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4 **PHYSIOLOGICAL CONDITIONS INFLUENCE STOPOVER**
5 **BEHAVIOUR OF SHORT-DISTANCE MIGRATORY PASSERINES**

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21
22 **Abstract**

23 During migration, birds spend more than 80% of the time at stopover sites to rest and refuel before
24 and after crossing ecological barriers such as deserts or seas. Since stopover has intrinsic costs in
25 terms of energy and time, birds should try to minimize its duration, which depends on the combined
26 effects of environmental factors, endogenous programmes, and physiological conditions. Previous
27 studies on long-distance migrants caught after crossing an ecological barrier indicated that body
28 condition strongly influences the decision whether to prolong stopover or resume migration with
29 lean birds staying longer than fat birds. In short-distance migrants, evidence for a determinant role
30 for physiological condition in stopover behaviour after crossing an ecological barrier is still scarce.
31 Here, we studied whether migratory restlessness (*Zugunruhe*) at a stopover site depends on
32 physiological condition in three European short-distance migratory passerines: black redstarts,
33 European robins, and European stonechats. In all species, an integrated measure of condition based
34 on body mass, amount of subcutaneous fat and thickness of pectoral muscles predicted the intensity

35 of *Zugunruhe*. Overall, our results confirmed the importance of energy reserves in determining
36 stopover duration, illustrating similar stopover strategies in short and long-distance migrants.

37 **Introduction**

38 Every year billions of birds migrate across areas where food and water are not available, with non-
39 stop flights that lead to a rapid exhaustion of energy reserves. Thus, stopovers for refuelling are
40 necessary to successfully continue migration. The duration of stopovers is influenced by a number
41 of factors including endogenous programmes, environmental parameters such as weather and food
42 availability, and physiological condition of each individual at arrival (reviewed by Jenni and Schaub
43 2003). Theory predicts that migratory strategies and stopover behaviour depends on fat deposition
44 (Alerstam & Lindström 1990; reviewed by Hedenström 2008), but evidence for a determinant role
45 of body condition for stopover duration has been reported only in long-distance migratory
46 passerines (Fusani & Gwinner 2004; Fusani *et al.* 2009; Goymann *et al.* 2010). To date, our
47 knowledge about stopover behaviour of short-distance migrants is still scarce.

48 In captivity, the extent of migratory disposition of nocturnal migrants is estimated by the intensity
49 of nocturnal restlessness, or *Zugunruhe* (Naumann 1795-1817). The duration and intensity of
50 *Zugunruhe* is correlated with the duration and intensity of migration in free-living birds (Berthold
51 1973). In garden warblers (*Sylvia borin*), it was noted that leaner birds show a diurnal pattern of
52 activity, whereas heavier birds show low diurnal activity and intense nocturnal activity, i.e.
53 *Zugunruhe* (Bairlein 1985). In northern wheatears (*Oenanthe oenanthe*), birds with large fuel loads
54 showed more *Zugunruhe* the night after capture at a stopover site and accumulated less fuel in the
55 subsequent two days than birds caught with small fuel loads (Eikenaar & Schläpke, 2013). These
56 observations match with the hypothesis that lean birds would spend more than one day at a stopover
57 site to refuel and recover, whereas fat birds would resume migration in the night following arrival
58 (Biebach 1985). This hypothesis was confirmed by laboratory studies in which a non-stop flight
59 followed by stopover was simulated in fasting-and-refeeding experiments (Biebach 1985; Gwinner
60 *et al.* 1988; Fusani & Gwinner 2004). In spring, the effects of the food regimen on nocturnal
61 activity during the night following food reintroduction were highly correlated with the amount of fat
62 reserves in blackcaps (*Sylvia atricapilla*). These results were confirmed later by field studies, in
63 which body condition was correlated with the extent of *Zugunruhe* in garden warblers, whitethroats
64 (*Sylvia communis*) and whinchats (*Saxicola rubetra*; Fusani *et al.* 2009). In particular, we observed
65 that birds with high fat reserves showed intense *Zugunruhe* at night and little activity during the
66 day, whereas birds with little fat reserves showed the opposite pattern, suggesting that the
67 physiological condition influences stopover duration in European long-distance migrants (Fusani *et*

68 *al.* 2009). Furthermore, we confirmed these results in a whole-island telemetry study, in which we
69 demonstrated the influence of fat reserves on real minimum stopover duration (Goymann *et al.*
70 2010).

