

The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover

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Received: 19 March 2007 / Accepted: 21 October 2007 / Published online: 6 December 2007
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Abstract Landscape context influences many aspects of songbird ecology during the breeding season. The importance of landscape context at stopover sites for migrating songbirds, however, has received less attention. In particular, landscape context may affect the availability and quality of food for refueling during stopovers, which is critical for successful migration. We evaluated the influence of woody habitat cover in the surroundings of stopover sites at several spatial extents on the hourly changes of body mass in two species of European-African forest-dwelling songbird migrants (Willow Warbler, *Phylloscopus trochilus*, and the Eurasian Redstart, *Phoenicurus phoenicurus*). Data were sampled by standardized methods from a network of ringing

stations throughout Europe during the falls of 1994–1996. In both species, hourly body mass gain calculated for first captures increased with woody habitat cover. We found a similar logarithmic relationship for both species, although for Willow Warblers mass gain was more strongly related to the habitat cover within 5 km, in contrast to 3 km for Redstarts. For Willow Warblers, where sufficient data are available for each year, the relationship is consistent over the years. The shape of the relationship suggests existence of a threshold of landscape suitability for refueling at stopover sites: in sites with less than 10% of woody habitat cover, birds tend to lose body mass or to gain mass at a lower rate.

Keywords Habitat cover · Landscape context · Mass gain · Refueling · Songbird migrants · Stopover

Electronic supplementary material The online version of this article (doi:10.1007/s10980-007-9177-4) contains supplementary material, which is available to authorized users.

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Introduction

Concepts and methods of landscape ecology are in common use in most ecological disciplines at the present time. The importance of landscape composition and configuration for ecological processes is widely recognized (Fortin and Agrawal 2005). Forest-dwelling songbirds are frequently considered as model species for studies of wildlife-landscape relationships because they are relatively well-known in terms of their basic ecology and taxonomy.

Furthermore, the methodology for the study of their ecology and behavior is well established. Most studies from a landscape ecology perspective are focused on the breeding season (Freemark et al. 1995). One of the main findings from such studies from the perspective of landscape is that many avian species have minimum requirements for habitat patch area and need a certain proportion of habitat cover to benefit in a given landscape during breeding (e.g. Freemark et al. 1995, Hinsley et al. 1995). Also, the composition of a landscape affects its suitability for occupying a territory within it, e.g. due to differences in nest parasitism (Robinson et al. 1995) and risk of predation (Chalfoun et al. 2002). While studies of habitat requirements of breeding birds are common, in stopover ecology the importance of landscape-level factors has been largely unstudied (Chernetsov 2006), despite the high potential for the landscape ecology approach for assessing the quality of stopover sites.

The few studies of stopover ecology in migrating songbirds in which landscape context was considered have focused mainly on species diversity and abundance patterns (Freemark et al. 1995). However, successful migration in most species depends on intensive fueling prior to and during the migration journey (e.g. Bairlein and Gwinner 1994; Berthold 1996). The quantity and quality of stopover sites along a flyway are important factors shaping fuel deposition patterns and migration strategies (Weber 1999; Chernetsov et al. 2004a). The potential importance of the availability of habitats optimal for fueling at the landscape level has been discussed (e.g. Dolnik 1990; Moore et al. 1995; Petit 2000). The importance of one landscape-related variable, namely the mud exposure index, has been shown recently for one shore bird species, the Western Sandpiper (*Calidris mauri*). It was one of the predictors of fueling efficiency at stopovers (Seaman et al. 2006). Moreover, Mehlman et al. (2005) suggested the classification of stopover sites based on their suitability for songbird migrants, and the landscape context of stopovers was pointed out as a factor influencing their quality. Nevertheless, to our knowledge, no attempt has been made to quantify possible dependence of fueling efficiency of songbirds in a landscape context.

