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# The good and the bad stopover: behaviours of migrant reed warblers at two contrasting sites

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**Abstract** Successful migration for passerine birds depends largely on the quality of stopover habitats, but we still lack complete knowledge of how migrants search for habitats en route and how they behave when landing at poor quality stopover sites. We compared the distance of exploratory movements and stopover durations of the reed warbler *Acrocephalus scirpaceus*, a reedbed habitat specialist, released at suitable (reed bed) and unsuitable (sand dune) stopover sites. Birds tape-lured during nocturnal migration to a sand dune were captured, radio-tagged, released and tracked at two sites of contrasting habitat quality. Lean birds were found to move further in the dunes (max. 300 m) than in reeds (max. 200 m), whereas ‘fat’ individuals at both sites remained stationary. Birds spent just 1 day in the dunes and up to 13 days in the reeds. Our results sug-

gest that some nocturnal migrants with restricted diurnal exploratory movements depend on stopover site selection when ceasing nocturnal flight.

**Keywords** Energy reserves · Exploratory movements · Habitat quality · Reed warbler *Acrocephalus scirpaceus* · Stopover duration

## Introduction

For most avian species, successful migration includes efficient refuelling at migratory stopovers (e.g. Berthold 1996). The theory of optimal migration assumes that decisions whether to stop or to continue migration are dependent on the fuelling rate at the current stopover site and on the fuelling rate expected at other stopover sites (Alerstam and Lindström 1990; Weber 1999; Chernetsov et al. 2004a, b). Habitat quality for food availability at stopovers is generally believed to be the main determinant of refuelling efficiency (Lindström 2003). Also, optimality models consider time and energy as important currencies of migration for birds (Alerstam and Lindström 1990; Hedenström and Alerstam 1997; Hedenström 2008); most of those currencies are spent at stopover sites (Wikelski et al. 2003). Search/settling time is a substantial component of such models and obviously contributes to stopover cost. However, little is known of how and when birds find a suitable foraging patch and make the decision to settle. The rapid discovery of good foraging habitats may be crucial for successful migration, since it decreases time and energy cost for migrants during stopover, contributing to increased speed of migration and reduced mortality during passage. Nocturnal songbird migrants are particularly constrained in their search for habitats by lack of time and information, as

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they cease flight mainly within a short time frame before dawn when visibility is limited (e.g. Bolshakov et al. 2003), and with only proximate cues available for suitable landing (Mukhin et al. 2008). They can find themselves in an unfamiliar place where they must explore their surroundings for food.

Our knowledge of how far nocturnal migrants move in search of habitat or feeding patch by day is confined to just a few studies (see Aborn and Moore 1997; Chernetsov et al. 2004a; Chernetsov 2005; Fransson et al. 2008, Paxton et al. 2008). The impact of habitat quality on the search distance has never been really studied. In most field experiments, stopover migrants are observed in 'ideal' feeding conditions, with ad libitum food supply, combined with remote weighing systems to measure fuelling rates of birds during stopover (e.g. Lindström et al. 1990; Fransson 1998; Dierschke et al. 2005; Bayly 2006; 2007). This approach has substantially advanced our understanding of stopover decisions. However, songbirds will hardly get lucky enough to find food available ad libitum at each stopover site. They are more likely to encounter environments that provide foraging conditions with limited food availability (e.g. Moore et al. 1995). In this paper, we consider this as 'back of the coin', namely the behavioural decisions of nocturnal migrants when confronted with suboptimal habitats of presumably poor foraging quality. We report the results of our field study designed to compare stopover duration and distance of exploratory movements in a nocturnal Palaearctic-African migrant, the Eurasian reed warbler *Acrocephalus scirpaceus* after landing in an suboptimal habitat (sand dunes), with birds on stopover in a habitat of higher quality (reed beds).

