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ORIGINAL PAPER

Influence of body condition and weather on departures of first-year European robins, *Erithacus rubecula*, from an autumn migratory stopover site

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Abstract How migratory birds decide when to leave a stopover site is important to the understanding of bird migration strategies. Our study looks at how body condition and the weather affect the decision to depart on nocturnal migratory flight. During two autumn migration seasons (2002–2003), we radio tracked 51 first-year European robins, *Erithacus rubecula*, at a stopover site on the Courish Spit (Eastern Baltic) from the first day after landing until their migratory departure. The tagged robins stopped over for 1–14 days. There was no clear relationship between stopover duration and energetic condition on arrival. Weather conditions (wind, precipitation, and cloud cover) on departure differed measurably between years. In 2002, robins took off mainly under following winds and clear skies. In 2003, there were mainly light head winds and partially cloudy or overcast skies. This could be explained by the year-specific role of weather factors in making the decision to depart. In both years, robins making short (1–2 days) stopovers took off in more varied weather situations than those individuals with long stopovers. This suggests that robins from the former group were more inclined to continue with migration than longer-stay birds that, apart from re-fuelling, could be waiting for favourable weather. The lack of a relationship between stopover duration and body condition and some departures under unfavourable weather conditions suggest that endogenous spatiotemporal programmes may play an important role in controlling stopover duration in robins.

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Introduction

In most cases, birds organise their migrations between breeding and wintering grounds in a repeated pattern of flight and stopover. Because most of the time is spent at the stopover sites (Hedenström and Alerstam 1997; Wikelski et al. 2003), the study of stopover behaviour is important to understand avian migratory strategies. A crucial focus of the study is on the decision by birds as to where and when to start a stopover period and when to end it (Alerstam and Lindström 1990; Weber et al. 1998; Jenni and Schaub 2003; Chernetsov 2003).

Many studies based on mist netting showed that a significant proportion of migrating passerines disappear from stopover sites during the first day/night after arrival. This suggestion is based on the low proportion of recaptures in the days after initial capture: 5.9–9.3% (Rappole and Warner 1976), 7–10% (Pettersson and Hasselquist 1985), 15% (Loria and Moore 1990), 3–12.2% (Kuenzi et al. 1991), 6.5% (Zimin 2003); and on estimates inferred from capture–mark–recapture statistics (Titov and Chernetsov 1999).

There are several suppositions explaining why the majority of birds leave the stopover site after a short time. Rappole and Warner (1976) suggested that such a pattern could be due to the dynamic between the two main physiological conditions in birds during migration: flight and energy accumulation. Most birds present at stopover at any given moment are, potentially, physiologically ready for flight and, hence, have a high motivation to continue with migration. This group of birds stops over for just 1 or 2 days, irrespective of stopover conditions. The second, much smaller, group consists of individuals that aim to make longer stopovers and to refuel. It is assumed that they develop a physiological capacity for energy accumulation, which is reflected in their behaviour. This group apparently shows rigid habitat quality requirements and display competitive behaviour towards other individuals (Rappole and Warner 1976; Dierschke and Delingat 2001). Furthermore, it is possible that a proportion of birds is forced to continue migration or to search for another place for stopover due to competition for food, shelter etc.

However, factors affecting the departure decision are still poorly understood. Optimal migration theory predicts that this decision is influenced by the migrants' actual body condition and re-fuelling possibilities (Alerstam and Lindström 1990; Houston 1998). It is hypothesised that the birds may need up to 2 days to assess habitat quality. Because most birds disappear during the first 2 days, the predictions of optimal migration theory mainly refer to the birds making longer stopovers. It is widely assumed that weather, mainly wind and precipitation, play a significant role in the decision to depart (Liechti and Bruderer 1998; Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Dierschke and Delingat 2001; Schaub et al. 2004). It has also been suggested that endogenous spatiotemporal programmes may, to a great extent, govern migratory behaviour, including stopover duration (Safriel and Lavee 1988; Jenni and Schaub 2003). A spatiotemporal programme is a complex interaction of circannual and circadian rhythms (e.g. rhythms of body mass and migratory locomotory activity) that form the migratory disposition and govern the birds' behaviour during migration (Dolnik 1975; Gwinner 1986). Earlier, it was assumed that spatiotemporal programmes rigidly regulate such parameters of migratory behaviour as the onset, duration and termination of migratory activity. Recent findings, however, suggest that external factors could have a significant role in the realisation of these programmes (Biebach 1985; Gwinner 1996; Thorup and Rabøl 2001; Jenni and Schaub 2003).