Foraging success and body mass gain vary substantially between stopover sites (e.g. Schaub and Jenni 2001; Dunn 2002), but the geographical position

of the site explains only a fraction of the observed variation (Schaub and Jenni 2001). Suitable habitat cover around stopover sites varies considerably, but effect of habitat availability at landscape scale remains largely unstudied. In some parts of a flyway, especially in a close proximity to ecological barriers, e.g. large water bodies or deserts, patches of stopover habitats such as woodlands may be small and isolated. Despite the current view that most songbirds on migration are flexible in habitat selection and foraging habits (Petit 2000), availability of suitable habitat in the environs of a site may be an important feature in assessing overall suitability of a stopover site.

This study aims to relate the hourly rate of body mass gain of two forest-dwelling migrant songbird species at different stopover sites to the cover of suitable habitats in the wide landscape vicinities of the trapping site. We hypothesized that landscapes with low woody habitat cover do not allow these migrants to refuel as efficiently as at stopover sites with high habitat cover, even though the area of suitable habitat cover may be large enough for an individual bird. Thus, we expect a positive relationship between body mass gain and the amount of suitable habitat in the surrounding landscape.

Materials and methods

Assessment of the role of landscape context in habitat use at migratory stopover sites and body mass gain during stopover requires a comparison of study sites showing variation both in fueling rates and in landscape structures. These sites should be studied following common and standardized routines. Such data is available from a large network of participating trapping sites. Between 1994 and 1996, the European Science Foundation Scientific Network on European-African songbird migration was set up (Bairlein 1998) to study migration strategies of songbirds. More than 30 research groups from 18 different countries were operating more than 50 sites ranging from northern Finland and Sweden across central and western Europe to western Africa. Some 400,000 birds of the 34 target species were recorded. These data provide a unique opportunity to examine the influence of landscape context on the quality of stopover sites for fueling songbird migrants at sites across wide geographical and ecological ranges.

Species studied

We selected two species which were common at many sites, the Willow Warbler (*Phylloscopus trochilus*) and Eurasian Redstart (*Phoenicurus phoenicurus*). Both occupy various types of woody habitats during migration (Bairlein 1983), follow long-distance Trans-Saharan migration routes when moving from Eurasian breeding grounds to winter quarters in tropical Africa and back. Although both species feed on insects, their foraging strategies differ. Willow Warblers forage mainly by pecking from branches and leaves, while the Redstart primarily uses aerial attacks (Cramp and Perrins 1988, 1992).

Study sites

Data from 22 sites were analyzed (Appendix, Fig. 1). Locations range from offshore islands and coastal sites to inland sites that provide a wide range of woody habitat cover in surrounding landscapes. The study sites are distributed over a wide geographical range but most are concentrated in Western Europe (Fig. 1). Of the British sites, only the eastern ones were included, because they are used by many transient migrants, unlike the western ones (Wernham et al. 2002).

Data sampling and selection criteria

Data were collected during fall migration 1994–1996. All sites were operated following a standardized protocol (Bairlein 1995). At most sites trapping was

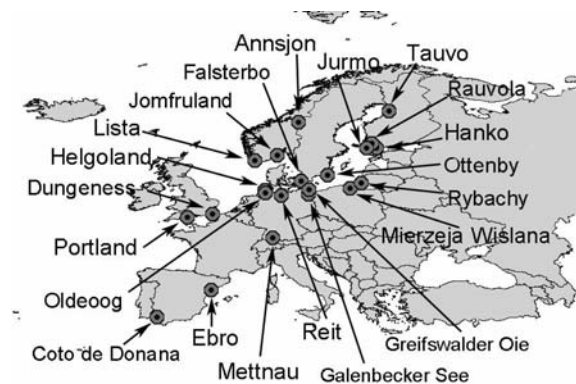


Fig. 1 Geographical locations of the trapping sites

carried out using mist nets, but some sites used funnel traps (Table 1). Birds were trapped during the entire fall migration season, every day from sunrise to sunset; nets or traps were checked at least every hour. All migrants were marked by aluminum bands in accordance with national banding rules. Among other data, the body mass, fat score, molt, wing length (maximum chord), age, date and time were recorded for each trapped bird.

