Chapter 5
Habitat Selection and Use by Passerine Migrants

Abstract In this chapter I emphasize that qualitative stopover ecology should be studied in a close association with the stopover behaviour, primarily with habitat use and selection by migrants. During stopovers, migrating songbirds are confronted with unfamiliar habitats, whereas they need to forage efficiently and refuel quickly. The habitat use of migrants is non-random, and I analyse the process of habitat selection and use on the basis of capture data and of radio tracking results of passerine migrants at stopovers. I discuss hierarchical decision making process when ceasing migratory flights and selecting stopover habitat, and whether this process is age-related. The importance of broader landscape context for stopovers, apart from the immediate habitat structure, is emphasized.

5.1 Introductory Remarks

Success of migratory stopover should actually be measured as survival rate during stopover. However, as daily survival rates are difficult to measure and they are anyway very close to 1, fuel deposition rate, or more directly food intake rate may be used as a proxy (under the condition that the migrant survives the stopover). These parameters are not identical for all migrants, but vary with sex and age (Wang et al. 1998; Woodrey 2000; Heise and Moore 2003; Yosef and Chernetsov 2004, 2005) and individually (Chernetsov et al. 2004b). Actual FDR that is reached at a particular site is a result of interactions between an individual migrant and stopover site characteristics, of which habitat quality is one of the most important ones. FDR and the pattern of its variation (local, global, or stochastic) is one of the crucial factors governing stopover duration and the whole organisation of migration (Hedenström and Alerstam 1997; Weber and Houston 1997b; Houston 1998; Chernetsov et al. 2004b). Optimal habitat selection and its subsequent exploitation are most important for successful migration.

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5.2 Scales of Habitat Selection at Stopover

When a landbird migrant makes a stopover, it usually finds itself in unfamiliar surroundings, with food demands and competition not infrequently high (Hutto 1985b; Loria and Moore 1990; Moore and Wang 1991; Chernetsov 2006). Therefore, selection of optimal habitats is of great importance for refuelling migrants. Many migrants which breed at temperate and/or high latitudes and winter in the tropics, have to be able to select the appropriate habitat in boreal forests, steppes, highlands, deserts and tropical areas. Even birds that breed and winter within temperate areas may be challenged. A European robin that breeds in boreal forests of Scandinavia or northern Russia may spend its winter in savannah-like cork oak stands in Portugal or in the cliffs on the Black Sea coast, i.e. in habitats very much unlike its preferred nesting habitat.

It is usually assumed that when selecting optimal stopover habitats, migrants use a hierarchical chain of cues (Hutto 1985b; Moore et al. 2005; Buler et al. 2007; Deppe and Rotenberry 2008). It is also assumed that because migrants in different condition may have varying stopover aims, they may rely on different cues for their condition-dependent habitat assessment. For example, lean birds may need to refuel urgently, even at the cost of accepting predation risk, whereas their fatter conspecifics may be more interested in good shelter (Moore and Aborn 2000; Dierschke 2003; Wang and Moore 2005). When crossing arid areas, like the Sahara or Central Asian deserts, water may be the crucial resource.

The problem of habitat assessment may be especially acute for songbirds that migrate at night and often solo. Captures in the early morning hours, i.e. immediately after ceasing migratory flights, show that the results of initial habitat (pre)selection that occurs prior to and during landfall are usually very 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 (Mukhin et al. 2005). 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. under the conditions of poor visibility, like rain of fog (Jenni 1996).

Habitat selection seems to occur during the daylight during and after landfall and is probably mainly based on visual cues. However, birds that land in twilight, i.e. in poor visibility, may also rely on visual cues. It has been reported that Eurasian reed warblers that were landing after a nocturnal flight have mistaken maize stands (a vertically structured habitat) for their optimal habitat, reedbed. This mistake was corrected in the daytime by movements to the optimal habitat (Degen and Jenni 1990). It should be however noted that plum aphids, the preferred food of *Acrocephalus* warblers, may occur in maize, and these birds are known to occur and to forage in maize fields (John Walder, “personal communication”). Therefore, landfall into a maize field may have been a deliberate decision by the birds and not a result of imperfect habitat assessment.

