ORIGINAL ARTICLE

Decision-making in migratory birds at stopover: an interplay of energy stores and feeding conditions

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Abstract

Migrating birds make stopovers to rest and fuel to prepare for their next flight. The decision when to continue migration significantly affects total duration of migration and thus arrival timing at the migratory destination. Departure decisions of migrants are therefore important to understand variation in arrival timing. Since the amount of energy can limit flight duration, feeding conditions and energy stores have a significant effect on the departure decisions. Unexpectedly though, various fasting-refuelling experiments controlling for these two parameters and using migratory restlessness as a proxy for departure probability did not find consistent patterns within and across different songbird species of departure decisions. Here we performed a fasting-refuelling experiment on four actively migrating songbird species during autumn, to assess the significance and consistency of the feeding conditions and energy stores on the bird's departure decision. We found no differences in the departure probability between low and favourable feeding conditions in all species. During the low food phase, however, birds with higher energy stores were more likely to depart than leaner birds. When fasted individuals encountered improved feeding conditions, they significantly increased their energy stores and showed a significant drop in migratory restlessness. This is tantamount to the decision of staying at stopover. The consistency of the patterns seems to be generalizable across species. Additionally, the results highlight the importance of the interplay of feeding conditions, changes in these and the bird's current energy stores for the stopover decision-making process.

Significance statement

Many migratory songbirds travelling thousands of kilometres do so by making several single nocturnal flights interrupted by resting periods on the ground. To decide when to continue migration, birds seem to follow general departure rules. Fat birds continue migration when they do not find food during their rest, while lean birds stay until the feeding conditions have improved. In this study, we show for the first time a generalizable consistent pattern that feeding conditions, changes in food availability and the current energy stores jointly influence the departure decisions of migratory songbirds at stopovers. This is in contrast to former studies showing inconsistent patterns on the reaction of a low food phase regarding the departure probability. Our experiment, therefore, advances our knowledge about the decision-making process of bird migrants and demonstrates the importance of favourable feeding conditions for migratory birds resting at a stopover site.

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Introduction

Songbird migrants usually alternate their migratory flights with stopovers, during which they rest and fuel for the upcoming flight (Delingat et al. 2006; Åkesson and Hedenström 2007; Newton 2008). Since energy accumulation during stopover is far slower than energy expenditure during flight (Alerstam and Lindström 1990; Hedenström and Alerstam 1997), considerably more time and energy are spent on the ground than in the air (Wikelski et al. 2003; Schmaljohann et al. 2012). Hence, variation in the rate of energy accumulation affects variation in stopover duration (Alerstam and

Lindström 1990), excluding the 1-day stopovers between two migratory flights. Variation in stopover duration, thus, affects migration speed (Nilsson et al. 2013; Schmaljohann and Both 2017; Schmaljohann 2018).

Since the amount of energy limits the duration of a migratory flight, the bird's actual energy stores should have a significant effect on the decision when to resume migration from stopover, reviewed in Schmaljohann and Eikenaar (2017). The current rate of energy accumulation is also thought to be an important departure cue (Alerstam and Lindström 1990) because this rate determines the stopover duration until sufficient energy is stored for the next migratory flight (e.g., Bayly 2006, 2007). Thus, the bird's migration speed is determined to a high degree by the rate of energy accumulation with high rates reflecting high migration speeds and low rates inducing the bird to set off in search of a more favourable stopover site (Lindström and Alerstam 1992; Hedenström and Alerstam 1997). Supportive evidence for this pattern is scarce due to the difficulties of obtaining energy accumulation rates across a bird's entire stopover period. It was shown for wild northern wheatears (Oenanthe oenanthe) that individuals experiencing a loss of energy stores or a low rate of energy accumulation had a higher departure probability than individuals experiencing high energy accumulation rates (Schmaljohann and Eikenaar 2017); see also Schaub et al. (2008) estimating simplified rates of energy accumulation based on capture-recapture data and finding similar patterns.

To get a better understanding of how the rate of energy accumulation affects departure probability, fasting-refuelling experiments were carried out with caged songbirds under controlled conditions (e.g., Berthold 1976; Biebach 1985; Gwinner et al. 1985, 1988; Fusani and Gwinner 2003; Bauchinger et al. 2008; Ramenofsky et al. 2008; Fusani et al. 2011; Eikenaar and Bairlein 2014). The fasting period is supposed to simulate the situation of migratory flight and/or a low food phase. These studies took advantage of the fact that caged migratory songbirds show nocturnal migratory restlessness at times of the year when they would normally migrate in the wild (Gwinner 1968, 1996; Bairlein and Gwinner 1994) and that the amount of restlessness is predictive of the bird's actual departure probability under free-flying conditions (Eikenaar et al. 2014a). Quantifying migratory restlessness, therefore, allows a relative comparison of departure probability between individuals (Eikenaar et al. 2014a). Whether birds with high amounts of restlessness would have resumed migration to further approach the migratory destination or in order to leave the stopover in search for a more favourable site (cf. Taylor et al. 2011) remains unknown.

In fasting-refuelling experiments, birds usually enter the fasting period with a large surplus of energy stores. During this low food period, birds usually show higher amounts of nocturnal migratory restlessness, i.e., an increased propensity to resume migration, than before and/or after the fasting period (refuelling). This pattern was found in spotted flycatchers (Muscicapa striata) (Biebach 1985), northern wheatears (Eikenaar and Bairlein 2014), and garden warblers (Sylvia borin) (Gwinner et al. 1985, 1988). Intriguingly, Fusani and Gwinner (2003) and Fusani et al. (2011) demonstrated the opposite effect in the latter species: birds in the fasting period showed lower amounts of nocturnal migratory restlessness, while Berthold (1976) and Bauchinger et al. (2008) found no pattern at all in this species. Likewise, Ramenofsky et al. (2008) found no effect of fasting on the amount of migratory restlessness in white-crowned sparrows (Zonotrichia leucophrys). For northern wheatears (Eikenaar and Schläfke 2013) and four North America thrushes (Hylocichla mustelina, Catharus fuscescens, C. ustulatus, C. minimus) (Yong and Moore 1993) not experiencing a fasting period, it was shown that energy stores at capture were positively correlated with the amount of migratory restlessness and negatively correlated with the rate of energy accumulation.

