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Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines

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During migration, a number of bird species rely on stopover sites for resting and feeding before and after crossing ecological barriers such as deserts or seas. The duration of a stopover depends on the combined effects of environmental factors, endogenous programmes and physiological conditions. Previous studies indicated that lean birds prolong their refuelling stopover compared with fat birds; however, the quantitative relationship between physiological conditions and stopover behaviour has not been studied yet. Here, we tested in a large sample of free-living birds of three European passerines (whinchats, *Saxicola rubetra*, garden warblers, *Sylvia borin* and whitethroats, *Sylvia communis*) whether the amount of migratory restlessness (Zugunruhe) shown at a stopover site depends on physiological conditions. An integrated measure of condition based on body mass, amount of subcutaneous fat and thickness of pectoral muscles strongly predicted the intensity of Zugunruhe shown in recording cages in the night following capture. These results provide novel and robust quantitative evidence in support of the hypothesis that the amount of energy reserves plays a major role in determining the stopover duration in migratory birds.

Keywords: bird; migration; stopover; migratory restlessness; Zugunruhe

1. INTRODUCTION

A large number of birds migrate every year crossing areas where food and water are not available or unpredictable such as seas and deserts. After crossing these areas, birds would have substantially reduced their energy reserves and might need to stop and refuel. The duration of a stopover is influenced by a series of factors including weather conditions, endogenous programmes and the physiological condition of the individuals at arrival (reviewed by Jenni & Schaub 2003). Birds with a large amount of fat reserves usually leave the stopover site on the evening of the arrival day, whereas birds with depleted reserves might interrupt migration for a period ranging from one day to several weeks (Bairlein 1985; Biebach 1985; Biebach *et al.* 1986). Despite the number of theories proposed to explain stopover duration, fuel load and migration speed (Alerstam & Lindström 1990; reviewed by Hedenstrom 2008), quantitative empirical evidence for stopover duration being related to body condition is scarce. Previous studies employed mathematical models to estimate stopover time from repeated captures of the same individuals. However, recent work, has suggested that such estimates of stopover duration might provide incorrect results because they do not take into account the different mobility—and thus likelihood of capture—of fat and lean birds (Salewski & Schaub 2007). When this factor was introduced into a model, there was no correlation between fat at first capture and (estimated) stopover duration (Salewski & Schaub 2007).

In nocturnal migrants, the extent of migratory disposition is shown in captivity by the intensity of nocturnal restlessness or Zugunruhe (Naumann 1795–1817). The duration and intensity of Zugunruhe in captive birds correlate with the duration and intensity of migration of birds of the same population in nature (Berthold 1973). In one of the early field studies with garden warblers (*Sylvia borin*), it was noted that heavier birds showed low activity during the day and intense Zugunruhe, whereas leaner birds showed the opposite pattern (Bairlein 1985). These observations suggested the hypothesis that lean individuals would stop to refuel upon reaching a suitable site, whereas individuals in good conditions would leave the following night (Biebach 1985). This hypothesis was further supported by laboratory studies in which we simulated a long migratory flight by depriving birds of food for two days, and a refuelling stopover by subsequently re-administering food. Such a food regime induces a temporary interruption of Zugunruhe in captive garden warblers and blackcaps (*Sylvia atricapilla*) on the night following food reintroduction (Biebach 1985; Gwinner *et al.* 1985, 1988; Fusani & Gwinner 2004, 2005). We found that the intensity of the response to the food deprivation–refeeding protocol was correlated with body condition as measured by the amount of fat reserves and body mass (Fusani & Gwinner 2004).

Here, we studied whether condition predicts the amount of Zugunruhe in free-living birds of three passerine species during their northward spring migration. After recording body mass and amount of fat and muscle reserves, the birds were set in custom-built cages for activity recording for one night and released the following morning. Our results show that the physiological condition of the birds predicts the intensity of Zugunruhe in all three species.

2. MATERIAL AND METHODS

The study was conducted in Ponza (Italy), a small island in the Tyrrhenian Sea (40°55′ N, 12°58′ E) located along one of the main Mediterranean migratory routes. A ringing station, directed by M.C., has been active on the island since 2002. We used 75 (unsexed) garden warblers, 70 male whitethroats (*Sylvia communis*) and 34 male whinchats (*Saxicola rubetra*), caught with mist-nets during ringing operations between 15 April 2006 and 18 May 2007. Birds were caught before 11.00 and a single observer (M.C.)