For the analysis we selected first-time outbound migrants in their first year (hatching year birds) were selected except for a few sites where birds of unknown age are included to increase sample size. As the majority of fall migrants are hatch-year, the bias of unknown-aged birds is low. Non-molting individuals were selected or birds with less than 25 molting body feathers in order to avoid the inclusion of birds not yet on migration. In general, birds separate molt and migration within their annual cycles (Jenni and Winkler 1994), however molting juveniles do take part in postfledging nocturnal movements prior to migration (Mukhin 2004). In addition, we included only periods after a substantial increase in the number of trapped birds at the particular stopover sites which indicated the start of the main migration period. Birds from Ottenby Bird Observatory, Sweden, were selected only by that criterion because molt was not recorded there. As this coastal site is rather isolated and does not provide much breeding habitat, the few, if any, local birds are unlikely to substantially influence the trapping pattern. At the two Spanish sites all Willow Warblers were included in the analysis because these sites are located south of the breeding range of this species.

A total of 18,379 records of Willow Warblers and a total of 3,052 records of Eurasian Redstarts were analysed from 22 and 15 trapping localities, respectively (Appendix). To compare between different years, we used data from 16 localities (Appendix).

Estimating body mass gain

In most stopover studies of songbirds, body mass gain was estimated from retraps. Although this method provides useful information about individual patterns of body mass change at stopover, it does not necessarily reflect site quality for the majority of stopover birds. At many sites most birds stay just for

Table 1 Models with lowest AICc values

Species	<i>N</i>	Model terms	Log-likelihood	K	AICc	ΔAICc	AICc weights
Willow Warbler	1	HC at 5 km radius (log-transformed)	-4.22	3	15.77	0.00	0.06
	2	Longitude + HC at 4 km radius (log-transformed)	-2.80	4	15.96	0.19	0.06
	3	HC at 4 km radius (log-transformed)	-4.40	3	16.15	0.38	0.05
	4	Longitude + HC at 5 km radius (log-transformed)	-3.13	4	16.6	0.83	0.04
	5	Longitude*latitude + HC at 4 km radius (log-transformed)	-3.14	4	16.63	0.86	0.04
Eurasian Redstart	1	HC at 3 km radius (log-transformed)	-0.45	3	8.22	0.00	0.09
	2	HC at 4 km radius (log-transformed)	-0.78	3	8.89	0.67	0.06
	3	HC at 5 km radius (log-transformed)	-1.16	3	9.66	1.43	0.04

one day, taking off the next night after landing (e.g. Rappole and Warner 1976; Bairlein 1988). Moreover, data from birds retrapped within the first day after capture may be biased due to handling. Birds recaptured within the first day frequently show negative or neutral body mass change (Schwilch and Jenni 2001). This leads to an underestimation of species- and site-specific values of body mass gain and fueling rates, possibly due to stress. Consequently, although migrants tend to gain weight according to analysis of first captures at a stopover site, analysis based on retraps alone may erroneously indicate that migrants are losing body mass (Winker et al. 1992). On the other hand, birds retrapped within several days after the first capture represent only a fraction of migrants using a particular stopover site. These birds may be the most successful ones through having obtained good feeding ranges (Rappole and Warner 1976), or conversely, they may be stragglers whose physiological state does not allow them to continue migration. As an alternative method, we applied a simple linear regression of body mass of first capture birds versus time of day of capture as follows: $CI = b_0 + b_1 H_c$, where CI is condition index, H_c is hour of capture in relation to sunrise, and therefore b_1 is a rate of hourly CI change during the daylight at stopover (Winker et al. 1992; Winker 1995; Dunn 2000, 2002). CI calculated as body mass (in g) divided by wing chord length (in mm) was used in order to account for size variation among individual birds (Winker 1995). We included in our regression analyses all hatching-year birds caught for the first time throughout the entire daylight period. Following Dunn (2001) we converted the

regression coefficients to body mass change per unit of time (g/h) as body mass change = b_1 *average wing chord. Average wing lengths were estimated for each species and site. For between-species comparison, the hourly mass change coefficients were expressed as the percent of lean body mass change per hour. Site-specific lean mass for each species at each site was obtained by calculating average body mass for birds seen without visible subcutaneous fat.