Despite some inconsistency in how the amount of energy stores and/or the rate of energy accumulation affected departure probability, it is generally accepted that they jointly regulate the corresponding decision-making process during stopover (Jenni and Schaub 2003; Hedenström 2008; Fusani et al. 2009; Alerstam 2011; Lupi et al. 2017; Schmaljohann and Eikenaar 2017). After having arrived at a stopover site, individuals may have depleted energy stores and initially experience a low rate of energy accumulation due to search and settling time/costs (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). If feeding conditions are good, individuals will experience high rates of energy accumulation. This will decrease their departure probability because they are assumed to exploit the food resources (Alerstam and Lindström 1990; Hedenström and Alerstam 1997). When sufficient energy for the upcoming migratory flight is stored, the rate of additional energy accumulation is reduced (Fransson 1998; Delingat et al. 2006). Such individuals will have a high departure probability, especially if environmental conditions in terms of wind, cloudiness, and precipitation are favourable for departure (Deppe et al. 2015). If individuals experience a low food phase, they will have a high departure probability (Schmaljohann and Eikenaar 2017). These rules become more complex because high energy stores may cause departure irrespectively of the experienced rate of energy accumulation, while low energy stores may prevent individuals from resuming migration. The current state of knowledge, however, is a patchwork of many mostly single-species studies across different songbird taxa, seasons, and areas/continents, performed on both wild and captive birds and following different protocols to access the effect of food availability on the probability of departure. To properly assess and generalize the departure rules described above, we need an experimental study on multiple species performed at one

location during a single season with a standard protocol to overcome site-specific (Fransson et al. 2001), potential seasonal-specific and protocol-specific (Berthold 1976; Biebach 1985; Gwinner et al. 1985, 1988; Fusani and Gwinner 2003; Bauchinger et al. 2008; Ramenofsky et al. 2008; Fusani et al. 2011; Eikenaar and Bairlein 2014) differences in the reaction to the food availability.

In this study, we caught and temporarily caged migrating individuals of four songbird species, namely, European robins (*Erithacus rubecula*; robin hereafter), northern wheatears (wheatear hereafter)*,* common redstarts (*Phoenicurus phoenicurus*; redstart hereafter), and garden warblers, at a stopover site during one autumn season. Birds were caged for five full days and six full nights (Fig. 1). During the day of capture and the first full day of caging, all birds had ad libitum access to food. Afterwards, one group experienced a low food phase (5 g of food) for 2 days (experimental group), while the other group still had ad libitum food supply (control group). During the last 2 days, all birds had ad libitum access to food (Fig. 1). We used quantitative magnetic resonance analysis to determine the bird's energy stores (Guglielmo et al. 2011; Kelsey and Bairlein 2019). During each night, nocturnal migratory restlessness was recorded (Eikenaar et al. 2014a).

With this experimental set-up, we assessed three main predictions (Table 1). If food availability affects the departure probability of songbirds, in which low food availability increases the departure probability and high food availability lowers the departure probability, we would predict the following: First, wild, temporarily caged songbirds experiencing an experimentally induced low food phase show more migratory restlessness, i.e., a higher propensity to resume migration, than

control individuals having continuous ad libitum access to food. Second, we predicted that individuals experiencing a change from low to ad libitum feeding conditions reduce migration restlessness to lower levels than control birds. Finally, we expected that the individual reaction, i.e., the amount of migratory restlessness, to the feeding conditions depends on the individual energy stores with large stores generally inducing high amounts of restlessness in both groups. We therefore predicted that during the low food phase, individuals with extremely low energy stores will show little to no migratory restlessness, while individuals with larger energy stores will show high amounts of restlessness.

Methods

Study site, species, and trapping procedure

The study was conducted on Helgoland (54°11'N, 07°55'E), a small island ca. 50 km off the German North Sea coastline. All study species are nocturnal migrants (Dorka 1966). They pass Helgoland in large numbers but rarely breed there (Dierschke et al. 2011), so all individuals studied can be safely assumed to be migratory. The robin is a medium-distance migrant which mainly winters in the Mediterranean, whereas the others are long-distance migrants wintering south of the Sahara. Birds were trapped using spring traps, funnel traps, and/or mist nets between 7 a.m. and 6 p.m. (local time) between mid-August and end of October 2017, the main migration period of the species (Dierschke et al. 2011) (see supplemental materials, Fig. S1). Wing length (maximum chord following Svensson (1992)) was measured to the nearest 0.5 mm and body mass to
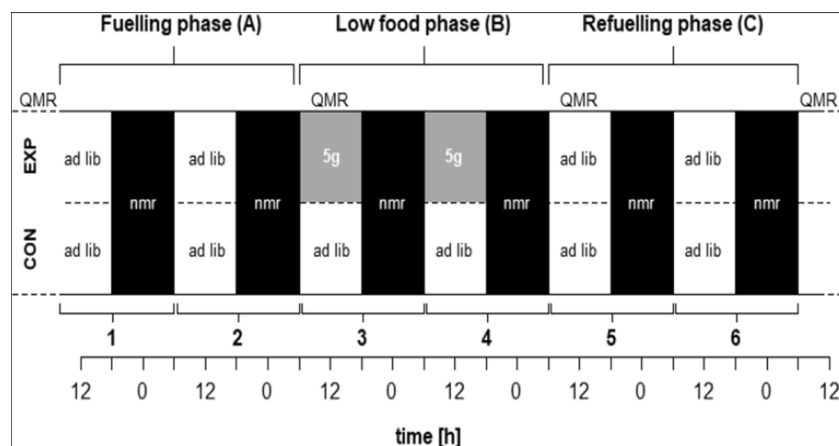

Fig. 1 Experimental design. Black bars indicate the nights when nocturnal migratory restlessness (nmr) was measured. White bars are the day time with ad libitum food supply of mealworms. Grey bars indicate days with restricted food supply (5 g). On day one, three, five, and seven QMR measurements were taken in the morning. Upon capture, birds were divided into experimental group (EXP) and control group (CON), respectively. Both groups received ad libitum food in the first 2 days, the fuelling phase. After the second night in captivity, the experimental group received a reduced food supply of 5 g for two consecutive days, and the control group continued to receive food ad libitum, respectively. After the fourth night, all groups received again ad libitum food. Birds were released in the morning of day seven. Migratory restlessness was measured in each night, but data of the first night were not considered because birds being caught at different times of the day had differently long access to the food on day one

Table 1 Predictions of how low food and refuelling conditions affect the amount of nocturnal migratory restlessness (left) and the reaction of our study species (right)

Predictions		Reaction
One	Experimental birds show more migratory restlessness in the nights following the low food conditions than control birds with ad libitum access to food throughout	No
two	After the low food phase, experimental birds show less migratory restlessness in the nights following ad libitum feeding conditions than control birds	Yes (European robin, Northern wheatear, Common redstart) No (Garden warbler)
three	Amount of migratory restlessness depends on the actual energy stores with high stores generally inducing high amounts of restlessness	Yes (European robin, Northern wheatear, Common redstart) No (Garden warbler)

the nearest 0.1 g. To minimize observer bias, blinded methods were used when all behavioural data were recorded and/or analysed. Measurements of nocturnal migratory restlessness and Echo MRI were recorded by electronic devices, and corresponding data were analysed by a standard procedure; see below. All procedures were approved by the Ministry of Energy, Agriculture, the Environment, Nature and Digitalization, Schleswig-Holstein, Germany.