A few studies that sought to investigate departure decisions in birds in the field used either feeding experiments (Lindström and Alerstam 1992; Fransson 1998; Dänhardt and Lindström 2001) or observations of individually marked singletons (Dierschke and Delingat 2001; Åkesson et al. 2002), or again capture–recapture analysis (Schaub et al. 2004). In most studies, the exact date of arrival and, hence, the body condition on arrival were not known, although the last parameter could greatly affect motivation to depart (Biebach et al. 1986; Titov 1999a). Some studies also assumed that the dates of last observations or last captures indicated the true date of departure. There are several observations, however, showing that birds may leave the study site, but stay in its immediate vicinity (Chernetsov and Mukhin 2006, this study). We suggest that unbiased estimates may be obtained by including only newly arrived birds into the analysis and following radio-tagged birds until departure. In such cases, we may be certain about the arrival and departure dates of the marked individuals, their body condition on arrival and the environmental conditions encountered at stopover.

We applied this methodology and analysed the role of endogenous factors (body condition) and weather conditions influencing departure on nocturnal migratory flight in first-year European robins, *Erithacus rubecula*, during the autumn migration season.

We started by analysing the relationship between body condition of robins on arrival and their stopover duration. It has been reported that the behaviour of robins after arrival at a stopover site was related to their fuel loads (Titov 1999a, b, 2000). Fat birds tended to continue migrating, whereas the lean ones remained for a longer time and tried to occupy a temporary home range and to refuel. We tested the hypothesis that, among robins that stop over for 1–2 days, a significant proportion were fat birds likely to continue migrating and that, among birds making longer stopovers, birds with depleted fuel stores prevailed. The threshold of 2 days was selected because, at our study site, robins either occupy small defined stopover areas or continue migration within a maximum of 2 days (Titov 1999b; Chernetsov 2005; Chernetsov and Mukhin 2006).

Secondly, we analysed weather conditions on departure. We tried to find out whether take-offs after stopovers of varying duration occurred under different weather conditions. The weather conditions vary from year to year, and the number of nights with favourable weather for migratory flight may differ markedly (Liechti and Bruderer 1998). We assume that, in situations with prolonged periods of unfavourable weather, birds could be forced to continue migrating despite the weather. Taking this and annual differences in weather dynamics into account, we might expect different reactions in different years. Therefore, we always considered weather condition separately for each year.

The European robin is a medium-distance migrant in which flight stages and migratory stopovers are clearly separated. The distance of diurnal movements after landing usually does not exceed 1.5 km (Chernetsov 2005, Tsvey, unpublished data). Birds that make prolonged stopovers occupy defined stopover areas (Mehlum 1983a, b; Titov 1999b; Chernetsov 2005; Chernetsov and Mukhin 2006). These birds gain weight at a higher rate than individuals that fail to occupy a small home range (Titov 1999b). This makes the robin a good model species for studying decision-making in migratory departures (Dänhardt and Lindström 2001; Schaub et al. 2004).

Materials and methods

The study was carried out in autumn 2002 and 2003 on the Courish Spit on the Eastern Baltic coast, at the Biological Station Rybachy (55°09′N, 20°51′E). The field site includes patches of wood- and marshland habitat on the shore of the Courish Lagoon, surrounded by an unimproved agricultural (and partly afforested) landscape. The vegetation consists mainly of reed (*Phragmites communis*) and willow (*Salix* spp.); some large trees are also present. The European robin is a common nocturnal migrant that makes stopovers at the study site.