71 Both long- and short-distance migrants are thought to migrate using a time-minimization strategy
72 (reviewed by Hedenström 2008). In spring, selection favours early arrival and onset of breeding
73 (Kokko 1999). Several studies suggested that the endogenous circannual mechanisms controlling
74 migratory parameters are particularly well developed in long-distance migrants (Bairlein &
75 Gwinner 1994). Across areas where refuelling stopover sites are available, endogenous factors
76 should dominate the duration and length of migratory flights, whereas condition and extent of
77 energy reserves are expected to determine the stopover duration before crossing an ecological
78 barrier (Jenni & Schaub 2003). Similarly, body condition is likely to be crucial in determining
79 stopover duration after crossing a barrier. In fact, when crossing ecological barriers, birds are
80 usually unable to stop and refuel. Furthermore, some field data suggest that long-distance migrants
81 deposit more fat before migration and also maintain fat reserves longer than short-distance migrants
82 (Bairlein & Gwinner 1994). Therefore, energy reserves are expected to strongly determine the
83 stopover behaviour in short-distance migrants. Previous studies on four different species of North
84 American thrushes, wintering in Central America or in the North of South America and crossing the
85 Gulf of Mexico, showed that lean birds are less active at night than fat birds just after the
86 overcoming of the ecological barrier (Yong & Moore 1993), revealing the priority of birds without
87 fat load to replenish energy reserves.

88 A few studies had previously demonstrated a simultaneous effect of body condition and weather
89 factors on stopover duration in short-distance migrants (Morganti *et al.* 2011; Bulyuk & Tsvey
90 2013). In fact, when weather condition are favourable (strong tailwinds, weak crosswinds, low
91 rainfall, high temperature, high pressure), fat black redstarts (*Phoenicurus ochruros*) are highly
92 likely to depart from the stopover site on the evening of the same day of arrival (Morganti *et al.*
93 2011), and although weather conditions alone do not determine the duration of stopover in robins
94 (*Erithacus rubecula*), birds that stop for longer than one night tend to depart when the wind is
95 favourable (Bulyuk & Tsvey 2013). We thus predict that short-distance migrants rest at the stopover
96 site in relation to their physiological condition, similar to long-distance migrants caught at the same
97 stopover site (Fusani *et al.* 2009). Here, we studied the relationship between physiological condition
98 and the amount of *Zugunruhe* of short-distance migrants after crossing the Mediterranean Sea. Birds
99 were caught at a stop-over site and placed in cloth cages to measure activity for one day and
100 released the following morning.

101 Our results demonstrate that the physiological condition predicts the intensity of *Zugunruhe* in all
102 three species of short-distance migrants.

103 **Material and methods**

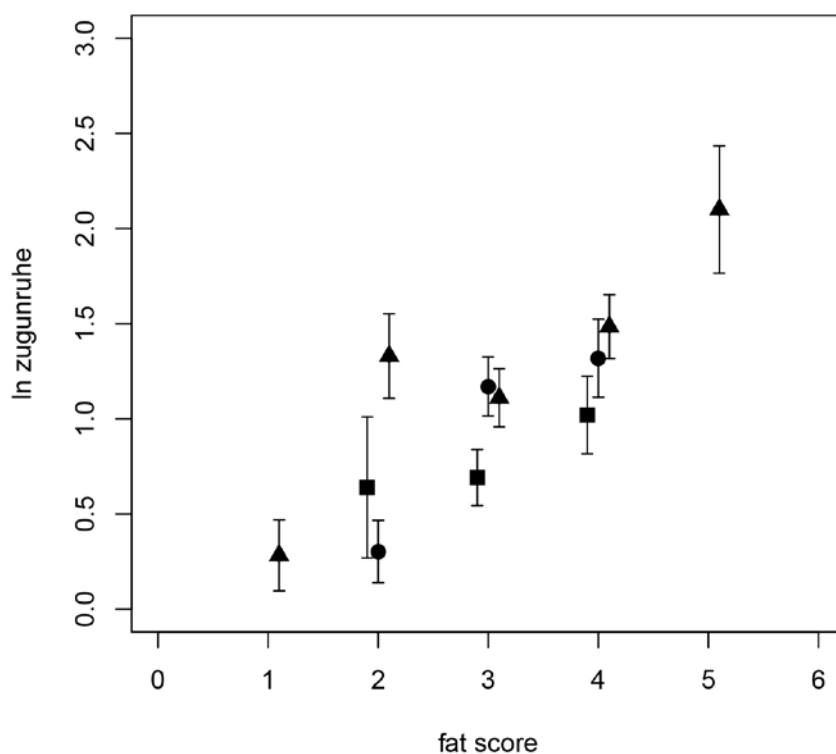
104 The study was conducted on Ponza (Italy), a small island in the Tyrrhenian Sea (40.855°N,
105 12.858°E) located along one of the main Mediterranean migratory routes. A ringing station has
106 been active on the island since 2002. We used 51 black redstarts (*Phoenicurus ochruros*), 98 robins
107 (*Erithacus rubecula*) and 17 stonechats (*Saxicola torquata*), caught with mist-nets during spring
108 ringing operations in March and April 2011 and 2013. These three species are short-distance
109 migratory passerines, which winter in the Mediterranean coasts of North Africa. Data from capture-
110 recapture studies suggest that in spring robins migrate to central-northern Europe, mainly to Sweden
111 and Baltic coasts, black redstarts migrate to central Europe, mainly to Germany, and stonechats
112 migrate to southern-central Europe, mainly to Italy, Austria and Hungary (Spina & Volponi 2008).
113 Data from the Ponza ringing station show that the peak timing of passage (median Julian day) in the
114 years 2007-2014 ranges from 82 to 97 in robins, 79-94 in black redstart, and 73-81 in stonechats
115 (Cardinale unpublished). Birds were caught in the morning between 7:30 and 11:30, subcutaneous
116 fat was scored on a 0–8 scale, the size of the pectoral muscles on a 0–3 scale, and body mass was
117 measured to the nearest tenth of a gram (Bairlein 1994). By 12:00, birds were placed in individual
118 cloth cages so that they were visually isolated from each other. Each cage was equipped with an
119 activity infrared sensor recording the locomotor activity. Birds were given only water ad libitum
120 and were exposed to natural daylight conditions. All birds were released the following morning
121 within one hour after sunrise.