In this study, we compared the distances of maximal linear movements of reed warblers in unsuitable vs. suitable habitats. We expected three possible outcomes. (1) In unsuitable habitats, birds need to move longer distances in search of food than in suitable ones (e.g. Delingat and Dierschke 2000). This should occur if reed warblers landing in sand dunes get access to food slower and are more motivated to explore their surroundings than birds landing in reed beds. (2) The reverse: in suitable habitats, birds move longer distances than in unsuitable ones. If for habitat specialists, like the reed warbler, unsuitable habitats represent a behavioural barrier for movements, as suggested by Harris and Reed (2002) and Bosschieter and Goedhart (2005), they might be reluctant to make diurnal movements in such habitats. (3) In both sites, they move the same distance. The latter should occur if reed warblers have a fixed template for exploration behaviour, and distances of diurnal movements are not influenced much by external stimuli.

An important factor which may influence decision-making when searching for resources is individual physiological condition (Bell 1991). The main reason in stopping

over for passerines, the Eurasian reed warbler included, is to replenish fuel stores (e.g. Rguibi-Idrissi et al. 2003; Yosef and Chernetsov 2005). Level of fuel stores may influence motivation for exploration. We expected that motivation for feeding should be higher in lean than in fat individuals, resulting in longer exploratory movements in the former group.

We expected birds released in an unsuitable habitat to stay until the subsequent night only and birds released in the suitable habitats to make stopovers longer than 1 day. We did not expect an effect of body condition in suboptimal habitats, since stopovers for longer than 1 day are neither beneficial for 'fat' nor for 'lean' birds. However, in the suitable habitats 'lean' birds may stay for a longer time in order to build up fuel reserves, whereas 'fat' birds may leave the stopover site shortly after arrival.

## Materials and methods

**Study sites and data sampling** The study was carried out on the Courish Spit of the Baltic Sea (55°00–09' N, 20°34–51' E) in the Kaliningrad Region of Russia in August and September 2004–2007. The distance between two study sites (field stations Fringilla and Rybachy) was about 11 km (Fig. 1a).

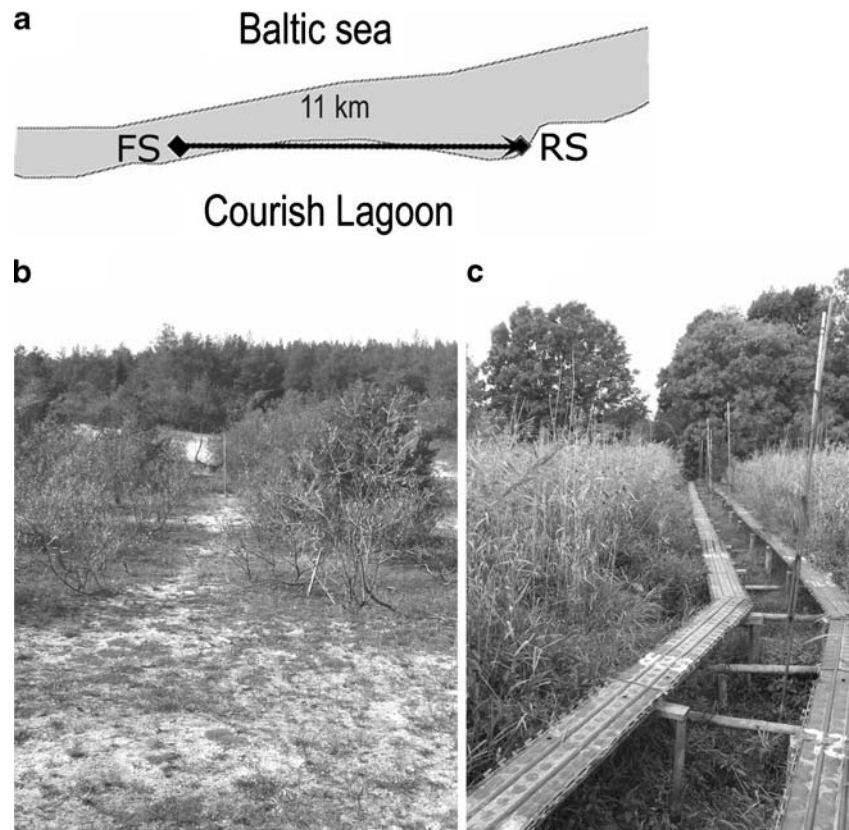
Habitats of the Fringilla field station (FS) was defined as an 'unsuitable' stopover site for the reed warbler being mostly composed of sand dunes, partly covered by dry willow scrub and pine forest with small patches of alder and birch. However, habitat patches are well connected and provide cover for the birds even at the release point (Fig. 1b). Reed warblers are not normally captured at this site which suggests that they avoid to landing here (Mukhin et al. 2008), while the nearest reed stands lie some 4 km to the southwest.