We studied the stopover behaviour of first-year European robins during autumn migration by radio tracking. We made every effort to fit transmitters only to birds with a known arrival date. The numbers of daily captures of small passerines at our study site, including those of European robins, is strongly variable (migration waves), as at many other coastal sites (Dolnik 1975; Titov and Chernetsov 1999; Chernetsov and Titov 2000). It has been shown by capture–mark–recapture analyses done at the same study site that the vast majority of European robins, initially captured in a standardised-effort mist-netting project on days when many new birds are ringed and after a day with low numbers of newly marked individuals, have indeed just arrived (Titov and Chernetsov 1999; Chernetsov and Titov 2000). Therefore, we only tagged the birds that were initially captured within the framework of the same standardised project on the morning of the first day of a migration wave. In 2002, most birds were radio tagged when recaptured in the afternoon of the day of initial capture; four individuals were tagged on the second and, in one case, on the fourth day after first capture. In 2003, most transmitters were fitted at first capture, i.e. in the morning soon after arrival. All birds, radio tagged at first capture or at recapture, were initially captured on the first day of a wave of arrivals. A stopover length of 1 day means that a bird has landed in the morning and departed during the following night, i.e. stayed for one daylight period.

The second selection criterion for radio tagging was the body condition of the robins. The birds tagged were either lean (body mass at arrival exceeded the size-specific lean mass by 0.5 g at maximum) or fat (arrival body mass exceeded the size-specific lean mass by at least 2.0 g). Size-specific lean mass was found from the linear regression of body mass (m_0) on the wing length (w) of robins captured in the autumn of 1994–2003 at the study site with a fat score of 0 (Kaiser 1993). The regression equation was $m_0=2.097175+0.180902\cdot w$ ($n=5348$; $R^2=0.14$, $p<0.001$). The difference between the actual body mass and the size-specific lean body mass was assumed to be the fuel load. In further calculations, the fuel load relative to the lean body mass was used.

We used LB-2N transmitters (Holohil Systems, Ontario, Canada) that have a life span of 21 days. Tags were fitted as backpacks with a Rappole harness (Rappole and Tipton 1991); the weight of a tag with harness was 0.49 g, which constitutes less than 5% of added mass—the upper permissible limit (Caccamise and Hedin 1985). We used receivers from Wildlife Materials® and Advanced Telemetry Systems® with Yagi antennae. Detection range at ground level was ca. 0.5 km and from an elevated point (e.g. the roof of the station building) at least 1 km. The radio-tagged European robins were surveyed once per hour during the daytime and continuously during the nighttime until their departure from the stopover site. During the daytime, every effort was made to look for birds likely to leave the immediate study area in the course of their daytime movements. Not a single bird was lost during the daytime (Chernetsov and Mukhin 2006). On the mornings subsequent to their departures, the tagged birds were searched for up to a limit of several kilometres from the departure site.

A total of 69 European robins were fitted with transmitters: 31 in 2002, between 2nd September and 17th October; and 38 in 2003, between 6th September and 20th October. All individuals were in their first year with completed juvenile moult. The nocturnal departure of 51 birds was directly observed; therefore, their exact stopover duration was known. One bird lost its tag, one was predated, two birds did not resume migration until the transmitters stopped working, and three birds left the study area during diurnal movements. Eight birds disappeared during morning twilight, so that their behaviour may not refer to departures for migratory flights. Finally, in three cases, the exact hour of departure remained unknown. All these birds were excluded from further analysis.

The weather parameters considered were wind, precipitation and cloud cover, as they have a serious influence on onward migration (Richardson 1978, 1990; Erni et al. 2002; Dierschke and Delingat 2001; Schaub et al. 2004). Wind conditions during take-off nights were characterised through the tailwind component (TWC, following Åkesson and Hedenström 2000). This parameter is measured in meters per second and was calculated as $V_w\times\cos(\varphi_t-\varphi_w)$, where V_w stands for wind speed, φ_t for the mean migratory direction of European robins on the Courish Spit in autumn, and φ_w for wind direction. Long-distance recoveries of European robins ringed on the Courish Spit during autumn passage and re-encountered on migration or in winter quarters before 1st November of the same year suggest the mean migratory direction of 230°. Wind measurements at the weather station at Rybachy at 15 m a.g.l. at 00:00 local time were analysed. Positive TWC suggests wind conditions favouring flights, i.e. following or side-following winds. Negative values indicate winds opposing migration in the preferred direction. TWC equal to zero means still air or a wind exactly perpendicular to the migratory direction. We have checked all the situations with very small TWC values. In our study, only one situation occurred when rather a strong side wind (330°, 4.7 m/s) resulted in a comparatively small TWC value (0.8). In the range of TWC values from −1 to 1, the mean wind speed was 1.0±1.0 (SD) m/s. Therefore, we conclude that, in our study, small TWC values correspond to weak winds and that extreme values correspond to rather strong following or head winds. It should be noted that robins took off mainly in weak wind conditions [limit, 0–5.2 m/s; on average, 2.3±1.5 (SD) m/s]. We used wind measurements at ground level, as we assumed that birds on the ground are not able to measure the wind situation at flight altitudes. This assumption is supported by our observations of the behaviour of departing robins.