122 We calculated the number of times the infrared sensor was activated during each 2 min period. We
123 then calculated the average activity during the intervals from 12.00–sunset (day activity) and from
124 sunset–sunrise (*Zugunruhe*) based on civil twilight times (Greenwich Mean Time +1). As the
125 activity data were saved every day at 24.00, we calculated the average activity during the intervals
126 sunset-24.00 (*Zugunruhe during the first part of the night*), and 24.00-sunrise (*Zugunruhe during*
127 *the second part of the night*), and we calculated *Zugunruhe* as the mean value of the two previous
128 variables. Finally, we transformed all the calculated values of activity (*Zugunruhe during the first*
129 *part of the night*, *Zugunruhe during the second part of the night* and *Zugunruhe*) by taking the
130 natural logarithms ($\ln(x+1)$). To test for the effects of body condition on *Zugunruhe*, we performed
131 first an analysis with the fat scores. We chose this approach because the fat score is a normalized
132 index which is directly comparable across species and previous studies have shown it to be a robust,
133 consistent predictor of migratory disposition (Fusani *et al.* 2009). It was not possible to use GLMs

134 (multiple regression) to study the relationship between fat score and *Zugunruhe* across species
 135 because of the study design, i.e. the species is a categorical variable with multiple levels. Therefore,
 136 we used a non-parametric approach. First, we performed a non-parametric Spearman correlation
 137 between fat score and *Zugunruhe* including all species. The effect of the species on the relationship
 138 between fat and *Zugunruhe* was then analysed by means of the Quade's Test, a non-parametric
 139 Analysis of Covariance. We also performed separately for each species a Pearson correlation test
 140 between *Zugunruhe* and the index CONDITION, which was extracted by means of principal
 141 component analysis (PCA) from body mass, fat score, and muscle score. All statistical analyses
 142 were performed with R v. 3.2.0 using a significance level of $\alpha = 0.05$.

143 Results

144 A global analysis across the three species considered together, on a total of 167 individuals (51
 145 black redstarts, 99 robins, 17 stonechats), yielded a significant positive correlation between
 146 *Zugunruhe* and fat score ($r_s = 0.263$, $n = 167$, $p = 0.001$) (Fig. 1).



147
 148 **Fig. 1** Log-transformed intensity of *Zugunruhe* (mean \pm SE) plotted against fat score for black redstart
 149 (circles), European robin (triangles) and European stonechat (squares). *Zugunruhe* was significantly
 150 correlated with fat score, with no specific effect of the species. See text for statistical details.