The suitable stopover site was the Rybachy field station (RS) where marsh habitats are dominated by reeds and wet willow shrub, with deciduous woodlands and rich herbaceous vegetation (Fig. 1c). Reed warblers are regularly trapped at this site in high numbers (Bolshakov et al. 2002) and retraps of ringed birds show they frequently make stopovers for several days and gain body weight here (Chernetsov 1998).

The study species, the reed warbler, is an insectivorous long-distance nocturnal passerine migrant which is one of the few migratory passerines that specializes in living in reed beds (Leisler et al. 1989), while also using them as an autumn stopover habitat in Europe (Bairlein 1983) and Asia (Gavrilov 1980).

Initially, reed warblers, while on migration at night or right after dawn, were tape-lured to mist nets by the playback of their song at the Fringilla field station study site (Herremans 1990; Schaub et al. 1999; Mukhin et al. 2008).

**Fig. 1** Study site. **a** Courish Spit. *Black diamonds* indicate study sites. In the SW—Fringilla field station (*FS*); in the NE—Rybachy field station (*RS*). **b** Tape-luring site at *FS*. **c** Trapping site at *RS*



This approach ensured us that all caught birds had just arrived at stopover and had not explored their surroundings. The birds were ringed, weighed and measured following the protocol of the international ESF project (Bairlein 1995). The length of closed wing from the carpal joint was measured to the nearest 0.5 mm, and the birds were weighed to the nearest 0.1 g. Only first-year birds which have or almost completed moulting were selected for tracking to exclude individuals which were not yet migrating, but performing post-fledging movements (Mukhin 2004; Mukhin et al. 2005).

Each bird was radio-tagged with a miniature LB-2N transmitter (Holohil Systems, Carp, ON, Canada), fitted as backpacks with a Rappole loop harness (Rappole and Tipton 1991). The weight was 0.61 g, which is below 5% of the bird's body mass and is believed to be the upper permissible limit (Caccamise and Hedin 1985; Naef-Daenzer 1993). We used receivers TRX2000S (Wildlife Materials Inc., Carbondale, IL, USA) and R2000 (Advanced Telemetry Systems, Isanti, MN, USA) with Yagi antennae. A total of 22 birds were radio-tagged on their first migration and had no prior experience of habitat quality at study sites.

**Release procedure** After radio-tagging, ten of the birds were released in the place of tape-luring near Fringilla field site (*FS*), eight birds were relocated to Rybachy field site

(*RS*) and four birds were captured at around sunrise and released in the *RS* in order to increase sample size. Birds at *FS* were released at sunrise, but at the *RS* the release time was sometimes delayed until the beginning of the third hour after sunrise due to displacement and/or tagging time (range is 80–197 min after sunrise). However, in both cases, birds were released during the time of day when exploratory movements normally take place (Moore and Aborn 2000; Chernetsov 2006).

**Tracking of birds after release** Movements of the tagged birds were continuously tracked during at least 4 h after release. In addition, the positions of the birds were checked at least once in the evening before sunset. The coordinates of the reference points from which the bearings were taken were recorded by GPS receiver Garmin E-Trex to the nearest 4–10 m. The coordinates of the birds were determined from the reference points by triangulation, using the software Locate III (Nams 2006). To identify location error, three independent observers took 30 locations of the stationary transmitter, which showed the highest concentration of calculated location points to be within the frame of the 50-m-diameter circle. Therefore, the error is estimated to be  $\pm 25$  m. The presence of all tagged birds was checked at least in the beginning of the night and early morning. As radio-tagged birds performed movements within a limited range (with one exception) and location error

was substantial, the only variable we used for analysis was the maximum linear distance (MLD) of movements from the release site. Generally, their movements were similar to the linear path, as far as could be judged with our location precision. Having covered some distance, the birds stopped and remained within a restricted area smaller than the spatial resolution of our location technique during the rest of the first stopover day.