Cloud cover and precipitation were recorded during each hour of the night. The overall cloud cover score across the night was used in the analysis: 0, generally clear night; 1, cloud cover varies between 10 and 100% given that, before departure, some stars were visible for at least 1 h; and 2, overcast during the whole night. Rain was scored as either 0 (no rain before departure) or 1 (at least some rain before departure).

Results

Stopover duration

Stopover duration of radio-tagged robins varied between 1 and 14 days (mean, 3.6±4.0 (SD) days; median, 2 days; n=51; Fig. 1). Most birds (32 out of 51, 62.7%) stopped over for 1–2 days. The frequency distribution of stopover durations did not differ significantly between 2002 and 2003 (Kolmogorov–Smirnov test, p>0.1).

Relationship between stopover duration and body condition

We radio-tagged 28 lean robins [14 in 2002 and 14 in 2003; mean fuel load, 1.6±1.7% (SD) of their lean body mass; range, −4.4 to 4.5%] and 23 fat ones [8 in 2002 and 15 in 2003; mean fuel load, 15.8±3.8% (SD); range, 9.9 to 24.6%].

We found no relationship between log-transformed stopover duration and fuel load at arrival (Pearson correlation, r=0.01, p=0.94, n=51; Fig. 2). We used log-transformation to normalise the distribution of stopover duration (Fig. 1). The proportion of fat birds did not differ between robins stopping over for a short time (1–2 days) and those making longer stopovers (χ^2=0.83, df=1, p=0.36).

In situations when several birds had arrived during the same night and were radio tagged in the course of one morning, it was possible to make a separate analysis of the relationships within the group between stopover duration and their arrival body condition. On 29th September, 6th and 20th October, 2003, we tagged 5, 6 and 7 individuals, respectively. In none of them did we find a significant relationship between stopover duration and body condition at arrival (Pearson correlation, 29.09.03, r=0.54, p=0.344; 06.10.03, r=−0.16, p=0.76; 20.10.03, r=−0.25, p=0.59; Fig. 2). The medium-size correlation in the first case is an artefact as the range of stopover durations was between 1 and 2 days (Fig. 2).

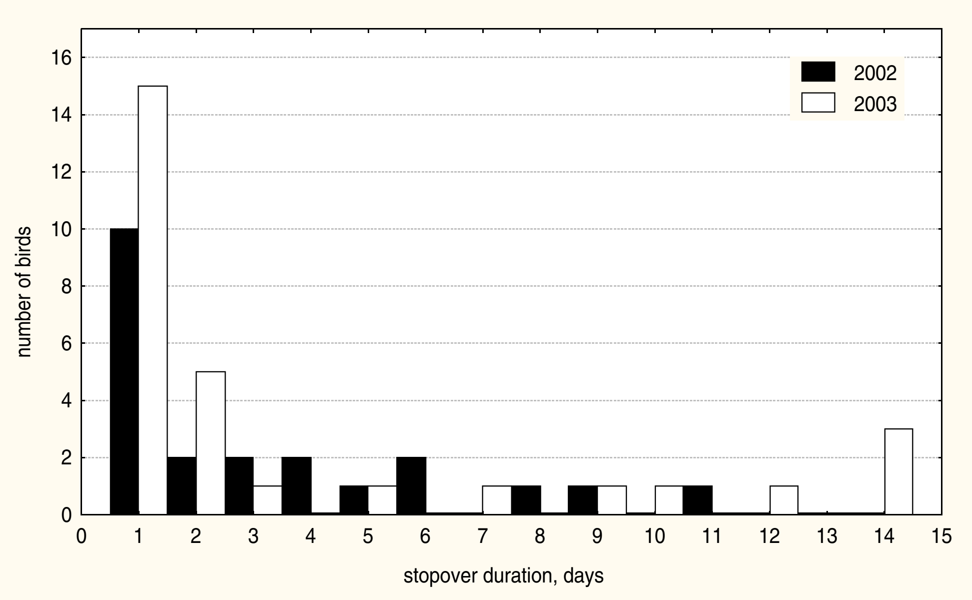

Fig. 1 Stopover duration in radio-tagged juvenile European robins in autumn 2002–2003