151 By applying a Quade's Test, a non-parametric analysis of covariance, we tested if the correlation
 152 found in this global analysis was influenced by the factor species. The analysis showed no

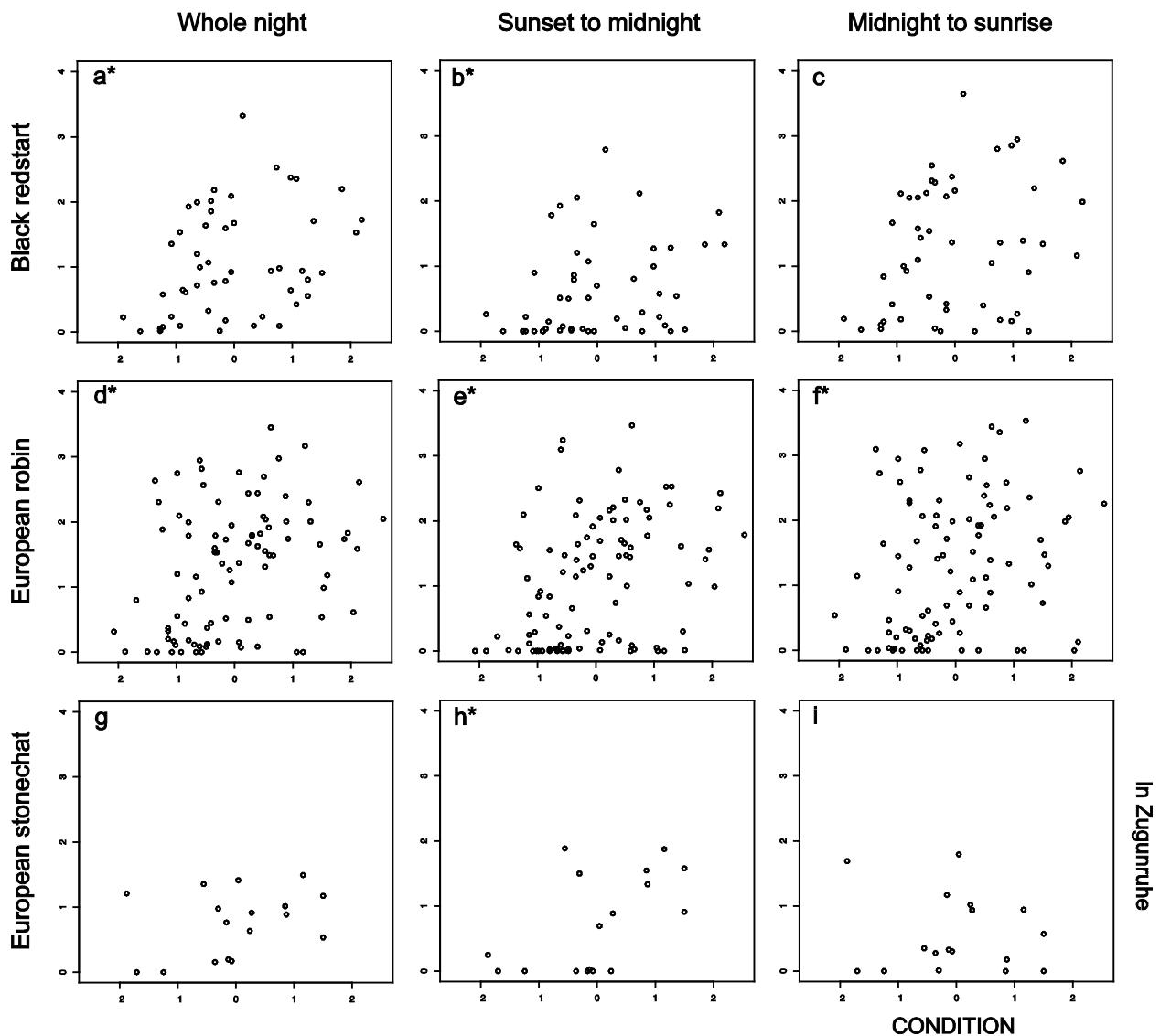
significant effect of the species on the relationship between *Zugunruhe* and fat ($F_{2,157} = 2,673$, $p = 0,072$).