Experimental design

After capture, birds were placed into individual bird cages (40 × 40 × 30 cm) with a maximum of 20 cages in a single room (24 m²). Throughout the study, the temperature was held constant at approx. 20 °C, and lights were switched on at local sunrise and switched off at local sunset. During the night, dim white light conditions of about 2 lx (20 lamps, 8.0 V, 50 mA; Barthelme, #00640850, Nuremberg, Germany) were provided throughout (cf. Zapka et al. 2009). All birds always had ad libitum access to water. Food (mealworms, *Tenebrio molitor*) was provided 1.5 h after lights were switched on, and food trays were removed when lights were switched off. Since it took at maximum 1.5 h to perform quantitative magnetic resonance (QMR) measurements of 20 birds (see below), we standardly put the food into the cages at this time to ensure that on a given day, all birds had the same time to feed. After caging, birds were randomly assigned to either the experimental group with a temporarily low food phase on day three and day four (Fig. 1) or the control group with ad libitum feeding conditions throughout (Fig. 1). At day one and day two, each bird received a food tray with ad libitum food (30 g of mealworms) (Fig. 1), which was never totally consumed by any bird. We termed the time period including day one and day two the "fuelling phase" (Fig. 1). On day three and four,

individuals of the experimental group received 5 g of food each day instead of providing no food at all because at this stage of the experiment, we were not able to predict whether the total lack of food would harm the individuals (cf. Corman et al. 2014). All individuals always completely consumed these 5 g of mealworms. Birds of the control group fed on average more than 12 to 18 g mealworms per day (robin, mean = 12.0 g, SD = 2.5 g, n = 525; wheatear, mean = 18.6 g, SD = 4.5 g, n = 174; redstart, mean = 14.3 g, SD = 3.1, n = 279; garden warbler, mean = 14.5 g, SD = 4.6 g, n = 286; Fig. S2). After the low food phase, the experimental birds again received ad libitum food for the final 2 days (hereafter "refuelling phase"; Fig. 1). Birds were released in the morning of day seven.

Recording of nocturnal migratory restlessness

During each night of housing, nocturnal migratory restlessness was automatically recorded using motion-sensitive microphones (Piezo-Scheibe 27 mm, Conrad Electronics SE, Hirschau, Germany) attached in the centre of the right cage wall. Each time a bird moved, an impulse was generated and transmitted to a recording device (developed by R. Nagel and T. Ubben, Institute of Avian Research, Wilhelmshaven, Germany). To avoid recording of occasional non-migratory activity, we set a threshold of three impulses per second before considering these as an activity count (Maggini and Bairlein 2010). Activity counts were summed up for 1-min periods over the entire night. We restricted the data to the first 10 h after sunset for all birds, which corresponds to the shortest night during the study. We excluded activity counts from the first 15 min of each night to avoid any potential effect of switching off the light (cf. Müller et al. (2018)). In subsequent

analyses, the number of all activity intervals was used as a proxy for departure probability (Eikenaar et al. 2014a).

Energy stores

Energy stores were estimated as the specific lean body mass (lbm) subtracted from its bird's actual body mass. Each day, all birds were weighed to the nearest 0.1 g at local sunrise and local sunset. In addition to fat, glycogen and protein also serve as energy stores during migratory flights. However, the contribution of energy derived from fat in relation to the total energy expenditure during flight is about 95% (Jenni and Jenni-Eiermann 1998). We therefore treat energy stores simplified as total amount of body fat.

To estimate lean body mass, we used a quantitative magnetic resonance body composition analyser (QMR; EchoMRI Body Composition Analyser E26–262-BH, Zinsser Analytic GmbH, Frankfurt am Main, Germany) (cf. Guglielmo et al. 2011). The QMR-unit was calibrated daily before sunrise with a 94 g canola oil standard. The room temperature was held constant at about 20 °C to secure sample stability given by the QMR-unit (Taicher et al. 2003; Guglielmo et al. 2011). One QMR-measurement can consist of several QMR-scans. Of each QMR-scan, we considered the bird's measured total body fat estimate (g) and wet lean mass estimate (g, lean body mass$_{QMR}$ hereafter). To reduce the time birds spent in the QMR-machine and with that the stress for the birds, two QMR-scans were taken per individual by the three accumulation software settings (cf. Seewagen and Guglielmo 2011). If any value between these two scans differed by more than 0.5 g, we performed a third scan and omitted the "outlier". The whole procedure lasted about 4–5 min, including taking the bird out of the cage and putting it back in. QMR-measurements started immediately after lights were switched on in the bird room. Since no food was provided during the night, birds had empty stomachs so that "no" gut contents could negatively affect the quality of the required QMR-data (Seewagen and Guglielmo 2011). QMR-measurements were carried out at day one, three, five, and seven and thus at the beginning and the end of each of the different phases (Fig. 1). Since lean body mass estimates of the QMR-measurements do not include the weight of skeleton, feathers, horn parts of bill, claws, etc., and since there is considerable between-individual variation in these due to significant individual differences in size, we estimated a corrected lean body mass separately for each species. For this, we run species-specific linear mixed-effect models (LMM) with body mass$_i$ as the bird's total body mass (weighed with a balance), minus total body fat estimate$_i$ (QMR-measurement) as the response variable representing the corrected lean body mass (lbm$_{cor}$), lean body mass$_{QMR}$

(lbm) as the explanatory variable, and bird ID as the random factor (intercept) to account for the non-independence of repeated measures from the same individual:

$$lbm_{cor,i}(body\ mass_i - total\ body\ fat\ estimate_i) \sim lbm_i \quad (1)$$

The species-specific equations to estimate the corrected lean body mass are:

$lbm_{cor.wheatear,i}$
$$= 1.06\ (95\%CrI:1.00/1.11)\ g*lbm_i - 2.80\ (95\%CrI:1.89/3.74)\ g \quad (2)$$

$lbm_{cor.robin,i}$
$$= 0.97\ (95\%CrI:0.91/1.04)\ g*lbm_i - 2.89\ (95\%CrI:2.16/3.63)\ g \quad (3)$$

$lbm_{cor.redstart,i}$
$$= 0.86\ (95\%CrI:0.81/0.92)\ g*lbm_i - 3.50\ (95\%CrI:2.90/4.09)\ g \quad (4)$$

$lbm_{cor.gardenwarbler,i}$
$$= 0.99\ (95\%CrI:0.93/1.05)\ g*lbm_i - 2.44\left(95\%CrI:\frac{1.61}{3.27}\right)g \quad (5)$$

Afterwards, we calculated for each individual the mean of the four lean body mass$_{QMR}$ measurements at day one, three, five, and seven (Fig. 1). We entered the corresponding value in the appropriate species-specific Eqs. (2–5) to calculate the bird's specific corrected lean body mass. By subtracting the bird's six evening body mass measurements (Fig. 1) from its individual corrected lean body mass and dividing the difference by the individual corrected lean body mass (Eq. 6), we obtained six values describing the relative amount of fat the bird had stored on the corresponding evening (energy stores hereafter). If birds had fed shortly before weighing, this could have yielded slightly overestimated energy stores.

$$Evening\ energy\ stores_i = \frac{(body\ mass_i - lbm_{cor,i})}{lbm_{cor,i}} \quad (6)$$

Statistical analyses

The statistical analyses were implemented using R, version 3.4.2 (R Core Team 2017). We excluded the first night (Fig. 1) because birds were caged at different times on day one, so that the potential food intake duration varied between individuals, i.e., 1–11 h. The continuous variables, energy stores and day of year (1 January = 1) were scaled and centred (z-transformed) prior to modelling for each species. We used LMMs and generalized mixed-effects models (GLMMs) run with functions in the R-package "lme4" (Bates et al. 2014).