**Data analysis** As a proxy for energy stores, a condition index was calculated as  $M/W=CI$  with  $M$  for body mass,  $W$  for wing length and  $CI$  for condition index (Winker 1995). Using this index, it was possible to take advantage of parametric statistical analysis, which is not applicable with fat scores (Benson and Winker 2005). Condition indexes correlated well with fat scores (Spearman's rank correlation,  $\rho=0.814$ ,  $p=0.000007$ ,  $n=21$ ). ANCOVA procedures were applied, with MLD as the dependent variable, sites as factors, CI as covariate and interaction term between factor and covariate. Julian date (JD) and time of release since sunrise (TS) were included as additional covariates. Fuel deposition rate may increase with progress of the season in autumn (Fransson 1998; Schaub and Jenni 2000; Bayly 2006); therefore, motivation of birds for exploration could vary with the season. Time of release ranged from 2 up to 197 min after sunrise. Time of release could potentially affect movements of birds; exploration in songbird migrants is usually more intensive in the early morning hours (Moore and Aborn 2000).

Models were compared with several possible combinations of predictors, ranging from an equation with a single predictor to the full model. We included in the set of competing models the equation without predictors, just with the intercept (the 'null' model), to justify if any measured variables influence distance moved at all (Anderson 2008). The most parsimonious model was selected, based on Akaike's information criterion corrected for small samples (AICc, Anderson 2008). The model with the lowest AICc value represents the best compromise between overfitting due to too many parameters and model bias due to too few parameters. We calculated Akaike's weights for each model. Akaike's weight is related to the likelihood that this particular model is better or worse than the others.

Weights of all models in the set sum up to 1 by definition, and candidate models with higher weights have better explanatory power compared to those with lower weights.

We used the same approach and predictors to evaluate difference in stopover duration at two stopover sites. Additionally, we used averaging of model coefficients across models with highest Akaike's weights, selected with the 'rule of thumb' ( $\Delta AICc < 2$ ; Anderson 2008).

Statistical analysis was performed with program R 2.9.0 (R Development Core Team 2009), using packages 'pgirmess' (Giraudoux 2009) and 'MuMin' (Barton 2009).

## Results

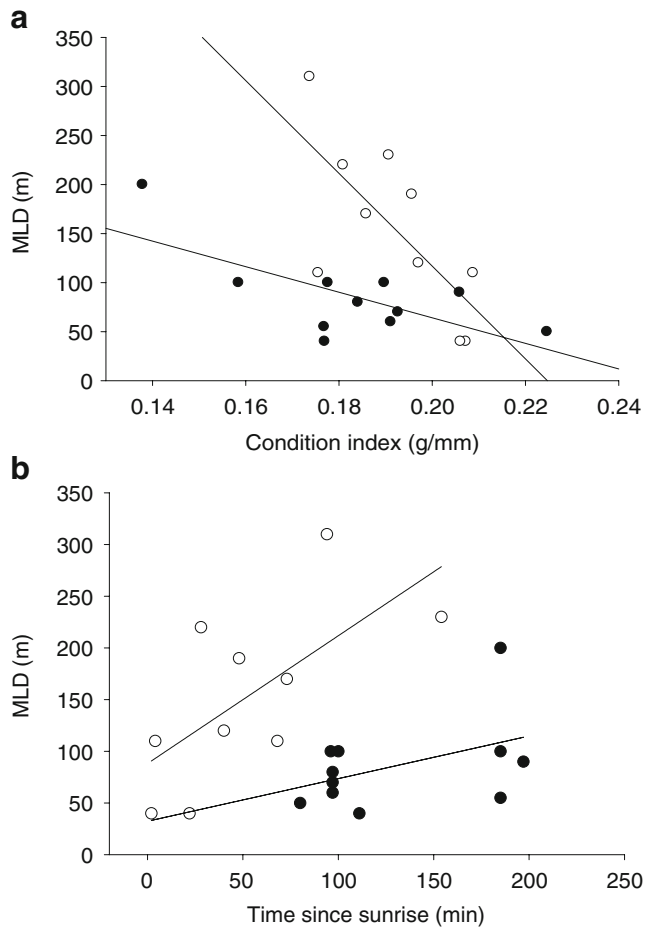
The MLD of movements was found to vary between 40 and 1,000 m ( $n=22$ ). However, there was one bird that covered 1,000 m by day. It was captured and released in RS, where the other released birds moved less than 200 m. After leaving the reed beds in RS, this bird crossed large grasslands, woodland, and 'settled' in a small reed fragment. Two days later, this individual was found 1 km away in a non-reed habitat. This individual was excluded from the analysis as due to the distance covered it was clearly an outlier. Probably the bird was local and familiar with the surroundings, still performing nocturnal post-fledging movements and consequently not yet migrating (Mukhin 2004; Mukhin et al. 2005).