For each species, we extracted a single PCA component from the variables fat score, muscle score and body mass, termed *CONDITION*. In black redstarts, *CONDITION* (eigenvalue 1.600) explained 53.0 per cent of the total variance, and its correlations with each variable were as follows: body mass, 0.890; fat, 0.900; and muscle, -0.030. In robins, *CONDITION* (eigenvalue 1.950) explained 65.0 per cent of the variance, and its correlations were as follows: body mass, 0.860; fat, 0.830; and muscle, 0.720. In stonechats, *CONDITION* (eigenvalue 1.690) explained 56.0 per cent of the variance, and its correlations were as follows: body mass, 0.920; fat 0.920; and muscle, 0.010. In black redstarts, *CONDITION* was significantly positively correlated with the amount of *Zugunruhe*; in particular, *CONDITION* was significantly positively correlated with *Zugunruhe* during the first part of the night, and positively, but not significantly, correlated with *Zugunruhe* during the second part of the night (Table 1; Fig. 2a, 2b, 2c). In robins, *CONDITION* was significantly positively correlated with the amount of *Zugunruhe*; specifically, *CONDITION* was significantly positively correlated with *Zugunruhe* both during the first and the second part of the night (Table 1; Fig. 2d, 2e, 2f). Finally in stonechats, the overall correlation between *CONDITION* and *Zugunruhe* was not significant; however, *CONDITION* was significantly positively correlated with *Zugunruhe* during the first part of the night, but not with *Zugunruhe* during the second part of the night (Table 1; Fig. 2g, 2h, 2i). The amount of diurnal activity was not significantly correlated with *CONDITION* in all species (Table 1).

173

	Black redstart (51)		European robin (98)		European stonechat (17)	
Statistics (r_P)	r	P	r	P	r	P
<i>Zugunruhe</i>	0.325	0.021	0.336	0.001	0.349	0.169
<i>Zugunruhe during the first part of the night</i>	0.297	0.036	0.349	0.0004	0.556	0.021
<i>Zugunruhe during the second part of the night</i>	0.255	0.073	0.253	0.015	-0.111	0.670
<i>Diurnal activity</i>	0.118	0.414	-0.167	0.100	-0.202	0.436

Table 1 Correlations (Pearson) between *Zugunruhe*, *Zugunruhe during the first part of the night*, *Zugunruhe during the second part of the night*, and *Diurnal activity* and the factor *CONDITION* extracted from the variables body mass, fat score and muscle score by means of Principal Component Analysis. Bold typeface indicates statistically significant correlations



178

179 **Fig. 2** Scatterplots of log-transformed activity variables against the principal component **CONDITION**
 180 extracted from muscle score, fat score and body mass. For each species (top: black redstart, a, b, c; middle:
 181 European robin, d, e, f; bottom, European stonechat, g, h, i) we show *Zugunruhe* across the whole night (left,
 182 a, d, g), from sunset to midnight (middle, b, c, h) and midnight to sunrise (right, c, f, i). The stars (*) beside
 183 the panel letter indicates a significant correlation. See Table 1 for the statistics.

184 Discussion

185 Our results show that in black redstarts and European robins caught at a spring stopover site body
 186 condition correlated with the amount of *Zugunruhe*. In stonechats, the correlation between body
 187 condition and *Zugunruhe* was significant only for the first part of the night. In all species,
 188 *Zugunruhe* was more strongly correlated with body condition in the first part of the night, and the
 189 lack of correlation with *Zugunruhe* across the whole night in stonechats was probably due to the

190 smaller sample size. Overall, our study confirms that condition is a good indicator of migratory
191 tendency in these three short-distance migrants.

192 The results support the hypothesis that energy reserves carried by birds when arriving at stopover
193 sites are good predictors of stopover duration (Bairlein 1985, Biebach 1985), an idea that we
194 confirmed in previous studies on long-distance migrants (Fusani *et al.* 2009, Goymann *et al.* 2010).
195 Thus, energy reserves appear to be one of the main determinants of stopover duration,
196 independently of the strategy of migration. Since we used an identical experimental approach and
197 setup in the present study on short-distance migrants and in the previous study on long-distance
198 migrants (Fusani *et al.* 2009), we are confident that the relationship between body condition and the
199 amount of *Zugunruhe* reveals actual similarities in the control of migratory programmes between
200 short- and long-distance migrants. One interesting difference is the possible contribution of the
201 muscle to overall condition: differently from what observed in three species of long-distance
202 migrants (Fusani *et al.* 2009), in black redstarts and stonechats the factor **CONDITION** was not
203 significantly accounted by the muscle score.