The hierarchical chain of events during habitat selection looks as follows: (1) habitat (pre)selection when still airborne; (2) landfall; (3) redistribution across (micro)habitats, or search; (4) settling; and (5) exploitation of the home range where the migrant has settled. The first link in this chain, preselection when still in flight, is often omitted, but it may be actually an important event that, if performed correctly, greatly simplifies the rest. Cochran et al. (2008) found a specific wingbeat pattern in two species of North American *Catharus* thrushes and in the wood thrush during what they called the final descent phase of nocturnal migratory flight. Wingbeat frequency and the percentage of pauses increased, suggesting slower ground speed, possibly to have a better look at the landscape beneath the birds.

All these events are most probably condition-dependent: individuals with different level of fuel stores may have different objectives during stopovers and different demands for the habitats. During flights across the eastern Sahara lean woodland Palaearctic migrants (e.g. willow warblers) were mainly found in the oases, whereas fatter individuals occurred across a wide range of habitats in the desert (Biebach et al. 1986; Biebach 1990). The same pattern was reported from the western Sahara (Bairlein 1985). It seems that fatter birds were not necessarily trying to refuel, but were just waiting for the night and cooler air temperatures to continue migration. The same reason could explain why in Central Asia most songbird migrants captured in oases were lean, whereas birds trapped in the desert were on average fatter (Dolnik 1990).

Migrants with large fuel stores may be not trying to further increase them, but to emphasize their safety and thus be inactive. They should prefer safer habitats, not necessarily proving good foraging opportunities. Leaner individuals that need to refuel may be more interested in occupying a temporary home range in an optimal habitat that would allow them to reach a high FDR (Chernetsov 2005; Chernetsov and Mukhin 2006). On the other hand, very lean, emaciated migrants may be in dire need to forage immediately and use any opportunity to refuel, without being too finicky about choosing the habitat.

5.3 Role of Individual Experience

Waterfowl and waders that often migrate with discrete stopover opportunity (i.e. they have a limited number of suitable stopover places along their migratory routes) apparently often use the same traditional stopovers year after year (Pienkowski 1976; Evans and Townsend 1988; Pfister et al. 1998; Fox et al. 2002). Whether passerines that usually enjoy continuous stopover opportunity do the same, is an object of discussion.

Long-term trapping project at the Biological Station Rybachy on the Courish Spit during 55 years (1957–2011) did not result in evidence of individual fidelity to stopover sites, in spite of large trapping figures (tens of thousands of individuals trapped annually, a total exceeding 2.7 million captures; Bolshakov et al. 2001, 2002, 2011). It is however worth noting the trapped individuals comprise just a fraction of birds that annually fly over the Courish Spit (Bolshakov 1981; Dolnik et al. 1981). It should be emphasized that flying over the same part of migratory route, known e.g. for Indian sparrows *Passer indicus* and Spanish sparrows *P. hispaniolensis* on Chokpak pass in western Tien Shan Mountains (Gavrilov 1998), is a matter of navigation mechanisms used on migration (Mouritsen 2003); we focus here on repeated using of the same stopover sites.

The often-cited studies that claimed that a substantial proportion of migrants repeatedly used the same stopover sites were performed in Spain (Cantos and Tellería 1994) and in Israel (Merom et al. 2000). The latter study reported a high stopover site fidelity in Eurasian reed warblers (22%, 27 birds out of 123) which is not significantly different from the breeding site fidelity of the same species at the same site (27%, 210 out of 773; $\chi^2 = 1.48$, $p = 0.22$). However, these authors excluded all birds that were only captured in one year which is an unorthodox assumption that might need re-evaluation, as stressed by Catry et al. (2004). A detailed and careful analysis of ringing data from Portugal performed by the authors of the latter paper showed that recurrence of songbirds at their previous year stopover sites was low and did not exceed the values that should be expected from random occurrence within the species-specific optimal habitats. Interestingly enough, birds of wetland habitats that occur sporadically in the Mediterranean region did not show a much higher stopover site fidelity than habitat generalists like e.g. willow warbler and pied flycatcher (Catry et al. 2004). Another report of stopover site fidelity in the bluethroat (Panov 2008) comes from the northern boreal forest of Karelia where these migrants occur in habitat islands in the sub-optimal taiga matrix (Panov 2012).

