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„Rest Study - Relationship between rest pattern and
physiological condition during spring migration in
whitethroats (*Sylvia communis*)“

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1. INTRODUCTION

1.1. *Behavioural changes in birds during migration*

Birds are migrating twice a year at about the same time due to seasonal environmental changes in their habitats. Once in spring they are migrating into their breeding area and then in autumn to their wintering sites because of the fluctuation in food availability. However, there are also other external factors, which are controlling migration, like the length of day/night, the weather as well as endogenous rhythms. Birds have different migratory strategies and most of them travel thousands of kilometres non-stop across areas where no food is available which consumes much energy. Therefore, stopovers are important to refill energy reserves and to handle migration (Rattenborg, et al., 2004; Lupi, et al., 2016).

The time that birds spend on stopover sites depends besides the environmental parameters, on the physiological condition. Studies show that birds with more fat reserves leave the stopover sites often during the same night and leaner birds stay longer to refuel and recover. Consequently, heavier birds show less activity during the day and more migratory restlessness (*Zugunruhe*) in the night in captivity. The opposite behaviour is demonstrated in birds with little fat reserves (Lupi, et al., 2016; Fusani, et al., 2009). Hence, the food availability on the stopover site is important because studies show that these behavioural and physiological adaptations during migration just happen when the stopover sites provide a high food amount. Sites with no food were abandoned on the same evening of the arrival by lean and heavy birds (Fusani & Eberhard, 2004) (Fig. 1).

When there is enough food on the stopover site birds also have to decide how much fuel to accumulate before departure. The more they eat, the heavier they get and therefore more energy is needed (Hedenström & Ålerstam, 1997). Consequently, for migrants also the flight (pectoral) muscle is important to transport the weight and to move and travel long distances, what also requires energy. Subsequently this muscle, which can constitute up to 35% of the total body mass in migrants, relies on oxidative metabolism for energy (Bicudo, et al., 2010). Therefore, birds are consuming more food with dietary antioxidants at a stopover site to prevent oxidative damage (Skrip & McWilliams, 2016) and to fly these long distances.

Nocturnal migration is a behavioural modification. Normally, in the non-migratory season birds are active during day and rest/sleep in the night. However, during migration birds are active during the day as well as during the night and therefore, less time is available to rest/sleep (Rattenborg, et al., 2004). The mechanisms controlling nocturnal migration are largely unknown and there are many hypotheses for this behavioural shift. For example, winning of time to forage for food during the day, reduction of predation and saving energy. Due to the fact that in the night there is cooler and denser air and the wind speeds are lower as well as the reduction of physiological stress (Bicudo, et al., 2010). Hence, migration during the night is associated with a switch in the circadian pattern of activity. For this reason, migration is carried out annually and depends on the circadian and circannual internal clock, which also has to be synchronized with the external conditions (Bergmann, 2010).

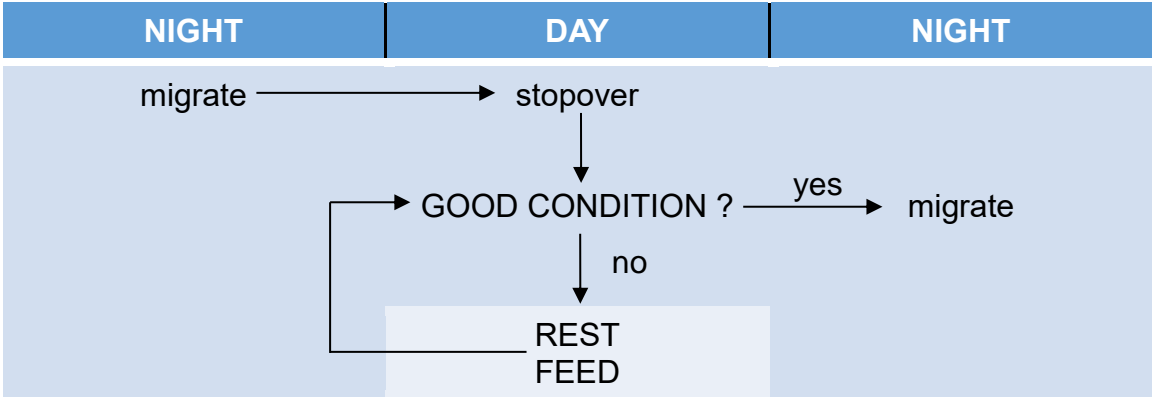


Figure 1: Behaviour of migrating birds during night and day with different condition. Arrows indicate gradual transition.

