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Habitat selection by nocturnal passerine migrants en route: mechanisms and results

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Abstract Habitat use and habitat selection are essential for successful stopovers. Passerine migrants use habitats in a clearly non-random manner, even if many species utilise a broader range of habitats during passage than during breeding or wintering. Habitat selection proceeds as a sequence of events: landfall; search/settling, including redistribution across habitats if necessary; and habitat exploitation, with all stages probably condition-dependent. This review is aimed at studying this sequence and also the factors which govern decision-making in nocturnal passerine migrants at all levels. In most cases, habitats are (pre)selected by migrants already at landfall using both visual and acoustic cues. After landfall, migrants start to perform direct sampling of habitats during which they may move constantly and perform fine-tuning of their habitat choice. Some species subsequently occupy a small home range in a particular (micro)habitats, whereas others continue to move broadly during the whole stopover period. An interaction of several factors shapes the use of habitats after landing, among which are migrants' innate preferences and functional morphology, foraging strategies and food resource distribution, habitat carrying capacity and exposure to predators. The large-scale spatial context probably also plays a role which might be currently underestimated.

Keywords Decision-making · Habitat choice · Nocturnal migrants · Passerines

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Introduction

When a landbird migrant makes a stopover, it usually finds itself in unfamiliar surroundings, with food demands and competition likely to be high (Hutto 1985b; Loria and Moore 1990; Moore and Yong 1991; Jenni and Schaub 2003). Therefore, selection of optimal habitats is of great importance for refuelling migrants. It is beyond doubt that correct habitat selection is important for survival and achieving the fuel deposition rate necessary for successful migration. Many migrants which breed in temperate and/or high latitudes and winter in the tropics, have to be able to select appropriate habitats in boreal forests, steppes, highlands, deserts and tropical areas. Habitat selection proceeds as a sequence of events: landfall; search/settling, including redistribution across habitats if necessary; and habitat exploitation. All these events are likely to be condition-dependent. Hutto (1985b) suggested the existence of a hierarchical chain of cues used by migrants when selecting stopover habitats. Individuals with different fuel stores might have different stopover aims and rely on different cues for their condition-dependent habitat assessment.

This review is aimed at studying this sequence and factors which govern decision-making in nocturnal passerine migrants at all levels. It is focused on passerines which migrate at night and stop for rest and foraging during daytime because in these species migratory flights and stopovers are clearly separated. The situation in daytime migrants is much more complex, as it may be difficult to separate flights and stopovers in these species (Chernetsov 2003).

It should be emphasized that the knowledge of habitat requirements of migrants during stopover is not only essential to understand their stopover ecology and principles of organisation of migrants, but is crucial for efficient conservation of billions of avian long- and medium-distance migrants (Moore 2000, Moore et al. 1995).

Landfall events

Our knowledge of how passerines complete nocturnal migratory flights is very limited. The existing generalised model assumes that when migrants do not have to cross ecological barriers, nocturnal passage of passerines almost completely stops soon after midnight (Kerlinger and Moore 1989). However, Bolshakov (1981) showed that during autumn migration, even though many birds cease flight in the beginning and middle of the night, most do not land until the last hours of the night. In spring, most Eurasian reed warblers *Acrocephalus scirpaceus* and sedge warblers *A. schoenobaenus*, and probably other long-distance migrants, do not cease flight until the end of the night (Bolshakov et al. 2003a, b). Ceasing flight at the end of the night may be adaptive, because increased visibility may permit better habitat selection and safer landing (Bolshakov and Bulyuk 1999).

It has been suggested that stopover locations are selected by migrants during daylight hours, most likely early in the morning (Moore et al. 1995; Moore and Aborn 2000). It is assumed that 'morning flights' reported for many passerine nocturnal migrants, when they fly low above the vegetation in the morning (Gauthreaux 1978; Bingman 1980; Wiedner et al. 1992), support this view. It should be stressed that the so-called 'morning flights' of nocturnal migrants usually occur above the vegetation, normally do not result in captures in mist-nets, and probably refer to wind drift compensation rather than to redistribution across habitats (Bingman 1980). The results of long-term trapping projects suggest that the initial habitat (pre)selection occurring prior to and during landfall, is usually already quite precise (Bairlein 1981, 1983). On the Courish Spit on the southeastern Baltic coast, 45 years of capturing migrants in stationary funnel traps located on the border between pine plantations and sandy dunes resulted in captures of 175 Eurasian reed warblers and 190 sedge warblers. Nine years of captures in mist-nets in an optimal habitat 11 km away from that site resulted in the capture of 8,918 Eurasian reed warblers and 6,748 sedge warblers (Bolshakov et al. 2003a, b). Song playback at the former site enabled capture of 1,521 Eurasian reed warblers and 342 sedge warblers in just 4 years (Mukhin et al. 2005a). Obviously, both species, which are quite common passage migrants in the area, were strongly underrepresented in an atypical habitat which implies that they rarely landed in it. However, accuracy of habitat recognition might be decreased, e.g. in the conditions of poor visibility (Jenni 1996). Degen and Jenni (1990) reported that landing Eurasian reed warblers had mistaken a vertically structured maize field for reed stands. This error was corrected after sunrise by daytime movements into the optimal habitat.