Variation in energy stores was modelled separately for each species using an LMM and assuming normally distributed errors. The model included the following fixed factors: experimental treatment (categorical; two levels, control group and experimental group), experimental night (ordinal scaled; five levels, 2, 3, 4, 5, 6), day of year (see above), and the two-way interaction of experimental treatment and experimental night. Bird ID was included as a random factor (intercept).

Variation in the amount of migratory restlessness was modelled separately for each species using GLMM and assuming binomially distributed errors. The response variable consisted of a two-column matrix with the number of active 1-min intervals per night ("success") versus the number of inactive 1-min intervals per night ("failure"). The model included the following fixed factors: experimental treatment, experimental night, day of year, and the two-way interaction between experimental treatment and experimental night (for details, see above; predictions one and two, Table 1); bird ID was included as a random factor (intercept). We also considered air pressure as an additional explanatory variable because of its general effect on departure decision in migratory birds (cf. Richardson (1990)). Since we found no effect of air pressure on the amount of migratory restlessness (Model estimations, robin, median 0.26, 95% CrI −0.04/0.55; wheatear, median −0.19, 95% CrI −0.46/0.08; redstart, median −0.02, 95% CrI −0.29/0.26; garden warbler, median 0.07, 95% CrI −0.45/0.59), we excluded air pressure from the model. To assess prediction three (Table 1), we additionally included energy stores as another fixed factor, the two-way interactions (between energy stores and both experimental treatment and experimental night), and the corresponding three-way interaction in another model. In all models, bird ID was included as a random factor (intercept). Model assumptions were visually assessed using residual diagnostics of the DHARMa R-package (Hartig 2017). To correct for overdispersion, we added an observation-level random term as a random factor to all GLMM (Harrison 2014). Visual inspection of standard diagnostic plots did not show deviation from model assumptions in any of the models.

To assess uncertainty of the model estimates and model predictions, we used Bayesian methods to obtain uncertainty estimates of the model parameters (Korner-Nievergelt et al. 2015). We used improper prior distributions, namely, $p(\beta)\sim 1$ for the coefficients and $p(\sigma)\sim 1/\sigma$ for the variance parameters in all models, following Korner-Nievergelt et al. (2015). To obtain posterior distributions of the respective models, we directly simulated 2000 values from the joint posterior distributions of each model's parameters applying the function "sim()" of the R-package "arm" (Gelman and Hill 2007). We used the median of the simulated values from the joint posterior distributions of each model's parameters as the respective model estimates and the 2.5% and 97.5% quantiles as limits for the 95% credible intervals (CrI), following Korner-

Nievergelt et al. (2015). We declare an effect to be significant if the corresponding 95% CrI does not include zero or if the 95% CrIs of the comparing groups do not overlap.

Results

Variation in energy stores

Energy stores on day two did not differ between experimental and control birds in wheatears, whereas energy stores were significantly higher in the former than in the latter group in robins, redstarts, and garden warblers (Table 2, Figs. 2, 4, S3). During the low food phase, experimental birds had significantly lower energy stores than during the initial fuelling phase and in comparison to control birds (Table 2, Fig. 2, S3). Wheatears and garden warblers of the control group significantly increased their energy stores from day two to day six (LMM with independent variable "day" [only day two and day six], cf. Figure 2; wheatears, median 0.12, 95% CrI 0.07/0.16; garden warbler, median 0.15, 95% CrI 0.11/0.20), but not robins and redstarts (robin, median 0.03, 95% CrI −0.005/0.06; redstart, median 0.02, 95% CrI −0.03/0.08; Fig. 2, S3). During the refuelling phase, experimental birds significantly increased their energy stores in all species except for two redstarts and one garden warbler (Table 2, Fig. 2, S3).

Variation in nocturnal migratory restlessness

Regarding the first prediction (Table 1), we found no differences in the amount of migratory restlessness between the control and the experiment group during the low food phase (Table S1, Fig. 3).

We found supportive evidence for the second prediction in robins, wheatears, and redstarts (Table 1): birds of the experimental group showed significantly less migratory restlessness on day five (start of the refuelling phase) than on day four (the last day of the low food phase), and they were significantly less restless on day five than the controls (Table 3, Fig. 3, S4). In the garden warblers, this pattern was not significant.

Regarding the third prediction (Table 1), we found significant positive effects of the corresponding three-way interactions between experimental treatment, energy stores, and experimental night during the low food phase, i.e., day 3 and day 4 (Table 3, Fig. 4). Experimental birds carrying relatively high energy stores showed more migratory restlessness than experimental birds with low stores in low food phase; see day 3 and day 4 in Table 3 and Fig. 4. We did not find an effect of energy stores on the amount of migratory restlessness in control birds over all nights except in wheatears during the last night (Table 3, Fig. 4).

Day of year only had a significant negative effect on the amount of migratory restlessness in robins, indicating that late

Table 2 Results of the linear mixed model of the effect of treatment and the experimental night on evening energy stores

	European robin (n = 35)		Northern wheatear (n = 37)		Common redstart (n = 28)		Garden warbler (n = 26)	
	Median	95% CrI	Median	95% CrI	Median	95% CrI	Median	95% CrI
Intercept	0.05	−0.23/0.34	0.00	−0.29/0.30	0.23	−0.09/0.58	**−0.48**	**−0.86/−0.11**
Exp.nExp.night (3)	0.01	−0.27/0.30	**0.46**	**0.25/0.69**	0.14	−0.17/0.48	**0.39**	**0.01/0.75**
Exp.nExp.night (4)	**0.36**	**0.09/0.63**	**0.81**	**0.58/1.04**	0.11	−0.22/0.45	**0.87**	**0.48/1.23**
Exp.nExp.night (5)	**0.43**	**0.16/0.72**	**0.86**	**0.63/1.08**	0.16	−0.17/0.49	**1.07**	**0.73/1.44**
Exp.nExp.night (6)	**0.38**	**0.10/0.66**	**0.99**	**0.75/1.21**	0.12	−0.21/0.45	**1.57**	**1.21/1.94**
Exp.group (EXP)	**1.07**	**0.65/1.48**	0.41	−0.02/0.81	**0.59**	**0.10/1.06**	**1.17**	**0.68/1.71**
Exp.group (EXP)*Exp.nExp.night (3)	**−2.14**	**−2.57/−1.71**	**−1.98**	**−2.29/−1.64**	**−1.93**	**−2.4/−1.46**	**−1.91**	**−2.39/1.37**
Exp.group (EXP)*Exp.nExp.night (4)	**−3.28**	**−3.70/−2.86**	**−2.85**	**−3.16/−2.53**	**−2.77**	**−3.24/−2.28**	**−3.09**	**−3.59/−2.59**
Exp.group (EXP)*Exp.nExp.night (5)	**−1.54**	**−1.95/−1.10**	**−1.49**	**−1.80/−1.17**	**−1.76**	**−2.24/−1.29**	**−1.57**	**−2.08/−1.06**
Exp.group (EXP)*Exp.nExp.night (6)	**−1.02**	**−1.44/−0.59**	**−0.99**	**−1.32/−0.67**	**−1.37**	**−1.89/−0.91**	**−1.59**	**−2.10/−1.10**

