A., Alan, R. R., Smith, A. D., Li, L., Seeram, N. P., & McWilliams, S. R. (2013). Birds select fruits with more anthocyanins and phenolic compounds during autumn migration. *The Wilson Journal of Ornithology*, *125*(1), 97-108.

Erni, B., Liechti, F., & Bruderer, B. (2002). Stopover strategies in passerine bird migration: a simulation study. *Journal of Theoretical Biology*, *219*(4), 479-493.

Fusani, L., Cardinale, M., Carere, C., & Goymann, W. (2009). Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. *Biology Letters*, rsbl-2008.

Fusani, L., Cardinale, M., Schwabl, I., & Goymann, W. (2011). Food availability but not melatonin affects nocturnal restlessness in a wild migrating passerine. *Hormones and behavior*, *59*(1), 187-192.

Gannes, L. Z. (2002). Mass change pattern of blackcaps refuelling during spring migration: evidence for physiological limitations to food assimilation. *The Condor*, *104*(2), 231-239.

Goymann, W., Spina, F., Ferri, A., & Fusani, L. (2010). Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. *Biology Letters*, *6*(4), 478-481.

Goymann, W., Lupi, S., Kaiya, H., Cardinale, M., & Fusani, L. (2017). Ghrelin affects stopover decisions and food intake in a long-distance migrant. *Proceedings of the National Academy of Sciences*, 201619565.

Hedenström, A., & Alerstam, T. (1997). Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of theoretical biology*, *189*(3), 227-234.

Hedenström, A. (2008). Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1490), 287-299.

Jenni, L., & Schaub, M. (2003). Behavioural and physiological reactions to environmental variation in bird migration: a review. In *Avian migration* (pp. 155-171). Springer, Berlin, Heidelberg.

Jenni-Eiermann, S., Jenni, L., Smith, S., & Costantini, D. (2014). Oxidative stress in endurance flight: an unconsidered factor in bird migration. *PLoS One*, *9*(5), e97650.

Kaiser, A. (1993). A new multi-category classification of subcutaneous fat deposits of songbirds (Una Nueva Clasificación, con Multi-categorías, para los Depósitos de Grasa en Aves Canoras). *Journal of Field Ornithology*, 246-255.

Klaassen, M., & Biebach, H. (1994). Energetics of fattening and starvation in the long-distance migratory garden warbler, Sylvia borin, during the migratory phase. *Journal of Comparative Physiology B*, *164*(5), 362-371.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology*, *68*(5), 940-950.

Lincoln, F. C., & Peterson, S. R. (1979). *Migration of birds* (No. 16). Fish & Wildlife Service, US Department of the Interior.

Lindström, Å. (2003). Fuel deposition rates in migrating birds: causes, constraints and consequences. In *Avian migration* (pp. 307-320). Springer, Berlin, Heidelberg.

Lupi, S., Goymann, W., Cardinale, M., & Fusani, L. (2016). Physiological conditions influence stopover behaviour of short-distance migratory passerines. *Journal of Ornithology*, *157*(2), 583-589.

Moore, F. R., & Simm, P. A. (1986). Risk-sensitive foraging by a migratory bird (Dendroica coronata). *Experientia*, *42*(9), 1054-1056.

Morganti, M., Mellone, U., Bogliani, G., Saino, N., Ferri, A., Spina, F., & Rubolini, D. (2011). Flexible tuning of departure decisions in response to weather in black redstarts Phoenicurus ochruros migrating across the Mediterranean Sea. *Journal of Avian Biology*, *42*(4), 323-334.

Rattenborg, N. C., Lima, S. L., & Amlaner, C. J. (1999). Facultative control of avian unihemispheric sleep under the risk of predation. *Behavioural brain research*, *105*(2), 163-172.

Rattenborg, N. C., Amlaner, C. J., & Lima, S. L. (2000). Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neuroscience & Biobehavioral Reviews*, *24*(8), 817-842.

Rattenborg, N. C. (2006). Do birds sleep in flight? *Naturwissenschaften*, *93*(9), 413-425.

Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M., & Benca, R. M. (2004). Migratory sleeplessness in the white-crowned sparrow (Zonotrichia leucophrys gambelii). *PLoS biology*, *2*(7), e212.

Rattenborg, N. C., Voirin, B., Cruz, S. M., Tisdale, R., Dell'Omo, G., Lipp, H. P., ... & Vyssotski, A. L. (2016). Evidence that birds sleep in mid-flight. *Nature communications*, *7*, 12468.