In the ANCOVA test where MLD was the dependent variable, one model received the highest Akaike's weight: with condition index, site, time of release and interaction between condition and site (Table 1, adjusted  $R^2=0.66$ ,  $n=21$ ).

MLD was inversely related to CI ( $\beta=-685.3504 \pm 644.5057$ ). However, at FS, influence of CI on MLD was higher than at RS (site— $\beta=-825.0385 \pm 243.5054$ , CI  $\times$  site— $\beta=-3,663.4186 \pm 1,268.0135$ ). 'Fat' reed warblers appear to have remained practically stationary at both sites, whereas the leanest individuals covered up to 300 m in the unsuitable site (FS,  $n=10$ ) and 200 m in the suitable site (RS,  $n=11$ ; Fig. 2a). However, contrary to expectations, MLD increased with the time of release since sunrise ( $\beta=0.6123 \pm 0.2311$ ; Fig. 2b). We report coefficients, SE and

**Table 1** Models with lowest AICc values, MLD as dependent variable (top six models out of 19 are shown): the number of parameters ( $K$ ), values of Akaike's information criterion (AICc), differences in AICc values corrected for low samples ( $\Delta AICc$ ) and Akaike's weights ( $w_i$ ) are shown for each model

No.	Model terms	Log likelihood	$K$	AICc	$\Delta AICc$	$w_i$
1	CI+site+TS+site $\times$ CI	-104.1580	6	226.3160	0.00	0.64
2	CI+site+site $\times$ CI	-107.8048	5	229.6097	3.29	0.12
3	CI+site+JD+site $\times$ CI	-106.0949	6	230.1899	3.87	0.09
4	CI+site+JD+TS+site $\times$ CI	-104.1440	7	230.9034	4.59	0.06
5	CI+site+TS	-109.1528	5	232.3055	5.99	0.03
6	CI+site	-111.5264	4	233.5529	7.24	0.02



**Fig. 2** Influence of fuel reserves (condition index, **a**), time of release since sunrise (**b**) and site on the maximum linear distance of exploratory movements. *Black circles* birds released at the RS ( $n=11$ ), *white circles* birds released at the FS ( $n=10$ )

significance values for the model where CI, TS, site and site $\times$ CI are included (CI— $\beta=-685.35\pm 644.5$ ,  $p=0.3$ ; JD— $\beta=-0.61\pm 0.23$ ,  $p=0.017$ ; site— $\beta=-825.03\pm 243.5$ ,  $p=0.004$ ; site $\times$ CI— $\beta=-3,663.41\pm 1,268.01$ ,  $p=0.0107$ ). Overall, the model is significant ( $F_{4,16}=10.67$ ,  $p=0.0009$ ).