Another parameter that affects spring migration is the competition to be at the breeding site as early as possible to establish a good territory, attract a mate and produce an early clutch (Agatsuma & Ramenofsky, 2006). Therefore, male birds leave the stopover site as soon as possible to increase reproductive success, which may cost more energy. Thus, they travel or leave with the least possible amount of energy to minimize the duration time of migration (Hedenström & Alerstam, 1997). Consequently, the body condition as well as the energy reserves influence the stopover duration and studies show that this correlates also with the intensity of “Zugunruhe” (Lupi, et al., 2016; Fusani, et al., 2009).

To find out more about these behavioural changes during migration, I studied the behaviour of captive whitethroats (*Sylvia communis*) who are normally active during the day but throughout migration they are also active at night until sunrise (Bairlein, 1991). These birds are nocturnal migrants and should show intense nocturnal

restlessness (*Zugunruhe*) (Fusani, et al., 2009). This means that they must have found a way to rest or sleep as effective as possible in a minimum amount of time (Rattenborg, et al., 2004).

1.2. **Characterization of the resting behaviour**

Songbirds change their behaviour during migration and migrate at night instead of resting/sleeping (Rattenborg, et al., 2004). It is difficult to study sleep during migration of free living birds because electrophysiological (electroencephalography EEG) recordings are necessary to be sure that birds sleep (Fuchs, et al., 2006). However, studies from Rattenborg (2006) show that sleep can be defined both behaviourally and electro-physiologically and that there is a relationship between a closed eyelid and sleep (Wellmann & Downs, 2009).

As Kavanau (1998) writes, resting happens before sleep and because I didn't perform electrophysiological tests I just studied the resting behaviour. That is a motionless state with overall or partially closed eyes and may serve to compensate sleep loss during nocturnal migration (Wellmann & Downs, 2009). Another hypothesis is that birds are digesting food during resting and herewith reduce weight for take-off (Agatsuma & Ramenofsky, 2006). The two main rest positions are: rest front (the head of the bird is retracted towards the body while facing forward) and rest back (the head is pointing backwards, resting on the bird's back and the bill is under the scapula feathers) (Wellmann & Downs, 2009; Fuchs, et al., 2006) (Fig. 2).

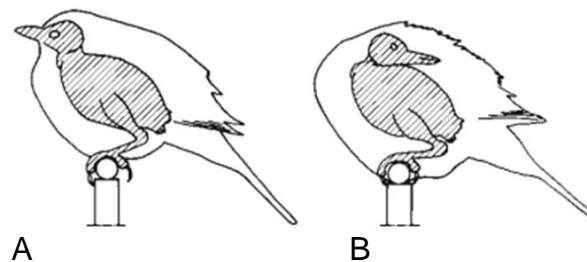


Figure 2: The head postures of the bird during the resting behaviour from Westheide & Rieger – Spezielle Zoologie 2. Schematic drawing of **(A) the rest front posture** where the head of the bird is retracted towards the body while facing forward and **(B) the rest back posture** where the head is pointing backwards, resting on the bird's back and the bill is under the scapula feathers.

There are many hypotheses for the rest function. The main role is to save energy by lowering the body temperature and by this to reduce the waste of energy. Possible is also the physiological restoring function of some body tissues which are

than required during the active phase. Hence, it can also be that a state of immobilization increases the safety against predators because then the resting birds are not easy prey (Amlaner & Ball, 1983; Wellmann & Downs, 2009).

As mentioned before, birds can regulate their body temperature in order to save energy resources, especially when it is cold and when there is lack of food. They change their position of the contour feathers to increase or decrease the body surface and thereby prevent heat loss. They are also often standing on one leg to warm up the other one or put their beak under the scapula feathers (Bergmann, 2010). Also the studies from Wojciechowski and Pinshow (2009) show that birds are decreasing their body temperature while resting at a migratory stopover to rebuild their energy stores and that many birds decrease their rest phase body temperature below normothermic values when there are unfavourable environmental conditions to buffer body mass and fat loss (Wojciechowski & Pinshow, 2009).