Generally, it may be concluded that the role of previous experience with a particular stopover site is mostly negligible even in experienced migrants.

5.4 Termination of Migratory Flights

Very few field data is available on when and how nocturnal passerine migrants complete their flights. It is commonly accepted that songbirds that are not crossing ecological barriers take off within a narrow time window after sunset, fly during several hours and cease their flight soon after midnight, i.e. in the darkness long before sunrise (Moore 1987; Kerlinger and Moore 1989). This idea is based on radar data; its critique and new data are given in Sect. 7.1. On the basis of this concept, and because nocturnal migrants usually select the landing habitat rather exactly, it has been hypothesised that habitat selection takes place after sunrise, most probably in the early morning (Moore et al. 1993, 1995). It is believed that 'morning flights', known for many species of nocturnal migrants, support this view (Gauthreaux 1978; Bingman 1980; Wiedner et al. 1992; Yaukey 2010). It should be however kept in mind that morning flight may not be mainly habitat-related, but aimed to compensate for orientation errors and wind drift during the preceding nocturnal flights (Bingman 1980; Moore 1990). The question when songbirds terminate their nocturnal flights is discussed in Sect. 7.3.

Rapid selection of high-quality habitat allows migrants to gain access to stopover resources ahead of competitors (Thompson et al. 2003; Mettke-Hoffmann and Gwinner 2004). Individuals that manage to make selection quickly get an advantage. Therefore, natural selection should probably support habitat selection at an early stage, maybe even before landing, i.e. when ending migratory flights. Two possible strategies of habitat assessment can be used: birds either sample the suitability of the habitat on their own (direct sampling) or use cues from other birds that are already present in a particular habitat (cue using according to Mönkkönen et al. 1999). Cue using allows birds to assess habitats from a distance without sampling, thus making the process more rapid.

Nocturnally migrating songbirds are known to respond to playback of conspecific (Herremans 1990b; Mukhin 2004; Alessi et al. 2010) and heterospecific song (Herremans 1990a) by landing close to the playback site. This response forms the basis of the tape-luring method (Herremans 1990a, b; Schaub et al. 1999; Bulyuk et al. 2000; Mukhin 2004; Mukhin et al. 2005, 2008). We made a study which showed that under some circumstances, in particular during landing before sunrise, acoustic distant cues may be used and prevail over visual stimuli. We have also shown that distant sampling on the basis of acoustic cues is more typical of habitat specialists, wetland specialists in particular, and that during autumn passage adults use acoustic information more actively than hatching-year first-time migrants (Mukhin et al. 2008).

We analysed capture data from two sites on the Courish Spit, at an optimal habitat on Cape Rossitten and at a suboptimal habitat in sandy dunes covered by willow scrub and compared them with historic data on birds killed at lighthouses in Denmark during nocturnal migratory flights in 1886–1939 (Hansen 1954). We tape-lured songbird migrants at a specially selected playback site situated in the transition gap between pine plantations and high sand dunes partly covered with willow scrub (Mukhin et al. 2008). The nearest wetlands were located 4 km to the southwest and 10 km to the northeast of the study site. We considered the dunes where the song playback experiment was performed as a suboptimal habitat for *Acrocephalus* species whose songs we played, because only 175 Eurasian reed warblers and 190 sedge warblers had been captured in stationary funnel traps located 150 m off over a 45 year period (see Sect. 5.2). These long-term trapping data indicate that this site is rarely used by wetland birds, in particular by *Acrocephalus* warblers, under natural conditions.