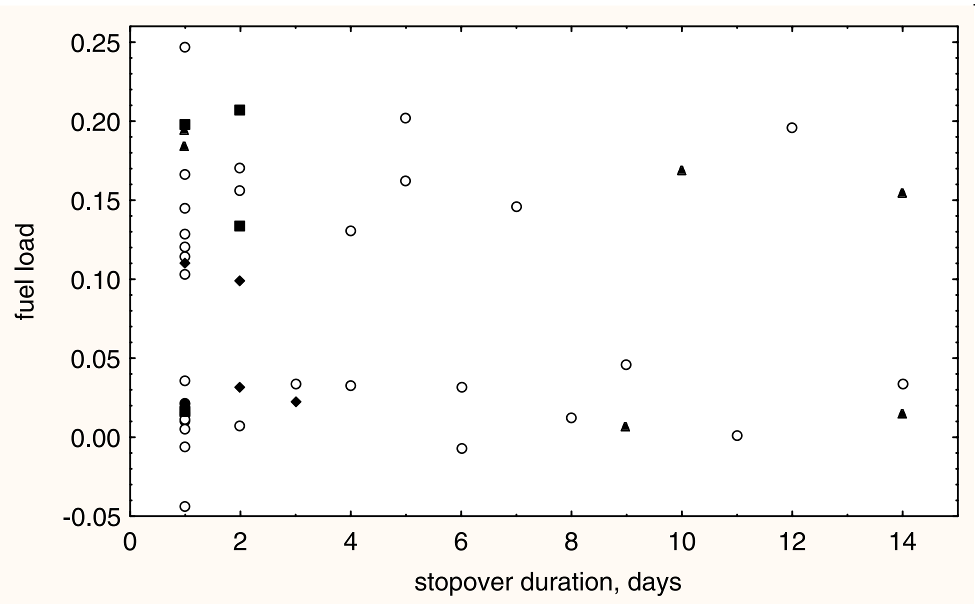

Fig. 2 Relationship between stopover duration and arrival body condition. Arrival body condition is expressed as proportion relative to lean body mass. The data pooled for all robins are shown (*open circles*), and three cases when more then four individuals were tagged in one morning: 29.09.06, n=5 (*filled squares*); 06.10.06, n=6 (*filled diamonds*); and 20.10.06, n=7 (*filled triangles*)

Weather conditions at departure nights

Wind

On average across both years, European robins departed on nights with weak tailwinds: TWC=0.31±2.16 (SD); n=51. In 2002, they took off under significantly more favourable wind conditions than in 2003: in 2002, TWC=1.2±1.93 (SD); n=22; in 2003, TWC=−0.36±2.7 (SD); n=29; t test, t=2.7, p=0.009. This was due to the overall difference in wind conditions between the years. In 2002, the proportion of nights with following winds or still air was 54.4%, whereas in 2003, it was just 36.8% (χ^2=4.3; df=1, p=0.039).

When both years are considered together, wind conditions under which robins took off after 1- to 2-day stopover and after longer stopovers, probably with refuelling, did not differ (Table 1). However, if the data for each year are analysed separately, in each year, departures after short stopovers took place under a broader range of conditions than after long stopovers (Table 1). Besides, in 2002, departures after long stopovers more frequently occurred under good wind conditions (Table 1). The lack of difference in mean wind conditions between shortly staying birds and birds with longer stopovers in 2003 was probably due to generally poorer wind conditions during that particular migration season.

We also analysed the relationship between body condition on arrival and the wind condition on the departure of the robins that only remained for a short stopover. Wind conditions at take-off did not differ between fat and lean individuals (2002 TWC, lean=0.18±2.24 (SD), n=6; fat=0.35±1.74 (SD), n=6; Mann–Whitney U test, z=−0.16, p=0.87; 2003 TWC, lean=−0.97±2.51 (SD), n=10; fat=0.76±2.33 (SD), n=10; Mann–Whitney U test, z=−1.70, p=0.09). We did not test for differences in birds departing after long stopovers, as their body condition might have changed in the interval.