Thus, resting also depends on the condition of the bird and is adapted to the time of other activities such as feeding. Accordingly, birds with enough fat reserves rest during the day while birds with little fat stores search for food during day and rest at night (Yong & Moore, 1993) (Fig. 1) because it may be a benefit to lower the energy expenditure at night while rebuilding tissues and energy reserves and start migrating the next morning (Wojciechowski & Pinshow, 2009). However, it could also be that birds gather information relevant for orientation cues from the setting sun during the rest phase (Agatsuma & Ramenofsky, 2006). Nevertheless, the overall principal advantage of resting is clearly recover from prior activities (Wellmann & Downs, 2009) and from the sleep loss accrued throughout migration (Agatsuma & Ramenofsky, 2006).

The overall objective of my study was to find out the relationship between rest pattern and physiological condition during spring migration in whitethroats (*Sylvia communis*). I expected that birds in bad condition spend more time at night resting back in order to save energy and recover than birds in good condition. Correspondingly, I anticipated that birds in bad condition also show more “active” behaviour during the day in order to search for food than birds in good condition. I also expected that birds in good condition have less oxidative damage than birds in bad condition.

2. MATERIAL AND METHODS

2.1. Study species

The whitethroat (*Sylvia communis*) is a sexually dimorphic long distant migrant and spends the winter in West Africa from the South of the Sahara up to the rainforest in east Africa. They show an increase in fat depots during migration. Their breeding zone reaches from Norway up to the Mediterranean area. Normally, the whitethroat is active during the day but during the migration season they are migrating at night. The migration from the winter habitats to the breeding sites starts at the end of March and has its peak in April until May (Bairlein, 1991).

2.2. Field work

The study was carried out at Ponza (Italy), a small island in the Tyrrhenian Sea (40.855°N, 12.858°E) on the west coast of Italy. It is located along one of the main Mediterranean migratory routes and a ringing station, where traditional bird ringing and monitoring activities are carried out. It has been active on the island since 2002. We collected data of two years from April to May 2015 and from March to May 2016. On different places and directions, we installed mist nets near the ringing station. The birds were trapped two hours after sunrise until 13:00 h and were bled within three minutes after nets entry. We took 150 µl blood of the wing vein and centrifuged the blood sample to collect the plasma. The red part and the plasma part of the blood were put into the liquid nitrogen (-20°C) within 13 minutes from capture and will be used for future analyses.

After the bleeding, the physiological and morphometric measures were taken at the ringing station. These measurements are the size of the pectoral muscles (scale 0-3), the subcutaneous fat (scale 0-8), the length of the 3rd primary cover, age, sex and the weight (to the nearest 0,10 g) following standardized European methods (Bairlein, 1994).

The birds were then put into a cage which was equipped with two to three cameras and they received water ad libitum and 3 g of mealworms (Fig. 3). These cages then again were put into a soundproof-box which had their own light- and air supply in order to be isolated from outside influences (Fig. 4). The activity of the bird was recorded from 13:00 h until the next morning.

Before the release of the birds, within one hour after sunrise, we took again the physiological and morphometric measures including tarsus length.



Figure 3. Cage from inside with the cameras and the perches.



Figure 4. Cage in the Soundproof-Box to be isolated from the outside environment.

2.3. Data analysis

For the analyses of the recorded videos, I used the program Solomon Coder (beta Version 17.03.22, 2006-2017). Therefore, I displayed the videos in parallel and analysed them from 13:00 h until sunrise. For the determination of the particular behaviour patterns I created an ethogram (Table 1). The analysed parameters were then transformed into an excel sheet (Microsoft excel) and the percentage of the particular activities during the day, night and 24 hours for every behaviour were calculated.

To have an overview of the different behaviour patterns that were analysed during the observed time I measured the mean percentages of all and displayed them in bar charts.

As all my analyses include the body condition of a bird I used the scaled mass index ($\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$) (Peig & Green, 2010) for the condition measurement. This is a body mass scaled on the size of the bird (body weight and 3rd primary cover in comparison to population mean) and is an indicator of an animal's health, quality and vigor.

In order to test the effects of the body condition on the rest position, the activity and the food intake, I performed a non-parametric Spearman correlation test for all three. Further, I visualised the relationship of these parameters separately in scatterplots. All statistical analyses were performed with RStudio v. 1.0.136 (RStudio, Inc., 2009-2016) using a significance level of $p < 0.05$.

Table 1. Ethogram to determine the particular behaviours of the recorded birds.