At night the songs of several passerine species (Eurasian reed warbler, marsh warbler *Acrocephalus palustris*, sedge warbler, pied flycatcher) were played by two car tape players with 30 W loudspeakers. After sunset, we checked the mist-nets on an hourly basis throughout the night. The birds captured earlier than two

Table 5.1 Numbers of birds tape-lured in the suboptimal habitat during the deep night in autumn on the Courish Spit as compared with the numbers killed at lighthouses in Denmark (from the nocturnal flow of migrants)

Species	Tape-luring		Lighthouses, night		χ^2	p
	n	%	n	%		
Great reed warbler	3	0.84	1	0.02	21.5	<0.0001*
Marsh warbler	5	1.40	7	0.13	19.9	<0.0001*
Sedge warbler	27	7.56	142	2.66	26.2	<0.0001*
Eurasian reed warbler	224	62.75	62	1.16	26.45	<0.0001*
Tree pipit	0	0.00	135	2.53	8.2	0.004**
Bluethroat	2	0.56	9	0.17	1.02	0.31
Icterine warbler	0	0.00	68	1.28	3.59	0.058
Red-backed shrike	1	0.28	16	0.30	0.19	0.66
Grasshopper warbler	**2**	**0.56**	**16**	**0.30**	**0.13**	**0.72**
Pied flycatcher	0	0.00	751	14.08	56.7	<0.0001**
Spotted flycatcher	0	0.00	17	0.32	0.32	0.57
Northern wheatear	0	0.00	765	14.35	57.9	<0.0001**
Common redstart	1	0.28	1178	22.09	95.6	<0.0001**
Willow warbler	0	0.00	757	14.20	57.2	<0.0001**
Whinchat	2	0.56	50	0.94	0.19	0.66
Blackcap	22	6.16	267	5.01	0.70	0.40
Garden warbler	61	17.09	854	16.02	0.21	0.65
Whitethroat	4	1.12	163	3.06	3.75	0.053
Lesser whitethroat	2	0.56	59	1.11	0.50	0.48
Barred warbler	1	0.28	15	0.28	0.26	0.61

*The proportion in tape-luring captures is significantly higher than in the flow of migrants
**The proportion in tape-luring captures is significantly lower
Habitat specialists are marked bold

hours before sunrise were considered to be trapped during the deep night, and those captured less than two hours before sunrise, at dawn.

Tape-luring data from a suboptimal habitat were compared with captures in reeds and scrub on the coast of the Courish Lagoon 11 km from site 1. At site 2 which was located in the habitat optimal for *Acrocephalus* warblers and other long-distance passerine migrants, captures occurred without playback. A total of 2,607 birds of 42 species were tape-lured; however, only 17 species were captured during the deep night, before twilight. These birds were with certainty diverted from the flow of migrants aloft by song playback, and not captured during morning movement. The bulk of birds was formed by the Eurasian reed warbler, sedge warbler, garden warbler, blackcap and grasshopper warbler (Tables 5.1–5.4; however, the latter species was only common in twilight captures in autumn). The proportions of other species were low. It is worth noting that such wetland non-passerines as one water rail *Rallus aquaticus*, two spotted crakes *Porzana porzana* and one common sandpiper *Actitis hypoleucos* were tape-lured attracted by Eurasian reed warbler song.

Table 5.2 Numbers of birds tape-lured in the suboptimal habitat in the morning twilight in autumn on the Courish Spit as compared with the numbers captured during daytime in the optimal habitat without song playback

Species	Tape-luring		Optimal habitat, day		χ^2	p
	n	%	n	%		n
Great reed warbler	3	0.47	1	0.38	0.14	0.71
Marsh warbler	10	1.56	10	3.82	3.38	0.066
Sedge warbler	147	22.97	33	12.60	12.5	0.0004*
Eurasian reed warbler	242	37.81	61	23.28	17.6	<0.0001*
Tree pipit	2	0.31	1	0.38	0.22	0.64
Bluethroat	5	0.78	5	1.91	1.35	0.26
Icterine warbler	1	0.16	1	0.38	0.02	0.90
Red-backed shrike	1	0.16	0	0.00	0.21	0.64
Grasshopper warbler	59	9.22	7	2.67	10.8	0.01*
Pied flycatcher	4	0.63	7	2.67	4.88	0.027
Spotted flycatcher	1	0.16	6	2.29	8.4	0.038**
Northern wheatear	3	0.47	0	0.00	0.22	0.64
Common redstart	8	1.25	17	6.49	17.04	<0.0001**
Willow warbler	7	1.09	29	11.07	45.7	<0.0001**
Whinchat	8	1.25	1	0.38	0.68	0.41
Blackcap	49	7.66	55	20.99	31.1	<0.0001**
Garden warbler	81	12.66	23	8.78	2.74	0.098
Whitethroat	6	0.94	0	0.00	1.26	0.26
Lesser whitethroat	3	0.47	5	1.91	2.9	0.089
Barred warbler	0	0.00	0	0.00	–	–