Precipitation

Most robins (71%) departed on nights without precipitation. The proportion of take-offs during rain did not differ significantly between birds departing after short stopovers (11 out of 32, 34.4%) and those leaving after longer periods

Table 1 Mean tailwind component on nights of migratory departures after short and long stopovers

Stopover duration	1–2 days			>2 days			Significance			
	Mean	SD	*n*	Mean	SD	*n*	t test		*F* test	
							t	*p*	*F*	*p*
Both years together	0.03	2.29	32	0.77	1.89	19	1.19	0.24	1.46	0.40
2002	0.27	1.91	12	2.31	0.92	10	3.18	0.006	4.33	0.04
2003	−0.11	2.52	20	−0.93	0.92	9	0.95	0.35	7.44	0.007

T test indicates the significance of differences between means, *F* test for equality of variances—between standard deviation, respectively.

Table 2 Number of take-offs of European robins after stopovers of different duration under different cloud cover

Stopover duration	1–2 days			>2 days			Significance		
	Cloud cover score			Cloud cover score			χ^2	*df*	*p*
	0	1	2	0	1	2			
Both years together	5	14	13	9	3	7	7.22	2	0.027
2002	2	3	7	7	1	2	6.43	2	0.04
2003	3	11	6	2	2	5	2.74	2	0.25

(4 out of 19, 21.1%; χ^2=1.02, *df*=1, *p*=0.31). There was no obvious difference between the 2 years. In 2002, the proportion of European robins taking off on nights with precipitation after short stopovers (five out of 12, 41.7%) was higher than the proportion of departures on nights with precipitation after long stopovers (1 out 10, 10%; χ^2=2.76, *df*=1, *p*=0.097). The difference is not significant, possibly due to a small sample size. In 2003, the proportions of departures on rainy nights were similar after both long and short stopovers [six birds (30%) and three birds (33.3%), respectively; χ^2=0.03, *df*=1, *p*=0.86).

Cloud cover

More than one half of the individuals (61%) took off under clear skies or with little cloud cover (cloud scores, 0 and 1), but some (39%) departed under complete overcast (cloud score, 2). Over the 2 years, the proportion of departures under overcast conditions after 1- to 2-day stopovers (40.6%) did not differ from the similar proportion after longer stopovers (36.8%, Table 2). The observed significant difference in the number of take-offs under different cloud conditions between short-stay robins and birds with longer stopovers was due to the difference between the proportions of take-offs under clear and partly clouded skies. There was a difference between the two study years. In 2002, seven birds departed under overcast conditions after short stopovers (58.3% of all individuals taking off after 1–2 days), whereas just two birds departed under overcast skies after prolonged stopovers, probably with re-fuelling (20% of all departures after long stopovers); the difference is statistically significant (Table 2). In 2003, this difference was not significant (Table 2). It should also be noted that, in 2002, a larger proportion of birds (41% of all departures) took off under clear skies than in 2003 (17%; χ^2=5.25, *df*=2, *p*=0.072). Cloud cover conditions did not differ between the years (χ^2=2.03, *df*=2, *p*=0.36).

Discussion

To study stopover duration and factors affecting decision-making in European robins, we radio tracked the birds from their arrival during migration waves until their migratory departure. We were able, in this way, to estimate some factors that could affect departure decisions.

In our study, the tagged robins remained for 1–14 days; 37% of all individuals were present for more than 2 days. This is a much higher proportion than reported in nocturnal passerine migrants (Rappole and Warner 1976; Pettersson and Hasselquist 1985; Loria and Moore 1990; Zimin 2003). Capture–mark–recapture estimates also suggest that 75–92% of European robins leave the stopover site during the first day/night after arrival (Titov and Chernetsov 1999; Chernetsov and Titov 2000). This variation could be due to differences of methodology: In 2002, we radio tagged birds at the end of the first day or on subsequent days after the first capture, i.e. the birds that had already spent at least one day on stopover and were likely to remain for re-fuelling. In 2003, most transmitters were fitted on the morning of the first day of the migration wave on first capture, and the proportion of birds stopping for 1 or 2 days was higher (Fig. 1).