Medians and 95% credible intervals (CrI) are given. 95% CrI not including zero are given in bold. Reference category for Exp. treatment is "Control" and for Exp.night "second night", respectively

individuals showed less migratory restlessness than early ones (Table 3).

Discussion

Our study shows that experimental birds of all species decreased energy stores during the low food phase and subsequently increased it during the refuelling phase (Table 2, Fig. 2, S3). Since the experimental birds did not show more migratory restlessness, i.e., higher departure probability (Eikenaar et al. 2014a), in the nights of the low food phase than control birds (Table 1, Fig. 3), we have to reject our first prediction. Contrary to this, we can confirm our second and third prediction: (2) Relatively low energy stores in combination with a sudden improvement in feeding conditions significantly decreases the bird's departure probability (Table 1). (3) Low feeding conditions in combination with low energy stores significantly reduces departure probability, whereas slightly higher energy stores increase departure probability (prediction three, Table 1, Fig. 4). This energy store-dependent shift in the departure decision suggests a certain threshold, below which staying and above which departing is more favourable. We argue that intrinsic (e.g., health, experience) and extrinsic (e.g., wind, predation) factors will individually modulate this context-dependent departure decision. The consistency of our results across the species suggests that these are general departure rules for migratory songbirds. Garden warblers showed relatively little restlessness compared to the others; this phenomenon is discussed at the end of this section.