STATES	
ACTIVE: Bird has open eyes.	Stationary: turns the head around, moves its body or body parts (i.e. stretching legs, cleaning beak), turns around on the perch or floor; the bird does not change its physical position in the cage (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: stretching, cleaning beak on the wood, pulling with the beak at the ring.
	Moving: Bird is awake, and 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: it is impossible to confirm if the eyes are open or not, but 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 rolled to one side or leans forward, occasionally dropping to the bird’s feet.	Resting-front: The head is retracted towards the body while facing forward. Also put if at least one eye is visibly closed.
	Resting-back: The head is pointing backward and resting at the bird’s back. Also put if at least one eye is visibly closed.
Out of sight: Bird is outside of the surveilled area (sitting on top of upper Camera).	
No Analysis: Behaviour and state of bird is not recorded.	
EVENTS	
Wingflap: the bird flaps its wings but the legs don’t leave the perch or floor.	
Eat: the bird swallows down a mealworm.	
Drink: the bird puts the beak into the water and then ups the head.	
Sun/Light: Marker for Daylight – to be put only once in each video, either 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 nighttime/darkness – to be put only once in each video, either in the instant when lights are turned off at the evening, or at the beginning of the video (if it starts during dark hours).	

3. RESULTS

In total 54 whitethroats in two sequent years were caught, 28 in 2015 and 26 in 2016. The ratio of the sexes in both years was balanced.

The bar chart displays an overview of the single particular behaviour patterns that were gathered (moving, stationary, rest front, rest back) during the light, dark and total time of observation. The whitethroats show more active behaviour during light hours than during the dark. Nevertheless, the rest back behaviour is the priority during dark hours while during the day captive birds rest almost with the head retracted towards the body while facing forward (rest front). In general, the rest front pattern stays the same during light and dark hours and the active behaviour during the total time in captivity is 50 % (Fig. 5).

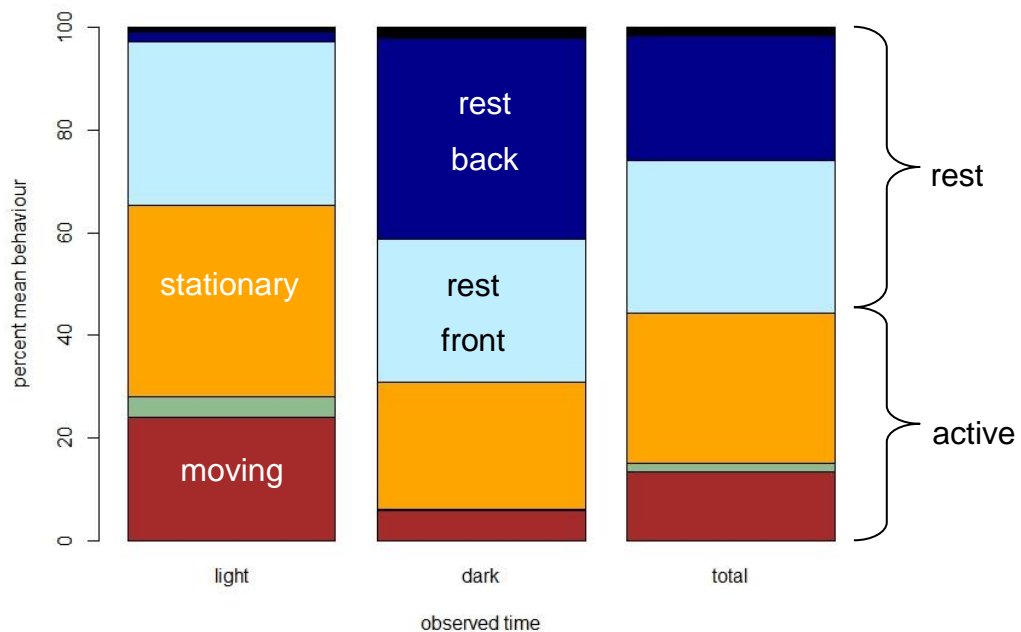


Figure 5: Bar charts of the percent mean behaviour patterns during the whole observed time separated in light hours, dark hours and total time. The rest behaviour is divided in rest-back and rest front. The active pattern contains the behaviour stationary, preening and moving.