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Table 1. Correlations between Zugunruhe and physiological variables, and between Zugunruhe and the factor CONDITION extracted from the physiological variables by means of PCA.

	whinchat (34)		whitethroat (70)		garden warbler (75)	
	r	*p*-value	*r*	*p*-value	*r*	*p*-value
muscle score (Spearman)	0.257	n.s.	0.192	n.s.	0.323	<0.005
fat score (Spearman)	0.342	<0.05	0.379	<0.001	0.651	<0.001
body mass (Pearson)	0.470	<0.005	0.423	<0.001	0.526	<0.001
CONDITION (Pearson)	0.474	<0.005	0.403	<0.001	0.601	<0.001

scored subcutaneous fat on a 0–8 scale, the size of the pectoral muscles on a 0–3 scale and measured the body mass (Bairlein 1994). By 12.00, birds were placed in individual fabric cages so that they were visually isolated from each other. Each cage was equipped with an infrared activity sensor connected with an activity recorder. Birds were given 10 mealworms, 20 g of a mixture of dry insect food, banana and boiled egg (Fusani & Gwinner 2004), and water ad libitum. The room received natural illumination through a large door. All birds were released the following morning after 07.00.

We calculated the number of times the infrared sensor was activated for each 10 min period. From these values, we calculated the average activity during the intervals 13.00–19.30 (day activity) and 19.30–04.30 (Zugunruhe) based on civil twilight times (Greenwich mean time+1) on 1 May in Ponza. Some of the birds were used as controls in other experiments, which will be reported elsewhere, and were handled for measurements at 24.00; therefore, for these birds, the activity after 24.00 was excluded from the analyses. Data were log transformed to correct for deviations from normality. We calculated then the correlations between Zugunruhe, physiological measures and an index of body condition extracted by applying principal component analysis (PCA) to body mass, fat score and muscle score (see §3). All statistical analyses were performed with SPSS v. 11.0 (SPSS, Inc.).

3. RESULTS

Correlations between Zugunruhe and physiological variables are reported in table 1. In all species, fat and body mass were positively correlated with the intensity of Zugunruhe. In garden warblers, the muscle score was also positively correlated with Zugunruhe. For each species, we extracted by means of PCA, a single component from the variables fat score, muscle score and body mass, which we named CONDITION. In garden warblers, CONDITION (eigenvalue=2.109) explained 70.3 per cent of the total variance, and its loadings (correlation with each variable) were as follows: body mass, 0.860; fat, 0.856; and muscle, 0.798. In whinchats, CONDITION (eigenvalue=2.414) explained 80.5 per cent of the variance, and its loadings were as follows: body mass, 0.923; fat, 0.903; and muscle, 0.864. In whitethroats, CONDITION (eigenvalue=2.088) explained 69.6 per cent of the variance, and its loadings were as follows: body mass, 0.862; fat 0.931; and muscle, 0.691. In all species, CONDITION was positively correlated with the amount of Zugunruhe (table 1; figure 1). The amount of diurnal activity (12.00–19.30) was negatively correlated with CONDITION in garden warblers ($r_P=-0.402$, $n=75$, $p<0.0001$), whereas in whinchat and whitethroat, the correlation was not significant (respectively: $r_P=-0.119$, $n=42$, $p=0.501$; $r_P=-0.184$, $n=80$, $p=0.128$).

The results suggested that the variability of Zugunruhe is higher for birds in worse conditions (figure 1). As the fat score is an ordinal variable, we calculated the CV of Zugunruhe for each fat category, separately for each species (figure 2). In all species, CV Zugunruhe was negatively correlated with the fat score (garden warblers: $r_S=-0.886$, $p=0.019$; whitethroats: $r_S=-0.829$, $p=0.042$; whinchats: $r_S=-0.900$, $p=0.037$).