204 Our study shows that individuals of the three study species express more intense *Zugunruhe* in the
205 first part of the night. Telemetric data on European robins have shown that the take-off time is
206 shifted towards the beginning of the night in birds having higher fuel loads and during shorter
207 nights (spring versus autumn), suggesting that departure time is dependent on fuel loads and on
208 night duration (Bolshakov *et al.* 2007). Moreover, data on caged birds have shown that migration is
209 stimulated by darkness (Gwinner 1967) and reported a quiescent aphasic phase during sunset, in
210 preparation to the migration (Ramenofsky *et al.* 2003). In this study, we used individuals with fat
211 score 2 or more, excluding thus very lean birds, and we conducted the fieldwork during spring
212 migration. Our results are in agreement with these observations and confirm that individuals having
213 a sufficient amount of fuel load preferably perform their migratory flights in the first part of the
214 night during spring migration.

215 Several external factors, such as weather condition and food availability, and internal factors, such
216 as endogenous programmes, interact and thus influence the migratory programme and the decision
217 of staying at a stopover site or resuming migration (reviewed by Jenni and Schaub 2003). Overall,
218 spring migration is thought to depend on a time-minimization strategy (reviewed by Hedenström
219 2008), because birds arriving earlier at the breeding grounds may obtain better territories and mate
220 earlier, thus enhancing their reproductive success compared to birds arriving late (Kokko 1999).
221 The results of the present study, however, suggest that migratory behaviour strongly depends on the
222 body condition of the animals and the time-minimization strategy should not overcome the

necessity for short-distance migrants in poor condition to regain energy reserves. Endogenous circannual mechanisms controlling migratory parameters are particularly well developed in long-distance migrants, leading to a high temporal precision (Bairlein and Gwinner 1994, Helm *et al.* 2005). In fact, the timing of migration in long-distance migrants probably mainly relies on endogenous rhythms and photoperiod cues (Both & Visser 2001; Coppack & Both 2002). On the other hand, migratory schedules in short-distance migrants, which are characterized by shorter migration routes between wintering and breeding grounds, may be more flexible and the total duration of migration may depend more on the physiological condition and environmental factors. According to this hypothesis, our findings show that migratory behavior of short-distance migrants is finely modulated by energy condition. Moreover, we confirmed previous observations revealing that lean birds are less active at night than fat birds just after the overcoming of the ecological barrier (Yong & Moore 1993).

A novel contribution of our study was the capacity of our approach of separating the influence of environmental factors from that of internal factors. Our study birds were kept indoor in cages and in similar conditions during the recordings. Therefore, their behaviour was not affected by factors such as wind or cloud cover. The capture and the experiments, moreover, were conducted across the entire migratory season, thus calendar day and weather conditions preceding capture had no systematic effects on the results. Although it is likely that these factors introduced variability in the sample, the large sample size allowed clear relationships between condition and migratory behaviour to be uncovered.

Eikenaar and Bairlein (2013) demonstrated that birds maintained in captivity under fasting conditions increase *Zugunruhe*, showing that the motivation to migrate, quantified by *Zugunruhe*, is affected by changes in food availability. This result is in line with observational field studies showing that migrants are more likely to depart from a stopover site when food is scarce than when food is plentiful (Bibby & Green 1981; Ottich & Dierschke 2003). Experiments suggest that stopover duration is very short if fuel deposition rate is low or negative (Biebach 1985; Gwinner *et al.* 1985; Yong & Moore 1993). Previous studies on three species of trans-Saharan migratory passerines found that all birds departed in the evening of the arrival day at sites with low food availability, whereas at sites with high food availability lean birds stayed at least one day (Biebach *et al.* 1986). Preliminary data from our research station on Ponza suggest that this stopover site probably provides opportunities to regain fat reserves (Trez *et al.* unpublished). Hence, it is likely that stopover duration is not influenced by the lack of food availability and that lean birds prolong stopover to replenish energy reserves.

256 A few studies had previously demonstrated the role of body condition on stopover duration in short-
257 distance migrants, although the influence of environmental factors could not be excluded. In black
258 redstarts, stopover duration is longer in individuals with low fat stores, and birds generally resume
259 migration when weather conditions are favourable (Morganti *et al.* 2011). Moreover, in European
260 robins departure decision depends on simultaneous action of both energetic and weather factors
261 (Bulyuk & Tsvey 2013).