A problem may arise if there is high inter-individual variation in body mass change within the stopover site. It could then be difficult to detect any significant change resulting from stopover site quality (Winkler 1995). Indeed, variation in individual weights not explained by regression equations is always high, which may be due to several factors (Dunn 2002). It is very likely that the main factor is the initial difference in body condition of landing birds. Lean birds usually intend to gain mass, while fat birds are less motivated in extensive foraging. However, most Willow Warblers and Eurasian Redstarts in our study carry low stores of subcutaneous fat. Therefore, we believe that the regressions provide comparable indexes of stopover site quality.

To check for consistency of the results, estimates were made of body mass change coefficients from the single ANCOVA model, with body mass as dependent variable, sites as a factors, wing lengths, time since sunrise and interaction term 'time since sunrise*site' as a covariates. Body mass change coefficients extracted from single model were very similar with those based on single regressions; therefore we report the last ones, as they are based on the simplest method and comparable with results

of other studies (e.g. Winker et al. 1992; Winker 1995; Dunn 2000, 2002).

An important assumption of the regression method is that all birds arrive to stopover before sunrise. At some sites birds continue to arrive after sunrise, e.g. when they are crossing large water bodies and have no chance for landing at the end of night. At such places the reliability of the method of analyzing first captures is questionable (Dunn 2000). We set all coastal or island sites situated behind the seas (in relation to the migratory direction) in one category, and all the rest (inland sites and coastal sites where birds are making stopovers before crossing the large water body) to the other one (Table 1). In case if position of the site is important, all sites situated behind the barrier would tend to have low body mass change coefficients. In order to control for possible methodological drawbacks we included position of the site in relation to a barrier (SP) in our analysis as a dummy variable (see below).

Habitat cover

To estimate the proportion of woody habitats in the landscape surrounding a trapping site we used Landsat TM images with a grain size 28.5 m. Taking into account locations of our study sites, we considered a spatial extent of 5 km radius centered in each trapping site. Since some coastal islands are situated about 5 km from the mainland and at chosen extent habitat covers shows high between-sites variation. This scale is in the range of spatial extents commonly used to assess impact of forest cover on breeding songbirds, from 10 km (e.g. Robinson et al. 1995) to 1 km radius (e.g. Hinsley et al. 1995) However, living organisms may respond to the landscape structure at different spatial scales (Wiens 1989), therefore we considered several additional spatial extents for our analysis, with radius of 4, 3, 2 and 1 km.

We categorized habitats for each site using Image Analysis 1.0 extension (ERDAS) for ArcView 3.2 (ESRI), and verified the method reliability using aerial photographs and vegetation maps. Because both Willow Warblers and Eurasian Redstarts are considered woody habitat generalists, we then combined all forest or shrub categories into a ‘suitable habitat’ class and all the remaining categories into an ‘other’ class. Using this binary classification, we

estimated the woody habitat cover (HC) as proportions of the circles of every chosen radius (5–1 km) around each trapping locality. Although more complicated indices of spatial heterogeneity have been developed, many studies have shown that the simple measure of habitat cover in a landscape is a good measure of ecological phenomena (Gustafson and Parker 1992; Gustafson 1998).