We registered the exact stopover duration for all birds from previous analysis except one. This was one of the

individuals relocated from FS to RS. The transmitter failed during the first night after tagging. Incidentally, this bird was recaptured 7 days later. Subsequently, we removed the transmitter and neither controlled the movements of this bird nor included it in the analysis of stopover duration.

All individuals in FS ( $n=10$ ), irrespective of their body condition, departed from the stopover sites during the first night. At RS ( $n=10$ ), most of the birds stayed more than 2 days at stopover site (range 1–13 days, median=4, median absolute deviation= $\pm 3.7065$ ). Among 19 models compared, three models received the highest Akaike's weights (Table 2). They all included stopover site as a factor, two included Julian date and one included condition of birds. We performed averaging of model coefficients, as recommended in cases when several competing models have similar Akaike's weights (Anderson 2008).

Averaged model include all three predictors, and we report averaged coefficient and unconditional standard errors for them. Site was included to all top models, proving that stopover site quality has a strong influence on stopover duration (site— $\beta=-5.2\pm 1.28$ ; Figs. 3 and 4). Progress of the season influenced stopover duration slightly (JD— $\beta=-0.1\pm 0.0716$ ; Fig. 3). Parameter estimate for the influence of energy reserves was smaller than associated SE (CI— $\beta=-19.7\pm 30.6$ ), showing weak evidence for importance of body condition for stopover duration (Fig. 4). In addition, we did not report averaged coefficients, SE and significance values for the model where CI, JD and site are included (CI— $\beta=-54.96\pm 33.2$ ,  $p=0.12$ ; JD— $\beta=-0.14\pm 0.05$ ,  $p=0.02$ ; site— $\beta=-5.21\pm 1.13$ ,  $p=0.0002$ ). Overall, the model is significant ( $F_{3,17}=8.914$ , adjusted  $R^2=0.54$ ,  $p=0.0009$ ).

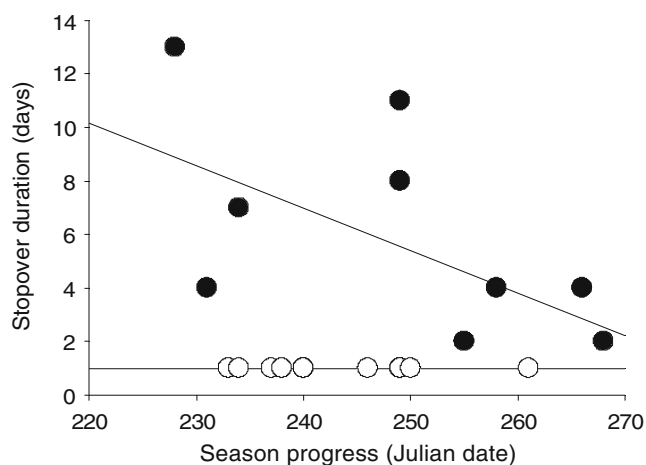
## Discussion

Our results suggest that reed warblers do not perform long-distance exploratory movements even in a habitat which is clearly suboptimal, at least when an optimal habitat is beyond their perception. Degen and Jenni (1990) reported movements of this species from a suboptimal habitat into

**Table 2** Models with lowest AICc values, stopover duration as dependent variable, data collected in the RS (top six models out of 19 are shown): the number of parameters ( $K$ ), values of Akaike's

information criterion corrected for low samples ( $AICc$ ), differences in AICc values ( $\Delta AICc$ ) and Akaike weights ( $w_i$ ) are shown for each model

No.	Model terms	Log likelihood	$K$	AICc	$\Delta AICc$	$w_i$
1	Site+JD	-48.07513	4	106.6503	0.00	0.30
2	CI+site+JD	-46.50352	5	107.0070	0.36	0.25
3	Site	-50.31384	3	108.0395	1.39	0.15
4	Site+JD+TS	-47.52685	5	109.0537	2.40	0.09
5	CI+site+JD+TS	-46.07164	6	110.1433	3.49	0.05
6	Site+TS	-49.99571	4	110.4914	3.84	0.04