Rapid selection of high-quality habitat makes it possible for migrants to start refuelling as soon as possible and to avoid the costs (in terms of time, energy and

security) of prolonged habitat sampling. Individuals get a greater benefit when they make a correct habitat assessment quickly, therefore it may be expected that initial assessment of landfall habitats occurs while still aloft. Two possible strategies of habitat exploration can be used: direct sampling and cue using (Mönkkönen et al. 1999). Cue using allows the birds to assess habitats from a distance without sampling, making the process quicker and cheaper.

It has been recently argued that, in addition to visual cues, acoustic cues (both conspecific and heterospecific ones) can be used by some species when making landfall decisions (Mukhin et al. 2005a). Tape-luring is known to be an efficient method to capture some nocturnal migrants both in spring and in autumn (Herremans 1990a, b; Schaub et al. 1999; Bulyuk et al. 2000; Mukhin 2004). This is evidence that acoustic cues are used by at least some migrants when making landfall decisions. The relative importance of visual and acoustic cues remains unclear. It most probably varies quite broadly among different species. Attraction by acoustic cues is more pronounced in passerines of wetlands, which supports the claim that these cues are most important for birds of naturally fragmented habitats (Mukhin et al. 2005a). However, attraction by song playback during nocturnal flights is not restricted to this group of species (Herremans 1990a). Individuals that cease flight in the darkness, when the use of visual cues is hampered, are probably more likely to rely on acoustic cues than birds that fly until twilight.

It should be emphasised that tape-luring data can only prove the role of acoustic cues in habitat selection of migrating birds ceasing flight if: (1) trapping is conducted in an atypical habitat, and (2) only birds captured in the darkness before the onset of daytime movements are included into analysis (Mukhin et al. 2005a). Otherwise, one should be extremely cautious when assuming that birds captured at a tape-luring site were indeed attracted to cease flight from the flow of migrants aloft and not from the pool of stopover migrants in the vicinity of the song playback location (cf. Schaub et al. 1999; Schilch and Jenni 2001).

Results of several studies show that selection of habitats prior to landing might be condition dependent. For example, only lean individuals of forest dwelling migrants were founded in desert oases with appropriate habitats, whereas fat individuals used any habitat in desert since they did not intend to forage (Biebach 1990).

Search/settling

After landfall, migrants start to perform direct sampling. Woodland passerines often make movements within the habitat which are manifested as the morning peak in captures (Brensing 1989; Berthold et al. 1991; Titov 1999b). As discussed above, this peak, well known to every bird ringer, is mainly due to fine-tuning of habitat choice by migrants, and to attempts to establish a

defined home range / temporary territory within the preferred habitat (Titov 1999a; Chernetsov et al. 2004a; Chernetsov 2005). The very fact that it is possible to attract birds into very unsuitable habitats by song playback at night (see above) suggests that rough habitat choice occurs when ceasing migratory flights.

In some nocturnal migrants, e.g. European robins *Erithacus rubecula*, longer-range movements are largely restricted to a period after landfall, typically several hours, but up to 2 days, as shown by radio tracking (Chernetsov 2005; N. Chernetsov and A. Mukhin, submitted). Summer tanagers *Piranga rubra* also seem generally to follow this pattern (Aborn and Moore 1997). However, in other species, e.g. in pied flycatchers *Ficedula hypoleuca*, comparatively long-range (several kilometres) movements may occur during any stage of stopover, even several days after arrival (Chernetsov et al. 2004a; Chernetsov 2005). They should not be treated as extended search/settling, but rather as a strategy of stopover resource exploitation based on much movement. In the European robin, search/settling probably usually occurs within several hours after arrival to a stopover, up to one or in some cases two days. Time which a migrant is ready to invest in searching for a good stopover site and settling has serious consequences for its optimal stopover strategy (Weber and Houston 1997a; Chernetsov et al. 2004b) and is most probably condition-dependent (Chernetsov et al. 2004b). As suggested by Aborn and Moore (1997), time spent exploring probably depends on the costs of acquiring information and the benefits to be gained. Both costs and benefits are most likely condition-related.