3.1. Relationship between condition and active behaviour

To see if birds in bad condition show more active behaviour during the day I analysed the data with the spearman correlation test. This analysis shows that there is no significant correlation between the condition of the birds and the activity during light hours ($n = 54$, $\rho = -0.010$, $p = 0.940$). Therefore, birds with bad or good condition show similar levels of activity during daylight (Fig. 6).

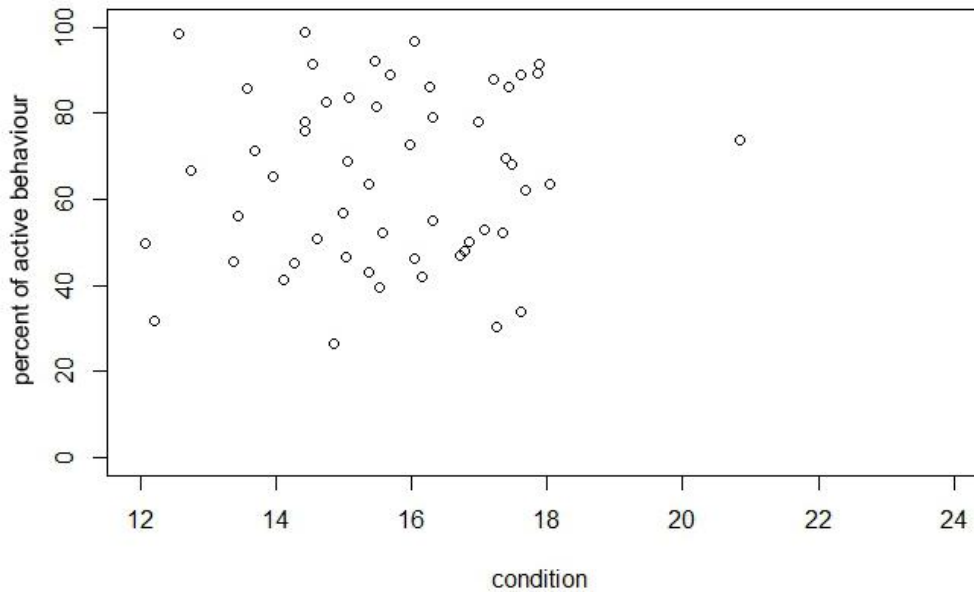


Figure 6: *Scatterplot* of the percentage of the behaviour active during light hours plotted against the condition of the birds using the scaled mass index. The behaviour active was not significantly correlated with the condition.

3.2. Relationship between condition and food-intake

I then went on to test whether birds in good condition eat less than birds in bad condition. The spearman correlation test displayed no significance between the condition of the birds and the food intake in gram ($n = 54$, $\rho = 0.063$, $p = 0.649$) and therefore birds in bad as well as in good condition eat many or all mealworms (Fig. 7).

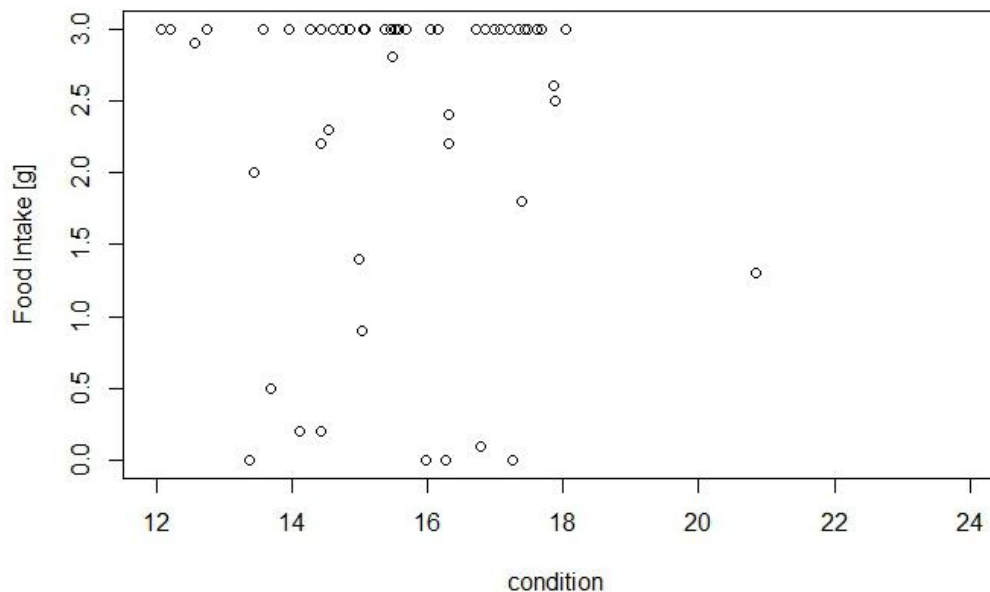


Figure 7: *Scatterplot* of the food intake in gram plotted against the condition of the birds using the scaled mass index. There is no significant correlation between the food intake of the birds and the condition.