Statistics

We assessed the relationship of body mass gain versus HC using ANCOVA procedure. We used body mass change coefficients obtained from regressions of body mass versus daytime as a dependent variable. In attempt to account for local habitat productivity, we also used GIMMS NDVI (Tucker et al. 2005), estimated for every site as median for the whole migration season (second half of August and September) and 3 years of study. This index serves as a proxy for primary productivity of vegetation at given site, and is assumed to be correlated with food availability in many ecological groups of animals, including insectivorous birds (Pettorelli et al. 2005). Resolution of NDVI composites was rather low (8 km grain), but it still may serve as estimate of large-scale habitat productivity of the geographic region, which is important to account for given the large geographical range of distribution of our study sites. Since the HC values from different spatial extents were not independent, we did not include them in the same model. We instead considered several full models, with SP as an indicator variable, latitude, longitude, interaction ‘latitude*longitude’, median of NDVI, HC values for one of five spatial extents, either not modified or log-transformed, as covariates.

We fitted models with all possible combinations of predictors, ranging from equation with single predictor to the full model. From the whole set of candidate models, we selected the most parsimonious model for every species, based on Akaike’s Information Criterion corrected for low samples (AICc, Burnham and Anderson 2001). We checked if geographical position of the site contributes to inter-site variation in fueling rates, if the large-scale habitat productivity, as measured by NDVI, affects the performance of songbirds at stopover sites, and if positions of the

sites influence our results. Maximum weight gain in migrant birds is clearly physiologically limited, so a simple linear increase of fueling rates with HC in surroundings is improbable. Therefore, the relationship is tested for shape at the chosen spatial scales, namely whether it is linear, or described by an asymptotic curve, e.g. logarithmic. Comparison of models with log-transformed and not-modified values of HC measured at different scales allowed us to select between these relationships, and to determine the spatial scale of habitat cover to which variation of the fueling coefficients is most closely related. Polynomial functions were not considered because we could not ecologically justify such relationships.

Estimation of fueling rates was performed with SPSS 11.5 (SPSS for Windows Rel. 11.5.1 (2002) Chicago: SPSS Inc.). Models fit and selection was performed with R 2.4.0 (R Development Core Team 2006), using package “pgirmess” (Giraudeau 2006). Differences between regression coefficients for comparison between years were evaluated by *t*-test and ANOVA for linear regressions (Zar 1999), using GraphPad Prism 4.03 for Windows, GraphPad Software, San Diego, California USA.

Results

Diurnal body mass changes varied considerably between study sites (Appendix), ranging from -1.05% to 1.67% of lean mass per hour in Willow Warblers, and from -0.23% to 0.56% in European Redstarts. Woody habitat cover ranged from 0.1% (Portland, UK) to 41% (Rauvola, Finland, Appendix).

Simplest models with log-transformed HC as single predictor received the lowest AICc values and highest AICc weights in both species. Given the large number of models involved in this comparison (359), results are presented only for models with Akaike weights higher than 0.04 (Table 1).

Although this weight is small, most of the other models received much smaller weights: 0.02 – 0.01 , or zero. Since best models include HC terms from different spatial scales and belong to different basic equations, a proper model averaging was not possible. Similar performance of models related to five, four and, for the Eurasian Redstart, 3 km radius scales shows that fueling rates are related to HC in the area within 3–5 km radius, but exact scale

identification is impossible with our dataset. For the simplicity, the first-ranked model for both species is used for further consideration. For those models, we report goodness of fit and F significance statistics, as suggested by Stephens et al. (2005). To illustrate the shape of the relationship, we consider logarithmic model with non-transformed HC values (Fig. 2).

For the Willow Warbler model $rate\ of\ mass\ change \sim HC\ (5\ km\ radius)$, $R^2 = 0.412$, $F_{20} = 14.02$, $P = 0.001$, $n = 22$ (Fig. 2a); For the Eurasian Redstart model $rate\ of\ mass\ change \sim HC\ (3\ km\ radius)$, $R^2 = 0.319$, $F_{13} = 6.1$, $P = 0.028$, $n = 15$ (Fig. 2b).