At least two different scenarios may occur. Emaciated individuals might be less choosy and ready to accept any stopover area that offers a positive fuel deposition rate, because they have no safety margin and cannot afford too long an exploratory period. In contrast, individuals with larger fuel stores might invest more in search for an optimal area. Alternatively, it may happen that fat individuals do not aim to refuel, but just are waiting for optimal departure conditions (or simply for the next night) and thus do not move constantly (e.g. Bairlein 1987). It is not impossible that Chernetsov (2005) and N. Chernetsov and A. Mukhin (submitted) failed to find a relationship between energy condition and stopover behaviour in migrating European robins because both these patterns were realised.

The amount of movements performed just after landfall is probably not only condition-related but also age-related. In thrushes on the Courish Spit, the coastal effect (age ratio of migrants skewed towards juveniles; Payevsky 1998) is partly due to higher mobility of juveniles (Bolshakov et al. 2003a, b). During 'active trapping', when the birds were flushed into the nets, proportions of adults in captures were significantly higher than in the standardised trapping project, but still lower than expected on the basis of annual fecundity of respective species. The reason for higher mobility of juveniles just after landing could be that they are socially

subordinate to adults as reported for a number of species (Gauthreaux 1978), stopover migrants included (Woodrey 2000), which makes it more difficult for them to gain a small home area.

However, in the European robin, the difference in proportions of adults in 'active' and 'passive' trapping at migratory stopovers on the Courish Spit was not significant either in spring (14.3 and 13.3%, $n=233$ and $n=389$, respectively; $\chi^2=0.14$, $P=0.70$) or in autumn (5.1 and 5.0%, $n=156$ and $n=685$, respectively; $\chi^2=0.01$, $P=0.93$). In this species, adults and juveniles seem to perform a similar amount of movements during the settling period. It is worth noting that dominance status is not always age-related in stopover migrants, e.g. in red-eyed vireos *Vireo olivaceus* it is not (Moore et al. 2003).

In the species which move constantly during their stopovers, at least under certain conditions, it is difficult to speak of search/settling period, just because they may never settle. In species which gain a small home range (or a temporary territory) in order to be able to improve their condition, exploration results in either settling or departure. However, other species may be exploring their stopover area during the whole stopover period without finally settling. Some pied flycatchers adopted this strategy during their spring stopovers on the Courish Spit (Chernetsov et al. 2004a), even though the same species held temporary territories during autumn stopovers in Portugal (Bibby and Green 1980). Obviously, this can occur either when exploration costs were low, or when benefits of exploring new areas were high. It has been suggested that clumped and unpredictable patterns of prey occurrence in both space and time could benefit such 'constant exploration' (Chernetsov et al. 2004a).

Exploitation of habitat

When migrants are settled (or continue to move broadly in the case of the constant exploration model) they obviously show a certain pattern of habitat use and habitat selection. Habitat use by stopover migrants is clearly non-random (Bairlein 1981, 1983, 1992; Hutto 1985a, b; Ormerod 1990, Moore et al. 1990). This pattern of habitat use is stable between different years when different individuals occur at the same stopover site (Bairlein 1981), which strongly suggests that the patterns observed are not incidental and are a characteristic of a species. Juveniles generally occur across a wider range of habitats than adults, which has been interpreted as evidence that their habitat selection is imperfect (Bairlein 1981, 1983), possibly due to displacement into suboptimal habitats by socially dominant adults (but see Moore et al. 2003). Some species are known to shift their habitat preferences during migration as compared with the breeding period, e.g. sedge warblers, which generally do not breed in reed stands, clearly select them during the post-fledging and post-breeding period and migration (Ormerod 1990; Chernetsov 1998).

Use of habitat out of proportion at stopover sites (e.g. Moore et al. 1990) indicates habitat selection. Habitat selectivity during stopover varies among species. Parnell (1969) found that some species of New World warblers were more broadly distributed across habitat types than others. Similarly, Berthold et al. (1991) report very different distributions across habitat types in various passerine European migrants. At a stopover site in Israel, two *Sylvia* species differed greatly in the range of habitats where they could gain weight (Sapir et al. 2004). As shown by radio tracking, European robins utilise a broad range of habitats during both autumn and spring migration on the Courish Spit (SE Baltic coast), from willow scrub on sand dunes to different types of forest (A Tsvey and P Ktitorov, in preparation). In the same area, sedge warblers are only found in wetland habitats (Chernetsov et al. 2004a). In general, passerine migrants seem to use a wider range of habitats at stopovers compared to breeding season, behaving as generalists in terms of habitat selection.