3.3. Relationship between condition and rest position

To understand if birds save more energy while resting with the head pointed backwards I used also the spearman correlation test. It displays a significance between the condition of the birds and the resting position ($n = 54$, $\rho = -0.42$, $p = 0.002$). Birds in bad condition are more likely to rest with the head pointed backwards and resting at the bird's back than birds in good condition (Fig. 8).

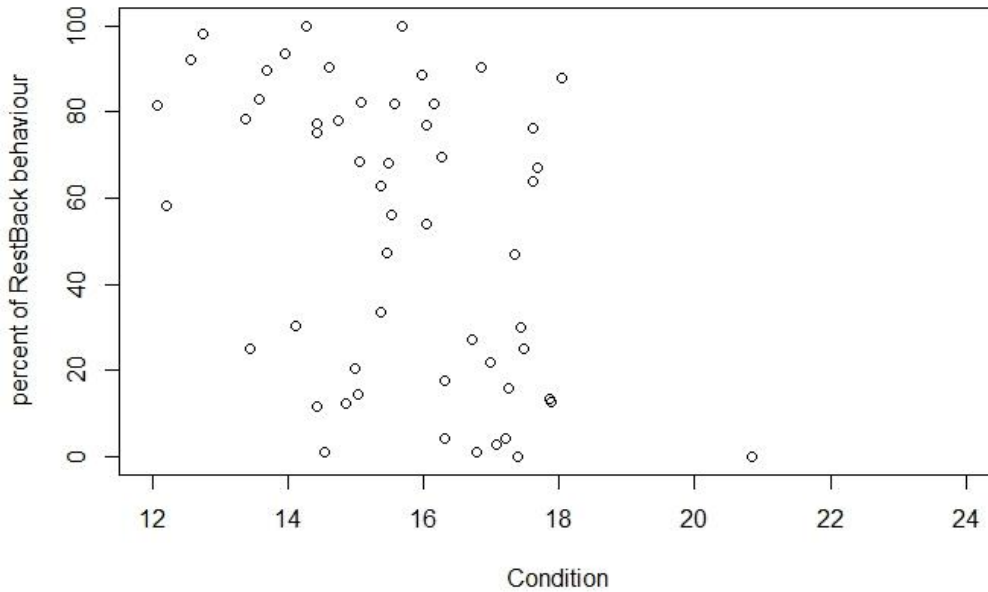


Figure 8: Scatterplot of the percentage of the behaviour rest back at night against the condition of the birds using the scaled mass index. The behaviour rest back was significantly correlated with the condition.

4. DISCUSSION

The aim of my study was to find out if there is a relationship between the rest pattern and the physiological condition during spring migration in *Sylvia communis*. Particularly, I was interested if there is a change in the rest position depending on the condition of the bird. Besides, I was also interested if there is a change in the active behaviour and in the food intake depending on the condition.

4.1. *Active behaviour and food intake*

My results show that whitethroats (*Sylvia communis*) in captivity rest a large percentage of the time and that they are in general more active during light hours than during the dark. The statistical analyses demonstrate that the diurnal activity is not significantly influenced by the condition of the birds as well as the food intake. Therefore, I couldn't confirm my hypothesis that birds in bad condition show more active behaviour during the day in order to search for food in comparison to birds in good condition. This is different from the study of Yong and Moore (1993) who found a higher diurnal activity among lean birds to feed and regain their fat depots at a stopover site. This leads to assertion that the migratory activity is also related to the energy stores and a decrease in daytime activity among lean birds depends also on other activities for example to avoid predation or to rest (Yong & Moore, 1993), which is of utmost importance before a repeated attempt to take off (Agatsuma & Ramenofsky, 2006). Nevertheless, also the food availability at a stopover site is a strong factor for activity and therefore influences the birds during migration (Fusani, et al., 2009). Thus, the experiments in laboratory differ from the natural environment because the birds in captivity have unlimited availability of food. This could decrease overall the need for general activity during the day (Fuchs, et al., 2006).