We have to reject our prediction one that experimental birds show more migratory restlessness in the nights following a low food phase than control birds (Fig. 2). Our results are in line with some studies (Berthold 1976; Bauchinger et al. 2008; Ramenofsky et al. 2008) but are in contrast to yet others (Biebach 1985; Gwinner et al. 1985, 1988; Eikenaar and Bairlein 2014). The inconsistency between these studies in the behavioural response to altered feeding conditions may be explained by different study species, dissimilar diet conditions, spring versus autumn migration, and wild birds versus those bred in captivity. An important explanation for not finding differences in the amount of migratory restlessness (Table S1, Fig. 3) and for the inconsistency of the results of former studies is the fact that the individual reaction to the feeding conditions significantly depends on the current individual energy stores (prediction three; Fig. 4). Therefore, prediction three can be confirmed. The experimental birds with no to low energy stores (Fig. 4, day three and four) showed little restlessness during the low food phase, whereas the others with higher energy stores showed large amounts of restlessness (Fig. 4). In the former, the currently low energy stores may be insufficient to reach any favourable stopover site in free flight. Such birds may die en route. From an evolutionary perspective, it is therefore a beneficial mechanism that no to low energy stores have a strong inhibitory effect on the motivation to resume migration and/or to leave the current stopover site. This is especially important if an ecological barrier has to be crossed, e.g., in our case 50 km across the North Sea, and/or species-specific habitats are only patchily distributed (Bairlein 1985; Biebach et al. 1986). Thus, spending the little remaining energy stores for staying until local feeding conditions improve offers a higher survival probability than spending energy for flying. In contrast, the individuals that have sufficient energy stores for a safe flight to another stopover will benefit from this decision. This is so because
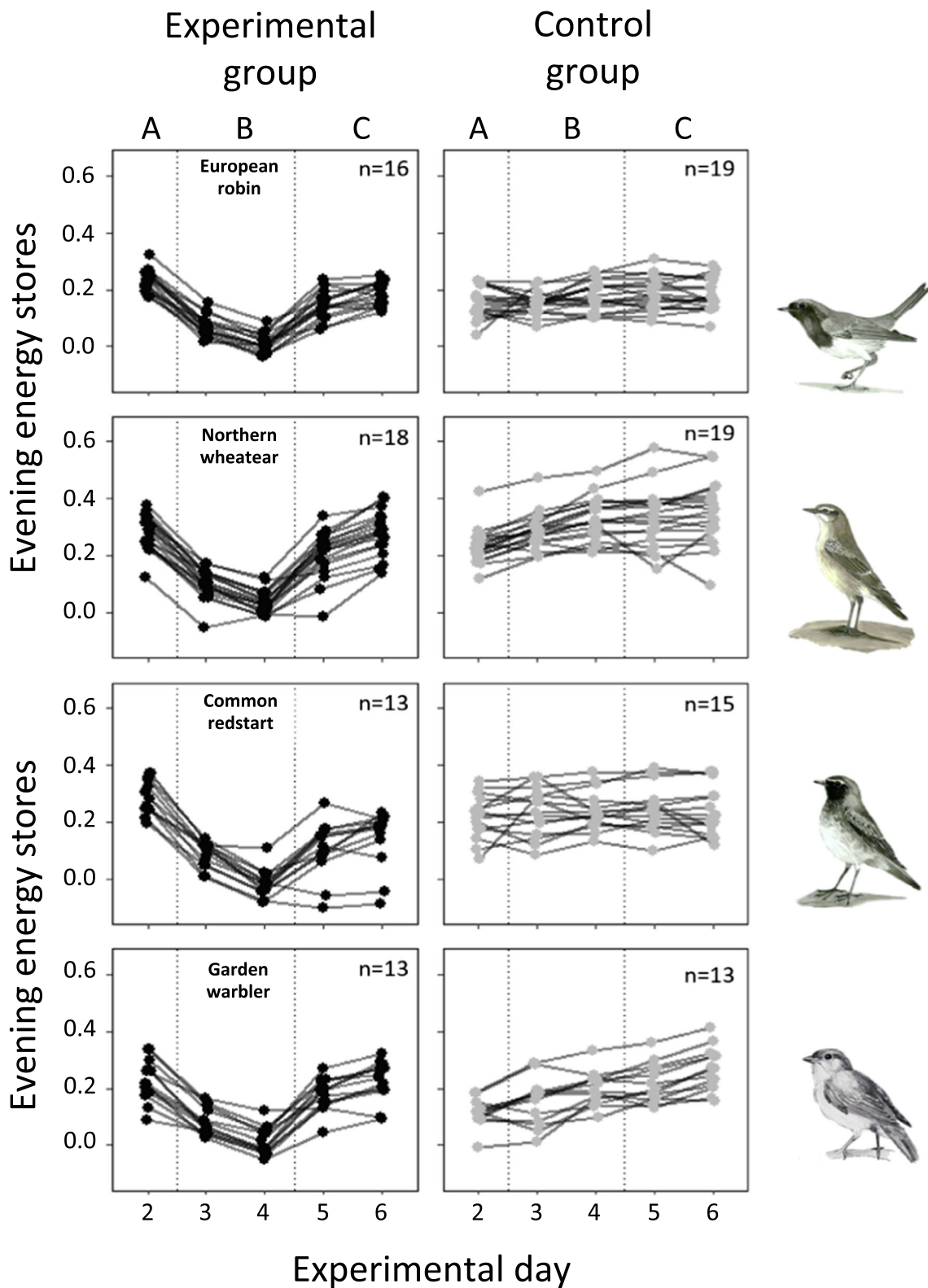
Fig. 2 Change in evening energy stores (proportional data) from day two to day six of the experiment of the four study species (European robin, northern wheatear, common redstart, and garden warbler). Black dots represent the experimental group receiving a restricted amount of food supply (5 g) on day three and four; grey dots are the control group which received ad libitum food during the experiment throughout. Dotted vertical lines representing the different phases of the experiment: (A) fuelling phase; (B) low food phase; (C) refuelling phase. Note that data of the first evening was not considered because birds being caught at different times of the day had differently long access to the food
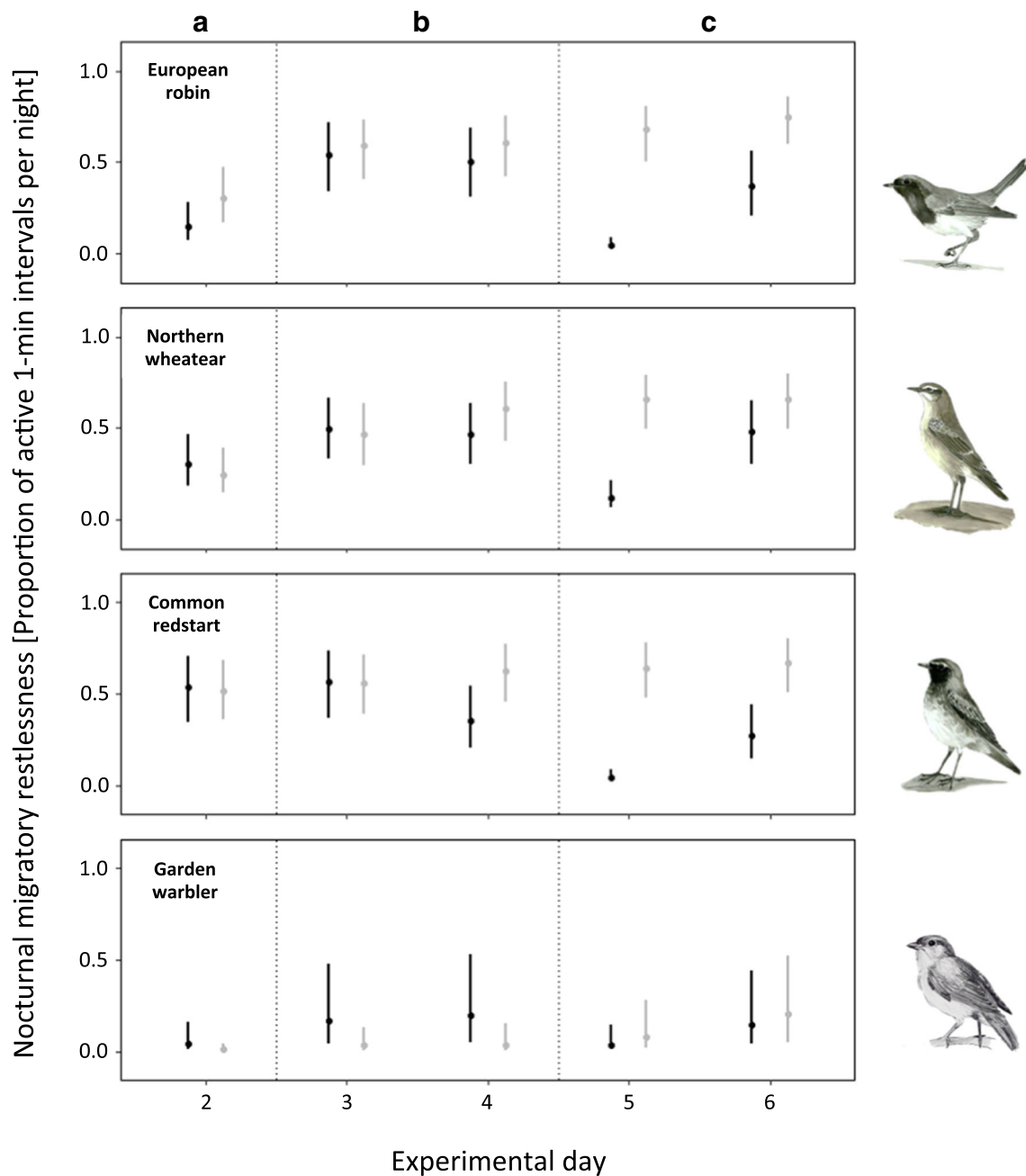
Fig. 3 The effect of the experimental treatment on nocturnal migratory restlessness for each species. Plotted are the respective medians (dots) and the 95% credible intervals (CrI) (solid lines) for each group (black, experimental group; grey, control group). Dotted vertical lines representing the different phases of the experiment: (A) fuelling phase (day two); (B) low food phase (day three and four); (C) refuelling phase (day five and six). To illustrate the effect of the experimental treatment on nocturnal migratory restlessness, we estimated 95% CrI using a GLMM with the two-way interaction experimental treatment*experimental night (Table S1). The variable day of year (scaled) was set to its mean. Sample sizes per species and group are given in Fig. 2

remaining at the current stopover with limited food supply can significantly slow down migration (Alerstam and Lindström 1990) and may even lead to starvation.

We propose that there is a critical "energy stores-threshold", below which survival probability is higher when continuing stopover and above which probability to reach the migratory destination in time is higher when departing. This threshold does not have a fixed, generally applicable value but is rather species-/individual-specific and strongly modified by current intrinsic (e.g., health, experience) and extrinsic (e.g., wind, temperature) conditions. Since we did not determine the bird's actual departure decision but only approximated the corresponding departure probability (Eikenaar et al. 2014a), our data do not allow for estimating such an "energy store-threshold".