Relationship between body condition and departure behaviour

The stopover duration of robins was not related to their body condition on arrival (Fig. 2): Lean birds could continue migration on the next night after arrival, and fat ones could make prolonged stopovers. This is in agreement with the data on nocturnal passerine migrants of other authors (Jenni and Schaub 2003). Among other possible explanations, it can be hypothesised that, if body condition on arrival does not govern stopover duration directly, take-off behaviour, including the decision to depart, should be controlled by the endogenous spatio-temporal programme (Safriel and Lavee 1988; Jenni and Schaub 2003). It seems plausible that an endogenous rhythm governs the behaviour of juvenile European robins that migrate for the first time and have no experience of how to behave in the changing environment.

The idea that spatio-temporal programmes could play an important role in making the decision to depart is further supported by the data on robins that were captured during the same morning and, thus, most likely have arrived at stopover site during the same, previous night (Fig. 2).

Although these birds migrated under the same conditions and experienced the same environment at stopover, their stopover durations varied. This variation was not related to their initial body condition, as was found overall. The results of experimental studies, when migratory activity and body-mass dynamics were recorded in caged migrants, also suggest the participation of an endogenous spatio-temporal programme in the regulation of the succession of flight bouts and pauses. A proportion of caged chaffinches *Fringilla coelebs* (Dolnik 1975) and garden warblers *Sylvia borin* (Bairlein 1986; Gwinner et al. 1992; Gwinner 1996) kept under constant experimental conditions showed fluctuations of body mass and the level of migratory activity: periods of high mass and activity were alternated with the periods of low body mass and low activity. Similar fluctuations were shown by a proportion of caged robins (Tsvey, unpublished data).

It should be also kept in mind that the migration of European robins generally takes place over the main ecologically favourable areas with a lot of opportunities for stopping over. Therefore, the relationship between arrival body condition and stopover duration might be less pronounced in this species than in many long-distance migrants before crossing ecological barriers (Biebach et al. 1986; Loria and Moore 1990; Sandberg 2003).

However, it cannot be ruled out that the absence of a clear relationship between body condition on first capture (and presumably on arrival) and stopover duration could be due to the effects of handling and of tagging on the robin's behaviour (e.g. stopover duration; Schwilch and Jenni 2001). Another possibility is that the duration of the previous flight, the influence of the previous experience of the individual bird at other stopover sites or the re-fuelling opportunities at the given stopover site could affect the stopover length more strongly than body condition at arrival.

Weather conditions on departure nights

Although many studies have focussed on the relationship between the weather conditions on the departure of migratory birds, the results appear to be ambiguous. Many robins initiated their nocturnal migratory flights under favourable weather conditions (slight winds, clear skies or limited overcast, no precipitation). This agrees with the results obtained in many other passerine studies based on estimating numbers aloft (Nisbet and Drury 1968; Richardson 1978, 1990; Erni et al. 2002) and results of the analysis of capture–recapture data obtained by Schaub et al. (2004). On the other hand, some robins departed into or close to a head wind, in rain and under overcast (Tables 1 and 2). Some other passerines in Europe and North America were also shown to depart not always with tailwinds (Hebrard 1971; Moore and Aborn 1996; Dierschke and Delingat 2001), or on clear nights (Cochran et al. 1967; Bolshakov and Bulyuk 1999; Dierschke and Delingat 2001). Overcast skies on departure seem not to hamper directional choice in migrants (Ottosson et al. 1990). The decision to depart under weather conditions unfavourable for flight and orientation may be explained, among other possible factors, by the role of spatio-temporal programmes in controlling migratory activity. As westerly and south-westerly winds predominate in Europe in autumn, many migrants have to fly with headwinds. In such conditions, slight head winds are rather more favourable than not (Liechti and Bruderer 1998; Erni et al. 2002). A study of autumn migratory departures of robins showed that after take-offs under moderate and strong headwinds, some birds migrated at very low altitudes and some terminated flights soon after departure (Bolshakov et al. 2007).

Weather conditions on take-offs after short (1–2 days) and long (>2 days) stopovers

The analysis of weather conditions on departure nights after stopovers of different duration showed that, after short stopovers, robins took off under a broader range of wind conditions and often under less favourable overall conditions (precipitation, cloud cover) than after prolonged stopovers. This agrees with findings from northern wheatears *Oenanthe oenanthe* that took off under stronger headwinds after 1-day stopovers than after longer stopovers (Dierschke and Delingat 2001). Departures under poorer weather after short stopovers may mean that such birds have a stronger motivation to continue migration than individuals resuming their migration after prolonged stopovers. The latter may wait for optimal flight conditions, apart from re-fuelling (Åkesson and Hedenström 2000; Dänhardt and Lindström 2001). The specific set of optimal conditions may differ between the years and depend on the overall weather dynamics during the migration season (see below).