**Fig. 3** Influence of progress of the season and site on stopover duration. *Black circles* birds released in the RS ( $n=10$ ), *white circles* birds released in the FS ( $n=10$ )

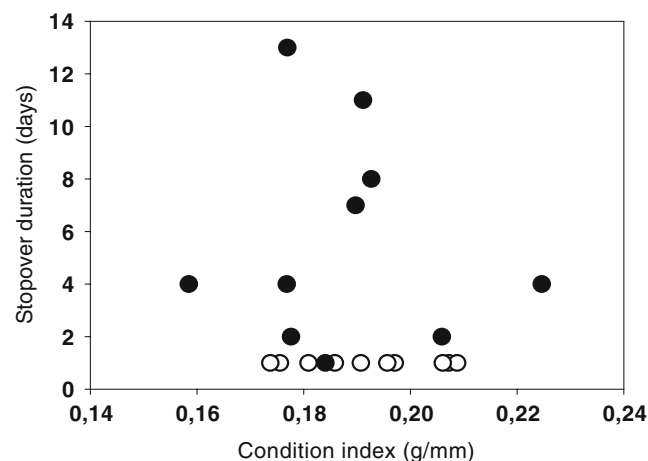
reeds, but this occurred when both habitats could be located in the close vicinity. Our results emphasise the importance of correct habitat recognition in this species when ceasing flight (Mukhin et al. 2008). In particular, it is experimentally shown that Eurasian reed warblers are generally reluctant to make diurnal movements across habitat gaps and unsuitable habitats, even though some individuals apparently move long distances over fields and woodland (Bosschieter and Goedhart 2005), as did one bird in our study. Consequently, this species is strongly dependent on its stopover decision made when ceasing nocturnal flight for finding suitable habitat and refuelling. It is safe to assume, that most of nocturnal migrants are restricted in diurnal movements by a few hundred metres (see Paxton et al. 2008 for review). The energetic cost of finding themselves in a poor (in terms of refuelling opportunities) stopover habitat patch, isolated from more profitable habitats, could be high in the abovementioned ecological group of birds since they must stay at the place where they land until the subsequent night. A previous study has shown that within landscapes with low proportion of suitable habitat cover, which correlates with high habitat isolation, nocturnal migrants may tend to lose body mass during daylight hours (Ktitorov et al. 2008).

The distance moved by the reed warblers is rather restricted compared with some other exceptional cases of small passerine nocturnal migrants radio-tagged at stopover sites. In pied flycatchers *Ficedula hypoleuca*, it may exceed 4 km; in European robins *Erithacus rubecula*, it reaches 3.5 km in exceptional cases (Chernetsov et al. 2004a, b; Chernetsov 2005). Some garden warblers (*Sylvia borin*) after tape-luring covered more than 1 km from one day to another (Fransson et al. 2008). Wilson's warblers (*Wilsonia pusilla*) in suitable riparian habitat moved up to 1.5 km (Paxton et al. 2008). Energy reserves of marsh habitat

specialist like the reed warbler tend to be higher than those of woody habitat species like the garden warbler (Bairlein 2003). This emergency store of energy by reed warblers might be an adaptation to both high fragmentation of reed habitats and low diurnal potentials for exploration of stopover site.

Comparing stopover site movement distances in FS and RS, it shows a combination of two expected outcomes. In accordance to expected outcome (1), the leanest birds tend to move further in the unsuitable stopover than in the suitable one. However, individuals with higher condition indices show less difference in MLD between stopover sites, which correspond to expected outcome (3), and suggest that fat birds have an innate template for very restricted diurnal movements. We did not record the intake rates or weight change over the day, but our results indicate that exploratory movements at stopover sites were related to resource availability or the need for resources, and when birds are able to find a foraging patch nearby, or they have sufficient fuel stores, they do not move further.