Studies also show that the duration of stopovers is influenced by surrounding stimuli as well as the weather conditions during migration (Fusani, et al., 2009). Subsequently, during unfavourable weather conditions the birds stay longer at a stopover site and wait until they continue migration (Zduniak & Yosef, 2012). Consequently, environmental stimuli, like the meteorological conditions, are important and may influence activity (Amlaner & Ball, 1983), which may be the reason why I haven't found any significant results. Due to the fact that in my study

the birds were isolated from external parameters by a soundproof box and therefore were not affected by factors such as wind or cloud cover.

An interesting point is that my results show that birds in good as well as in bad conditions eat many or all mealworms. I suggest that during migration birds have different strategies to refuel their fat depots. Therefore, the activity during the day to find food does not only depend on the condition or the external factors but rather on the food availability in order to refill their energy reserves in relation to migratory flights (Fusani, et al., 2009). The fat depots or energy status plays an important role in determining the duration of a stopover and so does the nighttime (migratory) and daytime (foraging) activity (Yong & Moore, 1993). I think that the migratory activity is influenced by the energy stores, the food availability as well as by the physiological condition of the bird. Also, Hedenström & Ålerstam (1997) showed in their study that the variation in food abundance at the stopover site is related to the departure fuel load. Also unlike birds in the field, birds in captivity had free access to food and therefore do not have to search for it to obtain energy (Agatsuma & Ramenofsky, 2006).

To sum this up the observed differences in daytime activity and feeding behaviour depending on the condition and the external parameters are consistent with the evidence that, in contrast to the field, just the effect of food availability and lacking impact from outside changes the behaviour in captive birds and therefore they just intersperse resting with feeding what leads to less activity during the day (Agatsuma & Ramenofsky, 2006; Yong & Moore, 1993). Nevertheless, to prove this, further investigations are necessary.

4.2. *Resting behaviour*

With the video analyses, I figured out that the resting position during the night is influenced by the condition. This confirms my hypothesis that birds in bad condition rest more with the head pointed backwards and resting on the bird's back than birds in good condition. Birds with bad condition reduce their energy expenditure at night during stopover while resting back and possibly also reduce their body temperature to rebuild energy stores (Wojciechowski & Pinshow, 2009) as well as reduce heat loss, as it decreases volume/surface ratio (Wellmann & Downs, 2009). Thus, it shows that the resting position is more important for birds in bad condition in context

with the energetically demand of migration and to control recovery (Liechti, et al., 2013).

The resting behaviour differs also between birds in captivity and the natural environment. Under natural conditions birds are stimulated by surrounding noises, which may trigger actions (Amlaner & Ball, 1983; Steinmeyer, et al., 2010). Under unnatural laboratory conditions they are unaware of external sounds and that might change the rest behaviour of animals. In my study, the birds were separated from each other and thus they were not able to hear their conspecifics or outside noise. Whereas in other studies, the birds were just trapped in individual cloth cages resulting in the birds being just visually isolated from one another (Fusani, et al., 2009; Lupi, et al., 2016). Consequently, it may be that receiving no environmental sounds or noise, changes the behaviour. As a result, that no sound from outside and therefore no predation risk as well as a safe holding environment leads to rest more. Hence, the rest duration and the quality is also influenced by external stimuli and therefore, birds conserve energy, digest food or compensate the sleep loss while in captivity (Steinmeyer, et al., 2010). However, the rest demand could also depend on the daytime activity and furthermore in order to reduce the predator risk they increase their resting phase during the day (Amlaner & Ball, 1983). This also leads to the assertion that possibly also the individual housing as well as the laboratory conditions are influencing the resting behaviour.

Another impact, on decreasing or increasing the rest-phase of the birds, are the environmental conditions like sunset and the sunrise (Steinmeyer, et al., 2010) as well as the weather conditions during migration. As in nature the darkness comes gradually, in our settings the lights were also switched on and off just after and before sunset and sunrise. Hence, there was always some form of light in the cage like in natural conditions, where complete darkness is uncommon. As the studies from Ramenofsky and collaborators (Ramenofsky, et al., 2008) show that slight changes in nocturnal illumination changes the behaviour of captive White-crowned Sparrows. Therefore, a variation in light intensity can change the decision of migrants to rest or depart from the stopover site. Consequently, the light intensity may provide information about the weather conditions and less illumination leads to less nocturnal activity. Taken together, the amount of moon- and starlight could affect migratory activity and so the birds in my study may rest more because there was no light from the moon, stars, or reflection of clouds (Ramenofsky, et al., 2008).