Table 3 Results of four generalized linear mixed-effects models explaining variation in amount of nocturnal migratory restlessness of European robins, northern wheatears, common redstarts, and garden warblers

	European robin (n = 35)		Northern wheatear (n = 37)		Common redstart (n = 28)		Garden warbler (n = 26)	
	Median	95% CrI	Median	95% CrI	Median	95% CrI	Median	95% CrI
Intercept	**−0.96**	**−1.64/−0.25**	−1.21	−1.84/−0.58	−0.14	−0.74/0.50	**−3.43**	**−5.22/−1.69**
Exp.treatment (EXP)	0.82	−0.95/2.46	0.12	−0.92/1.08	0.36	−0.98/1.71	0.42	−2.09/2.91
Energy stores	0.53	−0.33/1.37	0.05	−1.05/1.10	0.34	−0.46/1.17	**2.65**	**0.25/4.91**
Exp.nExp.night (3)	**1.15**	**0.35/1.98**	**1.1**	**0.34/1.92**	0.24	−0.58/1.07	0.07	−1.40/1.56
Exp.nExp.night (4)	**0.94**	**0.04/1.81**	**1.32**	**0.42/2.19**	0.41	−0.47/1.28	−0.84	−2.76/1.01
Exp.nExp.night (5)	**1.31**	**0.40/2.17**	**1.25**	**0.39/2.00**	0.28	−0.64/1.09	−0.24	−2.16/1.53
Exp.nExp.night (6)	**1.64**	**0.78/2.51**	0.77	−0.03/1.61	0.53	−0.30/1.33	0.69	−1.61/2.85
Day of year (scaled)	**−0.41**	**−0.71/−0.11**	−0.18	−0.54/0.19	0.15	−0.11/0.39	0.00	−0.93/0.87
Exp.treatment (EXP)*Energy stores	**−1.99**	**−3.55/−0.45**	0.35	−1.09/1.80	−0.62	−2.08/0.87	**−2.89**	**−5.57/−0.11**
Exp.treatment (EXP)*Exp.nExp.night (3)	−0.92	−3.32/1.47	**1.89**	**0.18/3.67**	**2.29**	**0.02/4.43**	1.19	−1.38/4.00
Exp.treatment (EXP)*Exp.nExp.night (4)	1.61	−1.75/5.05	**3.76**	**0.99/6.54**	**3.41**	**0.19/6.61**	1.76	−2.13/5.67
Exp.treatment (EXP)*Exp.nExp.night (5)	**−4.42**	**−6.34/−2.52**	**−2.10**	**−3.16/−0.98**	**−3.16**	**−4.85/−1.41**	−0.05	−2.41/2.45
Exp.treatment (EXP)*Exp.nExp.night (6)	−2.46	−4.48/0.50	**−0.17**	**−1.36/0.96**	−1.27	**−2.77/0.33**	0.10	−2.70/2.92
Energy stores*Exp.nExp.night (3)	−0.41	−1.85/1.12	−0.41	−1.6570.81	**−0.39**	**−1.56/0.72**	**−3.00**	**−5.26/−0.63**
Energy stores*Exp.nExp.night (4)	0.13	−1.10/1.27	0.11	−0.91/1.20	**−0.11**	**−1.40/1.15**	−0.39	−2.87/2.42
Energy stores*Exp.nExp.night (5)	−0.11	−1.33/1.07	0.43	−0.63/1.49	**0.30**	**−0.89/1.48**	−0.70	−3.05/1.68
Energy stores*Exp.nExp.night (6)	−0.13	−1.28/1.07	0.87	−0.12/1.91	**0.04**	**−1.11/1.19**	−1.48	−3.80/1.03
Exp.treatment (EXP)*Energy stores*Exp.nExp.night (3)	1.89	−0.44/4.33	**1.88**	**0.11/3.59**	**3.47**	**1.22/5.79**	**3.21**	**0.05/6.27**
Exp.treatment (EXP)*Energy stores*Exp.nExp.night (4)	**2.74**	**0.48/5.06**	**2.11**	**0.20/3.99**	**3.05**	**0.67/5.20**	0.31	−3.33/3.47
Exp.treatment (EXP)*Energy stores*Exp.nExp.night (5)	**3.79**	**1.74/5.90**	−0.40	−1.91/1.04	0.53	−1.31/2.25	0.63	−2.55/3.70
Exp.treatment (EXP)*Energy stores*Exp.nExp.night (6)	**2.23**	**0.12/4.41**	−0.53	−2.01/0.96	1.60	−0.21/3.35	2.26	−0.82/5.37

Medians and 95% credible intervals (CrI) are given for fixed factors included in the model. 95% CrI not including zero are given in bold. Reference category for Exp. treatment is "Control" and for Exp.night "second night", respectively

Nevertheless, our study clearly demonstrated that the current energy stores of the experimental birds strongly affect the decision-making process during low food phase (Fig. 4).

During the first night of the refuelling phase, experimental birds showed significantly less migratory restlessness than control birds. This supports prediction two (Tables 1, 3, Fig. 3, S4). The effect was apparent in robins, wheatears, and redstarts during the first night and in the latter two also during the second night of the refuelling phase. We did not find such an effect in any of these nights for the garden warbler (see below for discussion). Since three out of four species showed a consistent behavioural response to the improved feeding conditions, we are convinced that it is a general strategy in migratory songbirds to exploit favourable feeding conditions for at least 1 day after losing significant energy stores and/or being lean (Fig. 3) (cf. Eikenaar and Bairlein 2014; Eikenaar et al. 2014b). The results of our experiment, therefore, support the more general finding of correlative studies, demonstrating that

free-flying birds with low energy stores stopover longer than conspecifics with high energy stores (e.g., Bairlein 1985; Biebach et al. 1986; Goymann et al. 2010; Schmaljohann et al. 2013; Deppe et al. 2015).