Sillett, T. S., & Holmes, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, *71*(2), 296-308.

Skrip, M. M., Bauchinger, U., Goymann, W., Fusani, L., Cardinale, M., Alan, R. R., & McWilliams, S. R. (2015). Migrating songbirds on stopover prepare for, and recover from, oxidative challenges posed by long-distance flight. *Ecology and evolution*, *5*(15), 3198-3209.

Südbeck, P., Andretzke, H., Fischer, S., Gedeon, K., Schikore, T., Schröder, K. & Sudfeldt, C. (2005). *Methodenstandards zur Erfassung der Brutvögel Deutschlands.* Max-Planck-Institut für Ornithologie, Vogelwarte Radolfzell.

Szymczak, J. T., Helb, H. W., & Kaiser, W. (1993). Electrophysiological and behavioral correlates of sleep in the blackbird (Turdus merula). *Physiology & behavior*, *53*(6), 1201-1210.

Wellmann, A. E., & Downs, C. T. (2009). A behavioural study of sleep patterns in the malachite sunbird, Cape white-eye and fan-tailed widowbird. *Animal Behaviour*, *77*(1), 61-66.

Yong, W., & Moore, F. R. (1993). Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. *Condor*, 934-943.

APPENDIX

Zusammenfassung

Der Einfluss der physiologischen Körperverfassung auf die Aktivität von Vögeln wird oft mithilfe von Infrarot-Sensoren untersucht. Ich verwendete hier eine andere Technik, nämlich die der kontinuierlichen Video-Beobachtung. Ich untersuchte an einem kleinen europäischen Zugvogel während einer Zug-Pause, ob ein Zusammenhang von Aktivität, Nahrungsaufnahme und Schlafmuster mit der physiologischen Verfassung des Tieres gegeben ist. Während dem Frühjahrszug 2015 und 2016 wurden auf einer Insel nahe Neapel, Italien, 63 Gartengrasmücken mithilfe von Japannetzen gefangen und für 16 Stunden in schalldichten Stoffkäfigen vom Weiterzug abgehalten. Mehlwürmer (3g) und Wasser (ad libitum) wurden jedem Vogel zur Verfügung gestellt. Drei Kameras machten kontinuierlich Video-Aufnahmen des Verhaltens. Es wurde allgemeines Rastverhalten und allgemeine Aktivität kodiert. Zwei Unterformen waren jeweils relevant: 'Rest Back' und 'Rest Front' bei dem Rastverhalten, 'Stationär' sowie 'Bewegung' bei der Aktivität. Aktivität und Rastverhalten sind sich gegenseitig ausschließend, wie auch die jeweiligen Unterformen: Eine relative Zunahme von Rest Back bedeutet beispielsweise eine entsprechende Abnahme von Rest Front. Das Ausmaß der Unterhaut-Fettdepots und des Brustmuskels wurde gemeinsam mit dem Körpergewicht zu einem einheitlichen Index für die körperliche Verfassung des Tieres verrechnet. Vögel in guter physiologischer Verfassung zeigten während Tageslicht mehr allgemeines Rastverhalten und weniger Bewegung als Vögel in schlechter Verfassung. Die Menge an aufgenommener Nahrung folgte einem eindeutigen alles-oder-nichts Schema, bei welchem Vögel in schlechterer Verfassung eine signifikant höhere Wahrscheinlichkeit hatten, das gesamte zur Verfügung stehende Futter aufzunehmen. Während der Nacht zeigten Vögel in guter Verfassung tendenziell weniger allgemeines Rastverhalten im Vergleich zu Vögeln in schlechterer Verfassung. Die Menge an Rest Back (Rastverhalten, während dem der Schnabel nach hinten zeigt) war wesentlich niedriger bei Vögeln in guter Verfassung; die Menge an Rest Front (Rastverhalten, während dem der Schnabel nach vorne zeigt) war wesentlich höher. Meine Ergebnisse unterstützen vorherige Studien, die besagen, dass Vögel in schlechter körperlicher Verfassung während den Zug-Pausen tagsüber eine höhere Aktivität aufweisen, um nach Futter zu suchen. Doch sind diese Unterschiede in meinen Ergebnissen nicht stark ausgeprägt, das

Verhalten wird vermutlich von weiteren Faktoren beeinflusst. Zusätzlich unterbreite ich die Idee, dass nächtliches Rest Back Verhalten in Gartengrasmücken während dem Vogelzug als ein Indikator für tiefere Formen der Erholung und des Schlafs genutzt werden kann, während die relative Menge an nächtlichem Rest Front Verhalten die physiologische Bereitschaft zu einem Weiterzug reflektiert, ähnlich der bekannten Zugunruhe. Ich schließe mit der Aussage, dass Infrarot-Sensor Methoden verwendet werden sollten, um nach Unterschieden in Aktivität oder Zugunruhe zu suchen. Falls jedoch eine detailliertere Unterscheidung von Verhalten benötigt wird, sollten Video-Aufnahmen bevorzugt werden.