Pattern of habitat use differing between species is accompanied by varying pattern of spatial use. Linear size of home area at stopover might differ by at least one order of magnitude between different species of passerine nocturnal migrants, and the area may differ by two or three orders of magnitude (Fig. 1, Chernetsov 2005).

An interaction of several factors shapes the use of habitats after landing. During and after arrival at stopover, migrants select appropriate habitats in accordance with their innate preferences and functional morphology (Bairlein 1983, 1992), foraging strategies and food resource distribution (Hutto 1985a; Martin and Karr 1986; Chernetsov 1998; Chernetsov and Titov 2003), habitat carrying capacity (Hutto 1985b). Relative

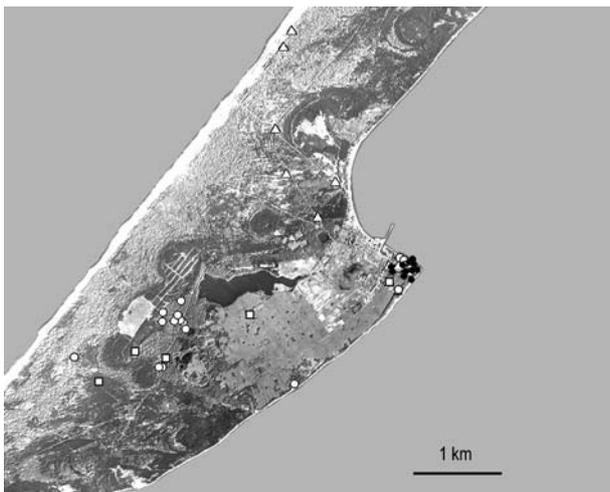


Fig. 1 Range of movements at daytime stopovers on the Courish Spit, SE Baltic, by radio-tagged pied flycatchers *Ficedula hypoleuca* (white symbols) and European robins *Erithacus rubecula* (black dots). Different white symbols refer to individual pied flycatchers in May 2003, and black dots refer to a single European robin in April 2003 with a typical movement pattern. Stopover duration 1–4 days in pied flycatchers, and 3 days in the European robin

predation hazard proved to be an important factor in trade-off between food supply and safety when birds select habitat type (Alerstam and Lindström 1990). Habitat selection during stopovers should be aimed at achieving at least two goals: to minimise the risk of predation and to maximise fuel deposition rate, or at least to achieve a certain threshold rate justifying the stopover. These two aims may compete (Fransson and Weber 1997; Dierschke 2003), i.e. (micro)habitats enabling the most rapid refuelling may leave foraging migrants more exposed to predators.

Another factor that can strongly influence habitat use and selection is competition. Strangely enough, there are not too many reports of food-based competition (Moore and Yong 1991, V. Salewski et al., submitted). However, I assume that this is mainly due to the difficulties of rigorously showing interference competition at stopovers rather than to the actual lack of competition. Density of conspecific and interspecific competitors may influence habitat quality and thus the pattern of habitat use by stopover migrants.

As already mentioned, the success of stopover, which probably should be measured as fuel deposition rate or, more immediately, feeding rate (assuming that the individual survives stopover), is not the same among all individuals. Age- and sex-related variation has been reported (Yong et al. 1998; Woodrey 2000; Heise and Moore 2003; Yosef and Chernetsov 2004, 2005), as well as a good deal of individual variation (e.g. Chernetsov et al. 2004b). Actual fuel deposition rate achieved at a given stopover site should be treated as a result of interaction between the particular individual migrant and the characteristics of the particular stopover location, among which habitat quality is one of the most important (Lindström 2003). In optimal migrations models, fuel deposition rate and the pattern of its variation between the sites (local, global or stochastic) is believed to be a major determinant of stopover duration and the whole organisation of migration (Hedenström and Alerstam 1997; Weber and Houston 1997b; Houston 1998; Chernetsov et al. 2004b). Therefore, habitat use and habitat selection appears to be very important for successful migration.