For the Willow Warbler, where sufficient data are available for each year, the body mass change/HC relationship is consistent among years (Fig. 3), although not significant in the fall of 1994. Between-year difference in slopes was not significant (ANOVA, $F_{2,36} = 0.06$, $P = 0.937$).

Figures 2 and 3 show fueling rates increased sharply with increasing HC up to 10%, and then

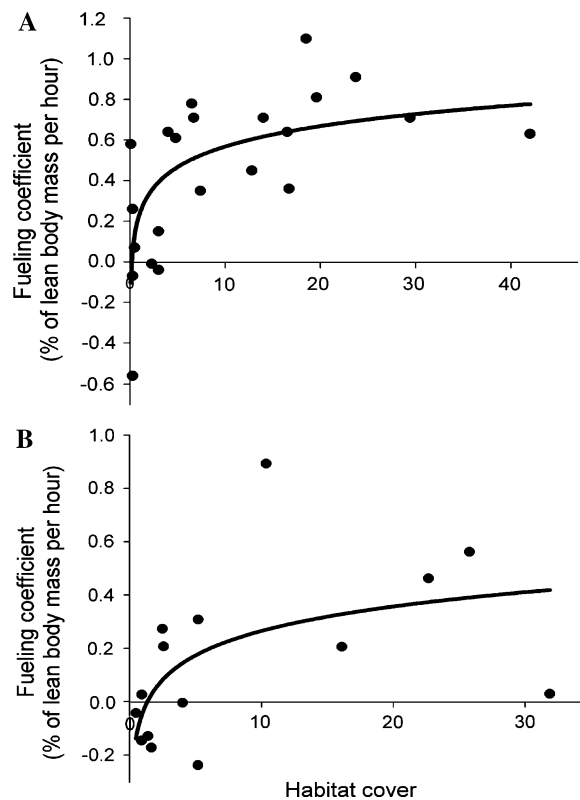


Fig. 2 The relationship between body mass gain in the Willow Warbler (a) and the Eurasian Redstart (b) and HC around stopover sites. (a) Habitat cover as percentage of 5 km radius circle, (b) Habitat cover as percentage of 3 km radius circle

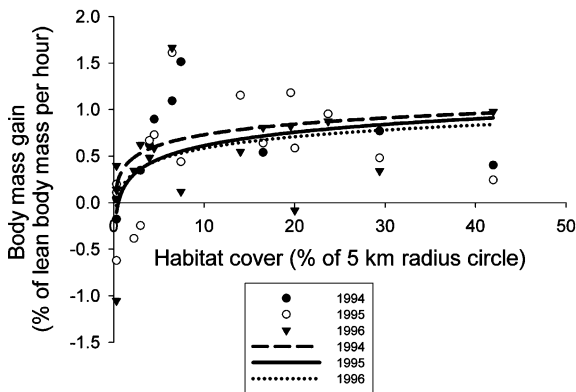


Fig. 3 The relationship between body mass gain in the Willow Warbler and habitat cover around stopover sites in different years

leveled off. These results agree qualitatively with our expectations.

Discussion

Pattern of HC–body mass gain relationship

The results reveal that the availability of suitable habitat in the landscape context surrounding stopover sites may better explain inter-site variation in fueling rates than geographical position—the only explanatory variable yet reported for fueling rates of songbirds compared on a large scale (Schaub and Jenni 2001). Diurnal mass gain rate increases steeply with the proportion of suitable habitats in adjacent landscape up to approximately 10% and levels off above this value of HC. This finding might be considered within the framework of the ecological threshold concept, which has now been applied to a variety of ecological subjects, including wildlife habitat requirements (Groffman et al. 2006). In many species of birds and mammals landscape context had a negative impact on performance of populations when HC was below 10–30% (Andrén 1994). Our results provide evidence that at least some species of songbirds during fall migration require a minimal HC for efficient refueling at stopover sites during migration just as they do on their breeding habitats. The response to landscape composition is similar for both species studied, although they differ in their foraging ecology. Moreover, in the case of the Willow Warbler the relationship is consistent between years.