To sum up, birds are well adapted in response to the energetic demands during migration and the video recording study revealed that the rest back behaviour depends on the condition of the birds and might be therefore more efficient to save energy. With the video observation, I was able to show a greater diversity of behaviours than with infrared activity monitoring systems although the video analyses require much more time (Wojciechowski & Pinshow, 2009).

5. CONCLUSION

In conclusion, this study shows that the resting position depends on the condition of the bird and therefore birds save energy by resting with the head pointed backwards but further studies are required to understand the causes of the different resting positions. While studies show that the rest position also depends on the temperature, it would be interesting to study the rest position in correlation with the temperature in the soundproof box to comprehend if the rest back position depends, beside the reduction of energy costs, also on the temperature as well as on the outside stimuli.

As I haven't found any significant results between the condition and the activity during daylight as well as in the food intake it is important to increase the sample size (n). It would be interesting if there is a significance in these studies if I had more birds in good condition.

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ABSTRACT

Many birds are migrating twice a year from their breeding sites to their wintering sites because of changes in their habitats. This requires a lot of energy, can produce oxidative damage, and results in alteration of rest/sleep cycle when migration takes place at night. Migration is influenced by external factors and modulated by endogenous cycles. Previous studies showed that body condition influences the duration of the bird stay at a stopover site as well as the resting behaviour. I used the whitethroat (*Sylvia communis*) as study species to find out if there are differences in the activity, food intake and rest behaviour of birds with different physiological conditions during spring migration.

The whitethroats refill their energy reserves while resting at stop over sites to complete their migration. I used the mist-netting method to catch the birds and took blood samples. Furthermore, morphometric measurements were taken at the ringing station. Therefore, field work was conducted from April to May 2015 and March to May 2016 at Ponza (Italy) during which birds were trapped in cages to film their behaviour.

My results show no significant relationship between the condition and the activity during light hours as well as in the food intake. Nevertheless, I found different strategies in the rest position relating to the condition of the bird.

Keywords: birds, migration, rest behaviour, physiological condition, stopover, activity, food intake, Ponza

ZUSAMMENFASSUNG

Zweimal im Jahr ziehen viele Vögel aufgrund von Habitatsveränderungen von ihrem Brutgebiet in ihre Überwinterungsgebiete. Dies ist sehr energieaufwändig, produziert oxidativen Schaden und minimiert die Zeit um zu rasten/schlafen. Der Zug wird von den Umweltfaktoren wie auch von endogenen Parametern beeinflusst. Weiters zeigen Studien, dass auch der körperliche Zustand die Dauer des Aufenthaltes sowie auch das Rastverhalten in einem Rastgebiet beeinflusst. Mit meinem Untersuchungsobjekt, der Dorngrasmücke (*Sylvia communis*), wollte ich herausfinden, ob es einen Unterschied in der Aktivität, der Nahrungsaufnahme sowie auch dem Rastverhalten in Zusammenhang mit dem körperlichen Zustand während des Frühjahrszuges gibt.

Die Dorngrasmücke füllt ihre Energiereserven für den Zug während des Zwischenstopps auf. Daher wurden die Vögel mit Japannetzen auf ihrem Rastgebiet gefangen. Weiters wurden Blutproben entnommen und die morphometrischen Maße wurden auf der Beringungsstation gemessen. Die Feldarbeit fand von April bis Mai 2015 und von März bis Mai 2016 auf Ponza (Italien) statt. Um die Verhaltensmuster der Vögel zu filmen, wurden sie in Käfigen, die mit Kameras ausgestattet waren, gehalten.

Ich konnte in meiner Studie keinen Zusammenhang zwischen dem körperlichen Zustand, der Tagaktivität sowie der Nahrungsaufnahme feststellen. Jedoch konnte ich durch die Videoanalysen feststellen, dass Vögel in schlechterem Zustand signifikant häufiger mit dem Kopf nach hinten rasten.

Schlüsselwörter: Migration, Rastverhalten, physiologischer Zustand, Zwischenstopp, Aktivität, Nahrungsaufnahme, Ponza