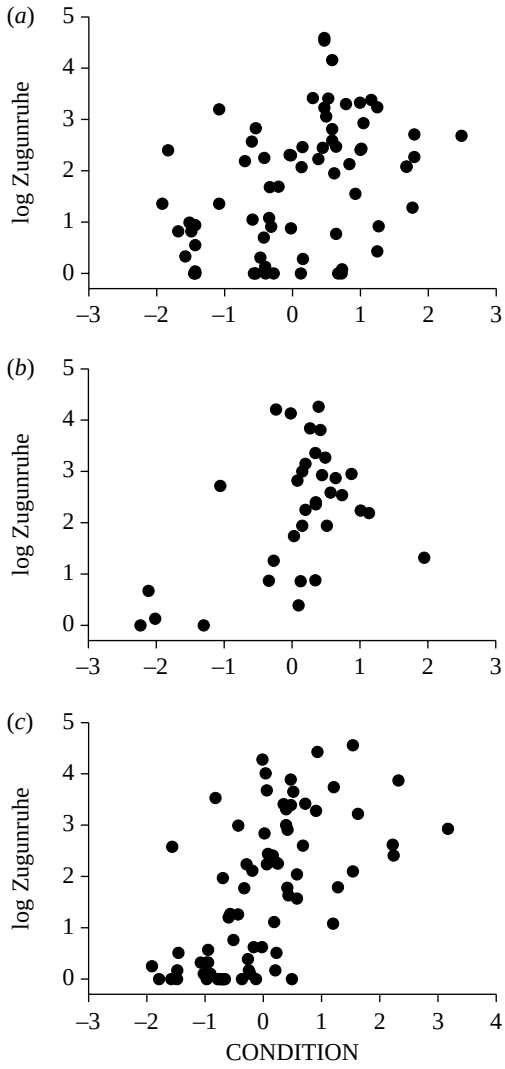

Figure 1. Scatterplots of log-transformed Zugunruhe intensity versus the principal component CONDITION extracted from muscle score, fat score and body mass for (*a*) whitethroat, (*b*) whinchat and (*c*) garden warbler. In all three species, Zugunruhe and CONDITION were positively correlated.

4. DISCUSSION

Our results show that measures of body condition correlate positively with the intensity of Zugunruhe

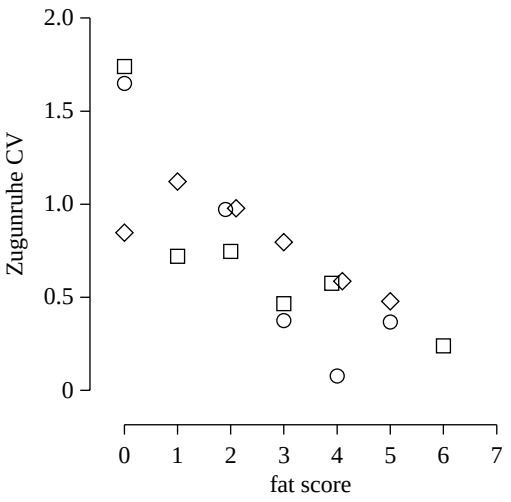

Figure 2. Scatterplot of the coefficient of variation (CV) of Zugunruhe versus the fat score. The two variables were negatively correlated in all species. Squares, garden warbler; circles, whinchat; diamonds, whitethroat.

recorded in cages in three species of wild migratory passerines caught at a spring stopover site. In all species, a single factor—that we named CONDITION—extracted by PCA of body mass, fat and muscle was strongly correlated with these three variables, and was negatively correlated with Zugunruhe. Thus, we conclude that a good measure of migratory state, Zugunruhe, is predicted by the condition of the birds. These data provide novel quantitative evidence in support of the original hypothesis that the amount of reserves at arrival determines the duration of the stopover (Bairlein 1985; Biebach 1985).

External factors such as weather conditions, predation risk and food availability, and internal factors such as energy reserves and endogenous programmes, influence the decision of staying at or leaving a stopover site (reviewed by Jenni & Schaub 2003 and Hedenstrom 2008). In spring, arriving earlier at the breeding grounds may increase reproductive success through acquisition of good territories or early mating (Kokko 1999). Thus, a migratory strategy that does not depend on energy reserves might be advantageous in spring because the risk of departing before having fully refuelled would be compensated for by the advantages of early arrival at the breeding sites (Salewski & Schaub 2007). The results of the present study, however, suggest that migratory behaviour is finely modulated by the condition of the animals. The interpretation of our results does not require determining or assuming whether the birds had arrived at the island on the same day of capture or earlier: the relationship between body condition and Zugunruhe may translate in nature to the likelihood of departing for each individual bird. Other factors, in particular the weather conditions, will then influence the final decision—to stay or to leave.

A candidate factor for regulation of migratory behaviour is melatonin, which is increased in blackcaps that interrupt Zugunruhe in response to food deprivation and subsequent refeeding (Fusani & Gwinner 2004, 2005). Alternatively, hormonal factors such as leptin released by the adipose tissue might act on receptors in specific brain areas to modulate stopover behaviour. Unfortunately, the existence of an avian leptin has been questioned recently (Sharp *et al.* 2008), and preliminary experiments in which birds were injected with 'avian' recombinant leptin showed no effects (W. Goymann & L. Fusani 2008, unpublished data). Nevertheless, the negative correlation between fat score and variability of Zugunruhe suggests that fat deposits play an important role in determining the duration of the stopover.

In garden warblers, day activity was negatively correlated with body condition. This confirms previous reports of a lower diurnal activity of fat birds at stopover sites (Bairlein 1985; Yong & Moore 1993), which could reflect a trade-off between refuelling needs and predation risk (Hedenstrom 2008). Interestingly, such a negative correlation was found only for garden warblers, whereas the positive correlation between nocturnal activity and physiological conditions was strong for all three species studied.

In conclusion, our study renders strong support to the hypothesis that the migratory strategy of small passerines is influenced by their physiological condition. Unlike previous results derived from capture–recapture studies, which may have been biased due to differences in mobility between fat and lean birds (Salewski & Schaub 2007), our results are based on direct behavioural measures of nocturnal activity and hence independent of such a potential methodological bias.

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