In agreement with our expectations, the distance of movement was evidently related to energy condition. This suggests that lean birds are more motivated to find a good foraging patch than fat ones. A similar tendency was reported in summer tanagers (*Piranga rubra*, Moore and Aborn 2000) at spring migratory stopovers. In the Sahara, passerine migrants show high spatial mobility and habitat selectivity when their fuel stores are small, whereas fat birds remain in suboptimal habitats and are inactive at daytime (Bairlein 1988). Birds with considerable fuel stores when encountering suboptimal or simply unfamiliar stopover habitats may prefer not to spend energy for exploration, but prefer to retain energy for nocturnal flight. However, Paxton and co-authors (2008) did not find any effect of



**Fig. 4** Influence of fuel reserves and site on stopover duration. *Black circles* birds released in the RS ( $n=10$ ), *white circles* birds released in the FS ( $n=10$ )

condition on the length of movements in the study of Wilson's warblers. In our study, condition index in the suitable habitats influenced length of movements less than in unsuitable habitats. We suggest that, in suitable habitats, short distance movements could be the feature of 'fat', not motivated for feeding birds, and 'lean' birds, in case they find food near the place of landing. This may blur the importance of individual fuel reserves for intensity of exploration. It is worthy of note that the absolute difference in lengths of movements between individuals in both sites was rather small.

Contrary to our expectations, MLD of birds released later was slightly longer than earlier releases. It is possible that birds explore more when visibility and the activity of arthropods increase. Alternatively, birds released later might be hungrier and/or stressed, which resulted in longer movements. On the other hand, it shows that shorter distances of movements in RS are not due to delayed release after transportation.

Stopover site quality evidently is the main factor affecting stopover duration of birds in our study. Even the leanest birds took off from FS during the first night, whereas in suitable habitats of the RS most of them stopped over for at least 2 days. This finding corresponds to the experimental results of Biebach (1985) and Gwinner and co-authors (1988) when food-deprived migrants showed Zugunruhe in cages. Similarly, by means of capture-recapture models, it has been shown that high and low fuelling rates cause early departure from stopover in three species of long-distant migrants, while birds with intermediate rates of body mass gain stay longer (Schaub et al. 2008). It is very likely that in our study the influence of habitat type on departure decisions is mediated by food availability, though we could not confirm whether food abundance or foraging substrate suitability is of major importance. It does provide an example of how external factors may override the influence of the intrinsic spatial-temporal program.

It remains unclear, especially for leanest individuals, if nocturnal departure of reed warblers from unsuitable stopover site is 'true' oriented migration, or if it is a large-scale search for a suitable stopover, performed by night. It was recently shown that reed warblers, probably in order to decrease risk of predation, use nocturnal flights to perform various large-scale spatial tasks (Mukhin et al. 2009). Observations and recoveries of ringed migrants show that birds stopped in unsuitable coastal areas can make 'reverse migration' for distances of tens of kilometres (Alerstam 1978; Åkesson 1999). The phenomenon known as a 'reverse migration' may represent a particular case of large-scale search for good stopover, taking place in situation when directions of flight are limited by an ecological barrier.

Individual variation in stopover duration in RS was substantial. However, comparison of different models based on

data collected at both stopover sites provided some support for the influence of season progress and amount of fuel reserves. Obviously, data from RS contributed to these tendencies. Birds trapped later in the season tend to leave stopover faster than those who migrate earlier. Time pressure despite our expectations did not influence motivation to explore stopover, but impacted the decision when to continue migration flight. Effect of body condition is weakly supported by averaged model, but still some tendency emerged for 'lean' birds to stay longer than 'fat' once.

Harper (1994) raised the ethical concerns about consequences for songbirds landing in poor stopover habitats due to artificially induced landfalls, considering that migrants urgently need to refuel at stopover. It was technically impossible to track the fate of tape-lured birds after departure from our trapping site. Nevertheless, from a previous study where tape-luring was used at the same site (Mukhin et al. 2008), some ringing recoveries are available. From approximately 400 post-moult reed warblers on migration, three were recaptured at a distance of approximately 700–1,000 km. Two ringed individuals were controlled in the year of trapping during autumn migration and one individual even 5 years later after surviving several successful winters. These data show that behavioural adaptations enable reed warblers to accomplish migration even when they sometimes use inhospitable areas as a stopover sites.

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