Large-scale spatial context

Whereas several responses to landscape structure have been discovered in migrants on breeding grounds, importance of large-scale spatial context is underestimated in studies of stopover ecology of passerines (Freemark et al. 1995). It is intuitively clear that migrants stopping over in, e.g., arid areas with very few stopover possibilities (Biebach 1990; Dolnik 1990) should select habitats on a different basis than birds which migrate across more ecologically hospitable areas. In the study by Martin (1980), density of migrants was inversely related to size of isolated shelterbelts during spring migration. At the same time, observations of

territoriality among stopover migrants (Rappole and Warner 1976; Kodric-Brown and Brown 1978; Bibby and Green 1980, 1981, Carpenter et al. 1983, 1993a, b) and density-dependence in settlement patterns and body condition (Viega 1986; Hansson and Pettersson 1989; Moore and Yong 1991; Shochat et al. 2002; Kelly et al. 2002; Ottich and Dierschke 2003) suggest that transients may compete with each other during stopovers. Since landscape features such as habitat area and patch isolation influence density and hence competition, it might be expected that fat deposition effectiveness depends on structure of habitat patch and adjusting landscape. Shochat et al. (2002) found that *Sylvia* warblers at stopovers in Israel were over-exploiting a poor habitat fragment as compared with a rich one. The pattern observed was different from prediction on the base of ideal free distribution model, and might be explained by effect of isolation (about 1 km distance between the patches).

Attempts were made to treat habitat selection on the landscape and regional scale (Simons et al. 2000). A most promising approach is to analyse stopover parameters, e.g. fuel deposition rate, stopover duration, etc., in relation to broader landscape context, and not just to the immediate vicinity of the trapping site (P. Ktitorov and F. Bairlein, in preparation). Habitat cover around the immediate location of the exact stopover site may be assessed by remote sensing and give a cue to overall habitat carrying capacity.

Temporary reverse migration in autumn has been discussed in the context of landscape and regional-scale habitat selection by migrating birds (Alerstam 1978; Åkesson et al. 1996; Åkesson 1999; Zehnder et al. 2002). When migrants confront an ecological barrier, e.g. a sea coast, some of them perform return movements. This allows them (particularly those with low fat reserves) to avoid intense competition for food and alleviate the risk of predation by moving inland to more suitable resting and feeding grounds before crossing a major barrier. This behaviour was reported for diurnal (Lindström and Alerstam 1986) and nocturnal migrants. However, a proportion of cases of northward movements by nocturnal migrants observed by radar and moon-watching in late summer/early autumn might not refer to return flights of emaciated nocturnal migrants, but rather to nocturnal postfledging movements. Such movements, long before migration and in different directions, including northerly ones, were found to occur in Eurasian reed warblers (Mukhin et al. 2005b), black-caps *Sylvia atricapilla* and garden warblers *S. borin* (A. Mukhin, unpublished data), and may be common in other passerine nocturnal migrants as well. As birds during postfledging movements carry smaller fuel stores than on migration (Bulyuk et al. 2000; Mukhin 2004), they may be mistaken for lean migrants performing temporary reverse movements. This is supported by the moon-watching data from the Balkan region where the proportion of reverse tracks decreased along the season from 35% in August to 18% in September and just 8% in October (Zehndjiev and Liechti 2003).

Zusammenfassung

Habitatwahl nachziehender Singvögel während des Zuges: Mechanismen und Konsequenzen

Habitatwahl und Habitatnutzung spielen eine wichtige Rolle für rastende Zugvögel. Zugvögel wählen ihre Rastplätze spezifisch, wenngleich auch viele Arten auf dem Zugweg von einer größeren Vielfalt an Habitaten Gebrauch machen als in den Brut- oder Überwinterungsgebieten. Die Rastplatzwahl lässt sich in eine Folge von Ereignissen untergliedern: Landung, Explorieren, Verteilen im und Nutzung des Habitats. Die Körperverfassung der Vögel hat Entscheidungseinfluss in wahrscheinlich allen diesen Phasen. Diese Arbeit untersucht diese Sequenz von Entscheidungsprozessen und die auf den verschiedenen Ebenen steuernden Faktoren für nachziehende Singvögel. Meist findet eine erste Habitatwahl bereits während der Landung statt, wobei visuelle und akustische Informationen benutzt werden. Nach der Landung in einem möglichen Rasthabitat explorieren die Zugvögel ihre Umgebung zunächst, um ihre Vorauswahl zu prüfen und weiter zu verfeinern. Während einige Arten dann schließlich die meiste Rastdauer über in einem eng begrenzten (Mikro-) Habitat verbringen, streifen anderen weiträumig und stetig umher. Ein Zusammenspiel verschiedener Faktoren formt die Habitatnutzung nach der Landung, darunter Instinktverhalten, funktionelle Morphologie, Fressstrategien, Nahrungsverteilung, Kapazität des Gebietes und Prädationsrisiko. Auch räumliche Zusammenhänge auf größerer Ebene scheinen bedeutsam zu sein, eine Komponente, die mehr Beachtung finden sollte.

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