It is noteworthy that the approximate scale of response to HC in our study is similar to that found by Buler (2006), who examined density of migrants as a response variable, and found that migrants respond to landscape context on the mean scale of 4.9 km during fall migration.

We found little evidence that geographical position or position of site in relation to barriers influences pattern of body mass change, as models including either of these terms received low ranks. One exception is that of longitude in combination with HC at 4 or 5 km radius in case of Willow warbler (Table 1). This finding is difficult to interpret biologically. Most of sites are concentrated at the center of the longitudinal range of our dataset, and influence of longitude might be caused by a few eastern and western sites.

Several studies of songbirds at stopover sites show that body mass gain may be linked to landscape context for different migration systems and flyways. In the study of variation in body mass change of Neotropical migrants across Canada, the site where more than half of the species studied did not gain mass effectively during fall season was a small coastal island (Dunn 2002). In the arid regions of Central Asia, where habitat fragments are surrounded by inhospitable matrix, migrants in oases were not able to refuel effectively during fall migration (Dolnik 1990). However, large oases in the Sahara desert provided fueling support for migrating songbirds (Bairlein 1988). Pairwise comparisons of coastal and mainland stopover sites based on retrapped birds revealed that fueling was more efficient inland, where woody habitat cover is likely to be higher than on the coast, for migrating Goldcrests (*Regulus regulus*) (Hansson and Pettersson 1989) and European Robins (*Erithacus rubecula*) (Ehnbom et al 1993).

The concept of ecological neighborhoods provides a conventional framework for scaling and interpretation of spatial relations of an organism (Addicott et al. 1987). Scale of neighborhood usually differs for different types of activity in the same species. As Hutto (1985) pointed out, songbirds select habitats among and within landscapes in several hierarchical steps which correspond to different spatial scales. The stages of this process are still poorly understood, which makes it difficult to interpret our results, i.e. which stage of this hierarchical process is responsible for the observed relationships.

One possible stage is selection of habitats aloft, prior to landing. Indeed, migrating songbirds change heading of flight in response to proximate visual cues when selecting landing location, and also increase wingbeat frequency prior to landing (Bowlin et al. 2005), which probably reflects searching effort. When ceasing nocturnal flight, songbirds are often constrained in habitat selection by many factors other than habitat (*sensu* Hutto 1985): for example fading darkness, level of fuel reserves, or synoptic weather pattern (see Jenni and Schaub 2003 for review), and therefore they may be forced to land in the nearest habitat patch. If the amount of suitable habitat is restricted, migrants may be attracted in higher numbers to available habitats from a wide surrounding area (Moore et al. 1995), especially at coastal sites and on islands. In such cases they may face intra- and interspecific competition, as reported in several studies (Moore and Yong 1991; Petit 2000; Kelly et al. 2002; Ottich and Dierschke 2003). Therefore the scale of response to landscape in our study may be determined by bird's behavior aloft, when songbirds are searching for available habitat patches, and also may be mediated by density-dependence of body mass gain. Unfortunately, density (trapping rate) of our study species among sites cannot be compared directly for several reasons: some sites used funnel traps and some—mist nets (Appendix); vertical structure (height) of woody habitats varies considerably between and within sites, but mist nets sampling birds on height of 2 m only; in some sites trapping was conducted mainly in reed stands, and density in this habitat not necessary reflects density in nearest woodlands or shrubs. Nevertheless, the maximum grand totals of trapped birds in the database come from small offshore islands.