In contrast to the other species, garden warblers showed relatively little migratory restlessness throughout the experiment. This made it difficult to interpret the results and compare their behavioural responses to the experimental treatment with the other species. One potential reason is that garden warblers may not have adjusted to the caging and feeding conditions as well as the other species. This, however, seems doubtful because experimental birds significantly increased energy stores during the refuelling period and control birds throughout their stay (Fig. 3). Alternatively, energy stores (max. 0.4, Fig. 2) were not sufficient to induce high restlessness, since it is known that garden warblers store large amounts of energy (often 0.5 and max. 1.0) before and during migration (Bairlein 1991; Ottosson et al. 2005). Whether any
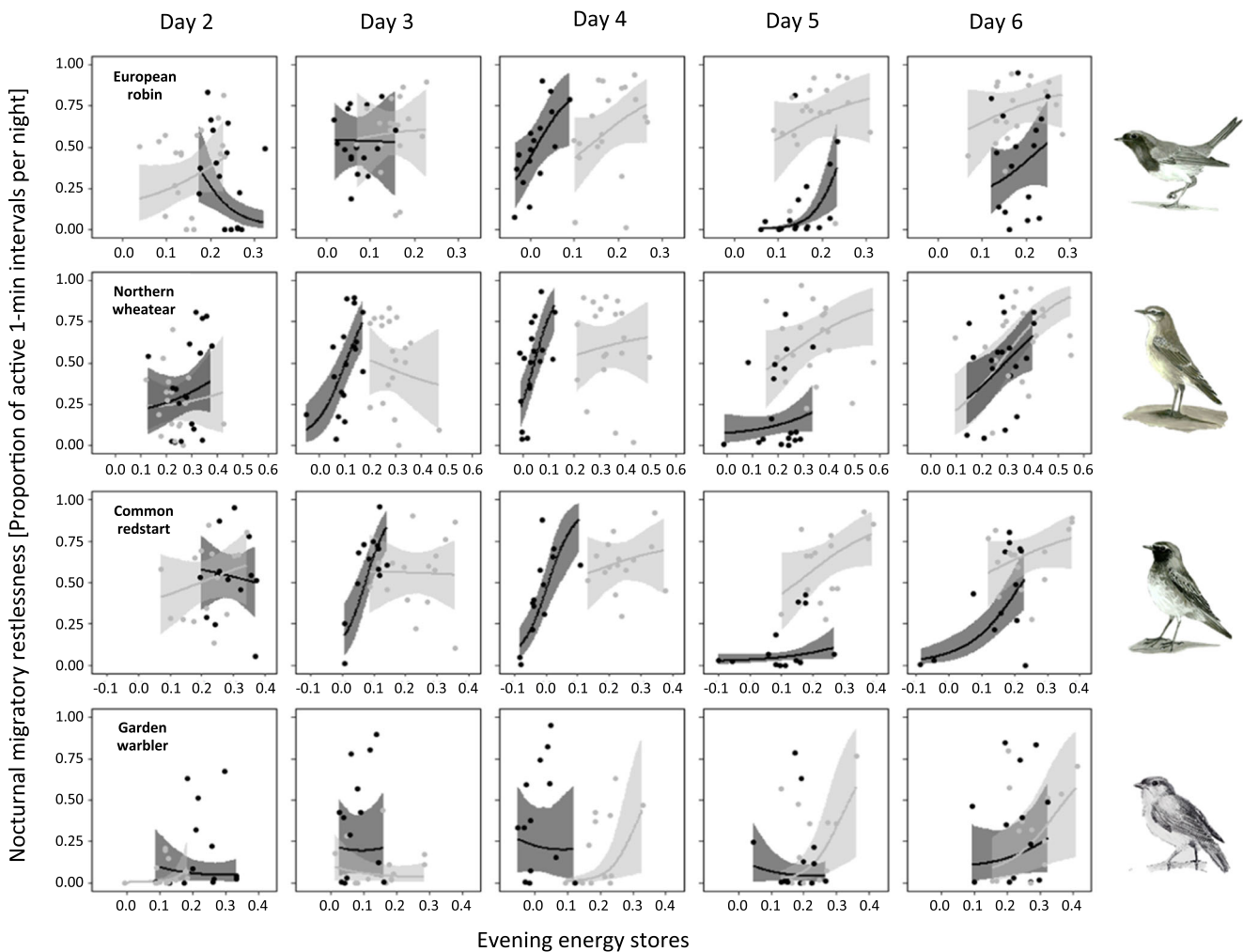
Fig. 4 Relationship of the three-way interaction between experimental treatment, evening energy stores (proportional data), and experimental night on nocturnal migratory restlessness of European robins, northern wheatears, common redstarts, and garden warblers. Black dots indicate the experimental group and grey dots the control group. Black (experimental group) and grey (control group) lines represent the fitted values of the corresponding models (Table 4) with the 95% credible intervals as the in dark grey (experimental group) and light grey (control group) area. The y-axis shows the proportion of 1-min intervals a bird was active during the night, while the energy stores a bird carried just before the night has started are given on the x-axis. Note, first night in captivity was excluded due to different caging time on the day of capture. Sample sizes per species and group are given in Fig. 2

of these reasons explain why most garden warblers showed low amounts of migratory restlessness in general and a few rather large amounts (Fig. 4) remains unknown to us. In addition, previous studies provided also inconsistent results in garden warblers (Berthold 1976; Gwinner et al. 1985, 1988; Fusani and Gwinner 2003; Bauchinger et al. 2008; Fusani et al. 2011), which illustrates the complexity of behavioural mechanisms even in a single species.

Control wheatears and garden warblers increased their energy stores as expected but not control robins and redstarts (Fig. 2, S3). The reasons for these differences are possibly related to different migration strategies, site-specific fuelling strategies en route, and/or adjustments to caging conditions between the species. The robin is a medium-distance migrant, while the other species are long-distance migrants. Long-distance migrants are expected to maximize speed of migration at the expense of relatively high energetic costs (Alerstam and Lindström 1990). Medium-distance migrants, in contrast, may be more prone to minimize energy expenditure during migration (Nilsson et al. 2014) and thus may limit the energy accumulation to a certain level even at ad libitum feeding conditions (Hedenström and Alerstam 1997), as observed here (Figs. 2, 4). This assumption and our results are supported from different field studies demonstrating that energy stores were in general low in migratory robins at stopover (Polak and Szewczyk 2007; Bulyuk and Tsvey 2013). Energy stores in ten robins using an artificial feeder (mealworms) were, in contrast, higher than in our experiment (energy stores of max. 0.70; Dänhardt and Lindström 2001). The migration strategy of redstarts does not appear to be considerably different from the other long-distance migrants (e.g., Ktitorov et al. 2008; Bayly et al. 2012; Gersten and Hahn 2016).

Nevertheless, free-flying redstarts seem to have generally lower energy stores than wheatears (e.g., Delingat et al. 2006; Schmaljohann et al. 2016) or garden warblers during migration (e.g., Chernetsov et al. 2007; Hama et al. 2013). This is similar to the pattern found in our study (Figs. 2, 4). Since migratory songbirds can use the Earth's magnetic field to locate their geographic position and adjust their migratory behaviour, i.e., fuelling and/or amount of restlessness, accordingly (Fransson et al. 2001; Kullberg et al. 2007; Bulte et al. 2017), robins and redstarts may have reached their individual-specific energy stores for Helgoland on day two, while the others were still eager to accumulate more energy. Additionally, the complex interplay of food predictability (Lindström and Alerstam 1992), time of season (Eikenaar et al. 2016), and seasonal switch in diet (Bairlein 1996) on the urge to fuel (Schaub and Jenni 2000) together with species-/individual-specific adaptabilities to the caging and feeding conditions may result in general different rates of energy accumulation between species and between individuals regardless of the food ad libitum conditions.

In conclusion, our study supports the predictions that decision-making in migratory birds at stopover is generally influenced by the interplay of bird's energy stores and local feeding conditions. The consistency of the behavioural responses to the fasting-fuelling conditions across one medium-distance and two long-distance migrants suggests that the departure rules elaborated in this study are probably valid for most songbird migrants. Yet, we find it likewise important to present results of the garden warbler that do not fit into the pattern of the other three species. This and the within-species variation in the response to different feeding conditions also illustrate the complexity of the decision-making process in migrant birds (Fig. 4) and the importance of more multi-species study on this topic.

Compliance with ethical standards

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