Ethogram

Definition of recorded behaviours, Ponza Rest Study 2015 + 2016

States

States Sub-states

Active: Bird has open eyes

> Stationary: Bird turns the head around, moves its body or body parts (comfort behaviour like stretching legs, cleaning beak, etc.), turns around on the perch or floor; the bird does not change its physical position in the cage, i.e. the feet stay on the ground and legs are not moved except turning or stretching.
>
> Preening: Bird is touching himself repeatedly with the beak, usually stroking through the feathers. Does not include: other comfort behaviour like stretching, cleaning beak on the wood, pulling with the beak at the ring, scratching the head with the feet.
>
> Moving: Bird is active, often seems restless, moves regularly on the perch or floor, jumps or flies through the cage, explores the cage. The position of the feet is changed often and the rest of the body is moved extensively.

Resting: Either one or two eyes are closed, or impossible to confirm if the eyes are open or not while one can exclude active states such as Stationary, Moving or Preening. Bird is sitting without motion, excluding breathing or reflex-like movements. It often stands on one leg. Feathers can be ruffled – which results in a "fluffy" or "round" appearance. The head is turned to one side or points forward, occasionally dropping to the bird's feet.

> Rest Front: The head is retracted towards the body while facing forward.
>
> Rest Back: The head is pointing backward with the beak resting on the bird's back or under the scapular feathers.
>
> Rest undefined: It can't be assessed in which state of Rest the bird is in.

Out of sight: Bird is outside of the surveyed area (e.g. sitting on top of upper Camera)

Events

Wingflap: the bird flaps its wings, but the legs don't leave the perch or floor
Eat: the bird swallows down a piece of food (mealworm)
Drink: the bird puts the beak into the water and then ups the head
Light: Marker for Daylight – only put once in each video, in the instant when Lights are turned on in the morning or at the beginning of the video (if it starts during light hours).
Dark: Marker for Night-time/Darkness – only put once in each video, in the instant when Lights are turned off at the evening, or at the beginning of the video (if it starts during dark hours).

4/3/2015

Sun or Moon Rise/Set Table for One Year

Location: E012 58, N40 55

PONZA
Civil Twilight for 2015

Zone: 1h East of Greenwich

= sun is 6° under Horizon

Astronomical Applications Dept.
U. S. Naval Observatory
Washington, DC 20392-5420