262 In all three species, day activity was not significantly correlated with body condition. These results
263 contrast with previous reports of higher diurnal activity of lean birds at a stopover site, observed in
264 the long-distance migrant, the garden warbler (Bairlein 1985), and in four species of North
265 American thrushes that cross the Gulf of Mexico to reach their wintering areas (Yong & Moore
266 1993), which could reflect the simultaneous needs of foraging and minimizing the exposure to
267 predators. In robins making stopovers on the Courish Spit, the proportion of recaptured individuals
268 is nearly 4-fold lower in fat birds than in lean individuals (Nikolay Titov 1999), suggesting a
269 diurnal pattern of activity in lean birds. One possible explanation for the discrepancy between our
270 results and previous work could lie in the pattern of migration and the frequency and distribution of
271 the stopovers, leading to different strategies of fat accumulation through the migratory flights and
272 different decisions during stopovers. Hence, diurnal activity is supposed to depend on the
273 simultaneous effect of numerous factors, not only body condition, food availability and predation
274 risk, but also the need to replenish energy reserves in relation to the stopover position along the
275 migratory route.

276 In conclusion, our study revealed the influence of physiological condition on stopover duration in
277 short-distance migrants. This adds evidence regarding the importance of fuel resources in
278 determining the decision of birds to resume migration or prolong stopover, and confirms that short-
279 and long-distance migrants follow similar stopover strategies after crossing an ecological barrier.

280

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286 ISPRA): paper No. 55. All experimental procedures were authorized by the Regione Lazio with
287 respect to Italian law.

288 **References**

- 289 Alerstam T, Lindström A (1990) Optimal bird migration: the relative importance of time, energy
290 and safety. In Bird migration: physiology and ecophysiology (ed. E. Gwinner), 331–351.
291 Berlin, Germany: Springer.
- 292 [Bairlein F \(1985\) Body weights and fat deposition of Palaearctic passerine migrants in the central](#)
293 [Sahara. Oecologia 66:141–146. doi: 10.1007/BF00378566](#)
- 294 [Bairlein F \(1994\) Manual of field methods. European–African Songbird Migration Network.](#)
295 [Wilhelmshaven, Germany: Institut für Vogelforschung.](#)
- 296 [Bairlein F, Gwinner E \(1994\) Nutritional mechanisms and temporal control of migratory energy](#)
297 [accumulation in birds. Annu Rev Nutr 14:187–215. doi: 10.1146/annurev.nutr.14.1.187](#)
- 298 [Berthold P \(1973\) Relationships between migratory restlessness and migration distance in six](#)
299 [Sylvia species. Ibis \(Lond 1859\) 115:594–599. doi: 10.1111/j.1474-919X.1973.tb01998.x](#)
- 300 [Bibby CJ, Green RE \(1981\) Autumn migration strategies of reed and sedge warblers. Orn Scand](#)
301 [12:1-12.](#)
- 302 [Biebach H \(1985\) Sahara stopover in migratory flycatchers: fat and food affect the time program.](#)
303 [Experientia 41:695–697. doi: 10.1007/BF02007727](#)
- 304 [Biebach H, Friedrich W, Heine G \(1986\) Interaction of body mass, fat, foraging and stopover](#)
305 [period in trans-Saharan migrating passerine birds. Oecologia 69:370–379.](#)
- 306 [Bolshakov C V, Chernetsov N, Mukhin A, et al \(2007\) Time of nocturnal departures in European](#)
307 [robins, *Erithacus rubecula*, in relation to celestial cues, season, stopover duration and fat](#)
308 [stores. Anim Behav 74:855–865. doi: 10.1016/j.anbehav.2006.10.024](#)
- 309 [Both C, Visser ME \(2001\) Adjustment to climate change is constrained by arrival date in a long-](#)
310 [distance migrant bird. Nature, 411:296–8. http://doi.org/10.1038/35077063](#)
- 311 [Bulyuk VN, Tsvey A \(2013\) Regulation of stopover duration in the European Robin *Erithacus*](#)
312 [*rubecula*. J Ornithol 154:1115–1126. doi: 10.1007/s10336-013-0981-0](#)
- 313 [Coppack T, Both C \(2002\) Predicting life-cycle adaptation of migratory birds to global climate](#)
314 [change. Ardea, 90:369–378.](#)
- 315 [Eikenaar C, Bairlein F \(2013\) Food availability and fuel loss predict Zugunruhe. J Ornithol 155:65–](#)
316 [70. doi: 10.1007/s10336-013-0987-7](#)
- 317 [Eikenaar C, Schläpke JL \(2013\) Size and accumulation of fuel reserves at stopover predict nocturnal](#)
318 [restlessness in a migratory bird. Biol Lett 9:20130712. doi: 10.1098/rsbl.2013.0712](#)
- 319 [Fusani L, Cardinale M, Carere C, Goymann W \(2009\) Stopover decision during migration:](#)
320 [physiological conditions predict nocturnal restlessness in wild passerines. Biol Lett 5:302–5.](#)
321 [doi: 10.1098/rsbl.2008.0755](#)