A second stage may be a bird's behavior after landing, when songbirds move relatively short distances while foraging during the day. A possible function of such movements is the search for suitable habitats on a smaller scale, using probing behavior, and avoidance of suboptimal fueling situations, e.g. dispersal from areas with high densities of migrants (Moore and Aborn 2000). Songbirds may need a mosaic of habitats at stopover sites to track changing resource availability. At a given stopover site, migrants change their habitat preferences within a season (e.g. Bairlein 1983). As habitat heterogeneity increases with area (Gaston and Blackburn 2000),

larger habitat blocks may provide more opportunities to migrants for switching to good fueling patches if in their current location food availability is low due to depletion or other factors, whereas in small disconnected patches songbirds should stay until night, since surrounding unsuitable habitat constrains the movements of forest-dwelling songbirds (Belisle et al. 2001). Data related to spatial scale of movements at stopover sites are somewhat contradictory. On the one hand, they may exceed 4 km in distance, as in the Pied Flycatcher (*Ficedula hypoleuca*, Chernetsov et al. 2004b). This is similar to the spatial scale found in our study. On the other hand, all other studies of movements at stopovers indicate that most migrants move only for short distances after landing (Buler 2006). Both mechanisms are possible and are not mutually exclusive.

Variation of fueling rates not explained by HC

Even though the influence of HC on fueling rates is significant, a substantial portion of among-site variation remains unexplained. This finding is not surprising, since many confounding factors influence fueling rates, and it is almost impossible to account for all of them. First of all, we use binary classification of habitats—woody versus non-woody habitats. This is a common practice in studies devoted to wildlife–landscape relationships, but the assumptions of this method are artificial. Quality of unsuitable (matrix) habitats, as well as differences in habitat types summarized to category of suitable habitat may be important, but binary classification assumes homogeneity within both habitat categories (Haila 2002). Being habitat generalists during migration, passerine forest-dwelling migrants still show clear patterns of habitat selection within a given stopover site (Bairlein 1983). At many woody stopover sites there is substantial between-species variation in fueling efficiency (Winker et al. 1992; Schaub and Jenni 2001; Dunn 2002, this study). This emphasizes that forest-dwelling songbirds, being overall flexible in habitat use at stopovers, nevertheless frequently have habitat demands more specific than simple availability of broad forest/shrub habitat. With regard to the large geographical extent of our study, it is clear that habitat heterogeneity may contribute to the high variation in fueling rates between sites with similar HC.

However, structural habitat heterogeneity may not be a good predictor of between-site variation in fueling rates. An example is provided by high between-sites variation in fuel deposition rates of Reed Warblers (*Acrocephalus scirpaceus*, Schaub and Jenni 2001), which are specialist foragers in reed beds (*Phragmites australis*). Habitat structure is quite similar among sites, but amount of food available for Reed Warblers may vary both spatially and temporally by a factor of 100 (Chernetsov 1998).

Finally, such factors as dietary nutritional quality, weather conditions, risk of predation and endogenous components are additional potential sources of between-site and between-year variation (see Lindström 2003 for a review). NDVI as a covariate did not help to explain variation in fueling rates among stopover sites. Therefore, we have no evidence that large-scale (8 km grain) habitat productivity influences much body mass gain at stopovers. However, we were not able to account for finer-scale differences in productivity of habitats, which is likely to be more important (see Seaman et al. 2006).

Overall, despite other variables not included in the current analysis, our results reveal that landscape context may serve as a predictor for fueling of songbird migrants during fall migration. HC alone explained a considerable portion of differences in fueling rates between stopover sites. This finding merits consideration in future studies of migration strategies and habitat use at stopovers.

Acknowledgements Legions of professional ornithologists, students and amateur volunteers took part in collecting and reporting trapping data. We are sincerely grateful to all of them, and ask them to accept our apologies that we cannot mention them all by name. Our colleagues from the Biological Station Rybachy and Institute for Avian Research gave invaluable assistance to this study with fruitful discussion and comments. Nikita Chernetsov, Michael Schaub, John Walder, Timothy Coppack, Anders Olson, Martin Griffiths, Kevin Winker and one anonymous referee helped significantly in the improvement of the early drafts of the manuscript. This study was supported by European Science Foundation within the Scientific Programme BIRD.

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