	Jan.		Feb.		Mar.		Apr.		May		June		July		Aug.		Sept.		Oct.		Nov.		Dec.	
Day	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End	Begin	End
	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m	h m
01	0702	1721	0650	1754	0615	1826	0525	1900	0437	1934	0406	2006	0406	2017	0433	1955	0506	1909	0537	1818	0610	1733	0642	1711
02	0702	1722	0649	1755	0614	1827	0523	1901	0436	1935	0406	2007	0407	2017	0434	1954	0507	1908	0538	1817	0611	1732	0643	1711
03	0702	1723	0648	1756	0612	1828	0521	1902	0435	1936	0405	2008	0407	2017	0435	1953	0508	1906	0539	1815	0612	1731	0644	1711
04	0702	1724	0647	1757	0611	1830	0520	1904	0433	1937	0405	2009	0408	2017	0436	1952	0509	1904	0540	1813	0613	1730	0645	1711
05	0702	1725	0646	1759	0609	1831	0518	1905	0432	1939	0404	2009	0409	2016	0437	1950	0510	1903	0541	1812	0614	1729	0646	1711
06	0702	1726	0645	1800	0608	1832	0516	1906	0431	1940	0404	2010	0409	2016	0438	1949	0511	1901	0542	1810	0615	1728	0647	1711
07	0702	1727	0644	1801	0606	1833	0515	1907	0429	1941	0403	2011	0410	2016	0439	1948	0512	1859	0543	1808	0616	1727	0648	1711
08	0702	1728	0643	1802	0605	1834	0513	1908	0428	1942	0403	2011	0411	2015	0440	1946	0513	1858	0544	1807	0618	1726	0649	1711
09	0702	1728	0642	1803	0603	1835	0511	1909	0427	1943	0403	2012	0411	2015	0441	1945	0514	1856	0545	1805	0619	1725	0650	1711
10	0702	1729	0641	1804	0601	1836	0510	1910	0426	1944	0403	2013	0412	2014	0443	1944	0515	1854	0546	1804	0620	1724	0650	1711
11	0702	1730	0640	1806	0600	1837	0508	1911	0424	1945	0403	2013	0413	2014	0444	1942	0516	1852	0547	1802	0621	1723	0651	1711
12	0701	1731	0638	1807	0558	1838	0506	1912	0423	1946	0402	2014	0414	2013	0445	1941	0517	1851	0548	1801	0622	1722	0652	1711
13	0701	1733	0637	1808	0557	1839	0505	1914	0422	1948	0402	2014	0415	2013	0446	1940	0519	1849	0549	1759	0623	1721	0653	1711
14	0701	1734	0636	1809	0555	1841	0503	1915	0421	1949	0402	2015	0415	2012	0447	1938	0520	1847	0550	1758	0624	1720	0654	1712
15	0701	1735	0635	1810	0553	1842	0501	1916	0420	1950	0402	2015	0416	2011	0448	1937	0521	1846	0551	1756	0625	1719	0654	1712
16	0700	1736	0634	1811	0552	1843	0500	1917	0419	1951	0402	2015	0417	2011	0449	1935	0522	1844	0552	1755	0627	1719	0655	1712
17	0700	1737	0632	1813	0550	1844	0458	1918	0418	1952	0402	2016	0418	2010	0450	1934	0523	1842	0553	1753	0628	1718	0656	1712
18	0659	1738	0631	1814	0548	1845	0457	1919	0417	1953	0402	2016	0419	2009	0451	1932	0524	1840	0554	1752	0629	1717	0656	1713
19	0659	1739	0630	1815	0547	1846	0455	1920	0416	1954	0402	2016	0420	2008	0452	1931	0525	1839	0556	1750	0630	1717	0657	1713
20	0658	1740	0628	1816	0545	1847	0454	1921	0415	1955	0403	2017	0421	2008	0453	1929	0526	1837	0557	1749	0631	1716	0657	1714
21	0658	1741	0627	1817	0543	1848	0452	1923	0414	1956	0403	2017	0422	2007	0454	1927	0527	1835	0558	1747	0632	1715	0658	1714
22	0657	1742	0626	1818	0542	1849	0450	1924	0413	1957	0403	2017	0423	2006	0456	1926	0528	1834	0559	1746	0633	1715	0658	1715
23	0657	1743	0624	1819	0540	1850	0449	1925	0412	1958	0403	2017	0424	2005	0457	1924	0529	1832	0600	1745	0634	1714	0659	1715
24	0656	1745	0623	1821	0538	1852	0447	1926	0411	1959	0403	2017	0425	2004	0458	1923	0530	1830	0601	1743	0635	1714	0659	1716
25	0655	1746	0621	1822	0537	1853	0446	1927	0411	2000	0404	2018	0426	2003	0459	1921	0531	1828	0602	1742	0636	1713	0700	1716
26	0655	1747	0620	1823	0535	1854	0444	1928	0410	2001	0404	2018	0427	2002	0500	1919	0532	1827	0603	1741	0637	1713	0700	1717
27	0654	1748	0618	1824	0533	1855	0443	1929	0409	2002	0404	2018	0428	2001	0501	1918	0533	1825	0604	1739	0638	1713	0701	1718
28	0653	1749	0617	1825	0532	1856	0442	1931	0408	2003	0405	2018	0429	2000	0502	1916	0534	1823	0605	1738	0639	1712	0701	1718
29	0652	1750			0530	1857	0440	1932	0408	2004	0405	2017	0430	1959	0503	1914	0535	1822	0606	1737	0640	1712	0701	1719
30	0652	1752			0528	1858	0439	1933	0407	2005	0406	2017	0431	1958	0504	1913	0536	1820	0608	1736	0641	1712	0701	1720
31	0651	1753			0526	1859			0407	2005			0432	1957	0505	1911			0609	1734			0702	1720