It may be argued that departures after short stopovers under unfavourable weather conditions may be a consequence of a possible failure to occupy a territory for re-fuelling (Titov 1999b; Chernetsov and Mukhin 2006). Our results, however, show that the large variation of wind conditions during take-offs of 'transient' individuals occurred in both lean and fat birds. This suggests that transients generally had a strong motivation to depart. Unfortunately, we cannot determine the nature of this motivation (Is it a function of the realisation of an endogenous programme or of the inability to refuel?).

In some situations when adverse weather conditions prevailed for several nights in succession, in many individuals with a strong motivation to fly, migration was arrested, so they were forced to stop over for more than 1–2 days (Bolshakov and Rezvyi 1998). Such cases should probably increase the observed variation of weather conditions on departures after long stopovers. Our analysis of weather conditions at take-offs after long stopovers showed that, only in a few cases, could long stays be explained by adverse weather after arrival (Tsvey, unpublished data). Together with the narrow range of wind conditions during take-offs, this suggests that, in our study, European robins taking off after long (>2 days) stopovers were individuals initially likely to stop over for more then 1–2 days.

Some data suggest that birds with a strong motivation to continue with their migration and those tending to re-fuel may differ physiologically (Klaassen and Biebach 1994; Hume and Biebach 1996; Karasov et al. 2004). The differences are related to adaptations for flight and for re-fuelling, respectively. The transition between these states may take some time. This is indirectly confirmed by the data on body mass change after arrival at stopover: The birds do not usually start to gain mass until 1–2 days after arrival (Mehlum 1983a; Muller and Berger 1966; Schwilch and Jenni 2001), and at the end of the stopover period, their body mass remains stable for some time (Fransson 1998; Klaassen and Lindström 1996). Most physiological studies of flight and the re-fuelling process were done on long-distance migrants and refer to long non-stop flights, i.e. crossing ecological barriers. It remains open whether this difference exists in robins and how strong it is.

Interannual variation in weather conditions at departure

We found no significant difference in weather conditions on departure of robins after short (1–2 days) and long (>2 days) stopovers when the data from 2 years were taken together. However, analysis of each year separately showed a considerable variation between the years in weather conditions during passage. In 2002, due to a higher frequency of tailwinds many more robins initiated flights under favourable wind conditions than in 2003 when headwinds predominated. Apart from this, in 2002, robins that took off after long stopovers did so under significantly more favourable winds than their co-specifics departing after short stopovers. In 2003, no significant difference in the mean TWC and in the proportion of departures during nights with precipitation and overcast conditions was found between birds with short and long stopovers. The reason for this was probably that, during a protracted period of adverse weather, the birds from both groups had to initiate flights under poor conditions.

Thus, our data suggest that, firstly, weather factors may influence the decision to start a migratory flight and, secondly, the sensitivity to weather may vary between the years. When the realisation of the endogenous migratory programme was not delayed by external (weather) factors and the position of a bird on the migration route was in agreement with the inner stimuli of the migrant (with programme expectations), weather factors could play a great role (see also Jenni and Schaub 2003). Annual captures in standard mist nets show that migration occurred later in 2003 compared to 2002 [median capture dates, 23rd September 2002 (n=3186) and 1st October 2003 (n=4816); Mann–Whitney U test, z=−9.3; p<0.0001). Robins that made stopovers in 2002 could be choosy about weather conditions on departure, whereas in 2003, they took advantage of any possibility to continue with their migration due to a time deficit and the high frequency of headwinds.

Therefore, the existence of an endogenous spatio-temporal programme governing the overall schedule of flights and stopovers may explain the lack of a clear relationship between stopover duration and (1) body condition at arrival and (2) weather factors. Such a programme may also explain the existence of two motivational conditions. It should be emphasised that an endogenous spatio-temporal programme is not a rigid mechanism controlling the migratory schedule, but rather a framework within which other factors play a part in shaping the particular behaviour (Gwinner 1996). The exact set of these factors and their relative importance remain, unfortunately, obscure.

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