322 [Fusani L, Gwinner E \(2004\) Simulation of migratory flight and stopover affects night levels of](#)
323 [melatonin in a nocturnal migrant. Proc Biol Sci 271:205–11. doi: 10.1098/rspb.2003.2561](#)

324 [Goymann W, Spina F, Ferri A, Fusani L \(2010\) Body fat influences departure from stopover sites in](#)
325 [migratory birds: evidence from whole-island telemetry. Biol Lett 6:478–81. doi:](#)
326 [10.1098/rsbl.2009.1028](#)

327 [Gwinner E \(1967\) Circannuale Periodik der Mauser und der Zugunruhe bei einem Vogel.](#)
328 [Naturwissenschaften 54:447–447. doi: 10.1007/BF00603157](#)

329 [Gwinner E, Biebach H, v Kries I \(1985\) Food availability affects migratory restlessness in caged](#)
330 [garden warblers \(*Sylvia borin*\). Naturwissenschaften 72:51–52. doi: 10.1007/BF00405336](#)

331 [Gwinner E, Schwabl H, Schwabl-Benzinger I \(1988\) Effects of food-deprivation on migratory](#)
332 [restlessness and diurnal activity in the garden warbler *Sylvia borin*. Oecologia 77:321–326.](#)
333 [doi: 10.1007/BF00378037](#)

334 [Hedenström A \(2008\) Adaptations to migration in birds: behavioural strategies, morphology and](#)
335 [scaling effects. Phil Trans R Soc Lond B 363:287–299. doi: 10.1098/rstb.2007.2140](#)

336 [Helm B, Gwinner E, Trost L \(2005\) Flexible seasonal timing and migratory behavior: results from](#)
337 [stonechat breeding programs. Annals of the New York Academy of Sciences, 1046:216–27.](#)
338 [http://doi.org/10.1196/annals.1343.019](#)

339 [Jenni L, Schaub M \(2003\) Behavioural and physiological reaction to environmental variation in bird](#)
340 [migration: a review. In *Avian migration* \(eds P. Berthold, E. Gwinner & E. Sonnenschein\), pp.](#)
341 [155–171. Berlin/Heidelberg, Germany; New York, NY: Springer.](#)

342 [Kokko H \(1999\) Competition for early arrival in migratory birds. J Anim Ecol 68:940–950. doi:](#)
343 [10.1046/j.1365-2656.1999.00343.x](#)

344 [Morganti M, Mellone U, Bogliani G, et al \(2011\) Flexible tuning of departure decisions in response](#)
345 [to weather in black redstarts *Phoenicurus ochruros* migrating across the Mediterranean Sea. J](#)
346 [Avian Biol 42:323–334. doi: 10.1111/j.1600-048X.2011.05331.x](#)

347 [Naumann JA \(1795–1817\) Naturgeschichte der Land- und Wasser-Vögel des nördlichen](#)
348 [Deutschlands und angränzender Länder. Köthen, Germany: Aue.](#)

349 [Nikolay Titov \(1999\) Fat level and temporal pattern of diurnal movements of Robins \(*Erithacus*](#)
350 [rubecula\) at an autumn stopover site. Avian Ecol Behav 2:89-99.](#)

351 [Ottich I, Dierschke V \(2003\) Exploitation of resources modulates stopover behaviour of passerine](#)
352 [migrants. J Ornithol 144:307-313](#)

353 [Ramenofsky M, et al \(2003\) Migratory Behavior: New Insights from Captive Studies. In *Avian*](#)
354 [migration](#) (eds Berthold P, Gwinner E, Sonnenschein E), pp. 97-111. Berlin/Heidelberg,
355 [Germany; New York, NY: Springer. doi: 10.1007/978-3-662-05957-9Spina F, Volponi S](#)

356 (2008) Atlante della Migrazione degli Uccelli in Italia. 2. Passeriformi. Ministero
357 dell'Ambiente e della Tutela del Territorio e del Mare, Istituto Superiore per la Protezione e la
358 Ricerca Ambientale (ISPRA). Tipografia SCR-Roma. 632 pp.

359 [Yong W, Moore FR \(1993\) Relation between migratory activity and energetic condition among](#)
360 [thrushes \(Turdinae\) following passage across the Gulf-of-Mexico. Condor 95, 934–943.](#)
361 [doi:10.2307/1369429](#)