*The proportion in tape-luring captures is significantly higher than in the optimal habitat
**The proportion in tape-luring captures is significantly lower
Habitat specialists are marked bold

In both migratory seasons the vast majority of captures during the night consisted of the Eurasian reed warbler (63% of captured in spring and 91% in autumn), whereas the proportion of this species in the flow of migrants was very low (Tables 5.1, 5.3). In spring other *Acrocephalus* warblers were also overrepresented in song playback captures as compared with the flow of migrants (Table 5.3). At the same time, the common redstart *Phoenicurus phoenicurus*, northern wheatear, pied flycatcher and some other songbirds were underrepresented in song playback captures (Tables 5.1, 5.3). This suggests that Eurasian reed warblers and to some extent their congeners were indeed lured by playing back the Eurasian warbler song to the sandy dunes where they normally do not occur (Mukhin et al. 2005, 2008). The same follows from comparisons of morning tape-luring captures in the sand dunes (site 1) and captures in the optimal habitat without song playback (site 2): in the former case, *Acrocephalus* warblers were more common (Tables 5.2, 5.4). Our data agree with the findings of Alessi et al. (2010) that yellow-breasted chats *Icteria virens* are also lured into unsuitable habitat by broadcast of their song.

Table 5.3 Numbers of birds tape-lured in the suboptimal habitat during the deep night in spring on the Courish Spit as compared with the numbers killed at lighthouses in Denmark (from the nocturnal flow of migrants)

Species	Tape-luring		Lighthouses. night		χ^2	p
	n	%	n	%		n
Great reed warbler	1	0.64	0	0.00	4.14	0.042*
Marsh warbler	1	0.64	1	0.03	1.63	0.20
Sedge warbler	4	2.56	162	5.61	2.1	0.15
Eurasian reed warbler	142	91.03	9	0.31	25.64	<0.0001*
Tree pipit	0	0.00	39	1.35	1.2	0.27
Bluethroat	0	0.00	11	0.38	0.01	0.93
Icterine warbler	0	0.00	5	0.17	0.24	0.62
Red-backed shrike	3	1.92	15	0.52	2.86	0.09
Grasshopper warbler	0	0.00	2	0.07	1.63	0.20
Pied flycatcher	0	0.00	414	14.34	24.7	<0.0001**
Spotted flycatcher	0	0.00	19	0.66	0.24	0.62
Northern wheatear	0	0.00	528	18.28	33.2	<0.0001**
Common redstart	1	0.64	523	18.11	30.5	<0.0001**
Willow warbler	1	0.64	734	25.42	48.2	<0.0001**
Whinchat	0	0.00	177	6.13	9.06	0.003**
Blackcap	0	0.00	31	1.07	0.79	0.37
Garden warbler	0	0.00	36	1.25	1.05	0.31
Whitethroat	1	0.64	135	4.67	4.74	0.029**
Lesser whitethroat	1	0.64	44	1.52	0.3	0.58
Barred warbler	1	0.64	3	0.10	0.45	0.50

*The proportion in tape-luring captures is significantly higher than in the flow of migrants
**The proportion in tape-luring captures is significantly lower
Habitat specialists are marked bold

Our data suggest an important role of acoustic cues in habitat recognition during both spring and autumn migration. It is noteworthy that in autumn, adult Eurasian reed warblers were more attracted by song playback than first-autumn birds. In 1999–2001, after 1 August adults made 15.6% of tape-luring captures ($n = 546$) and just 6.0% of captures at site 2 without song playback ($n = 801$; $\chi^2 = 33.4$, $p < 0.001$). The reason for this age-related difference might be that adults, unlike juveniles, have heard species-specific song and have better experience of using acoustic information in different contexts. On the other hand, in coastal areas (like the Courish Spit) the age ratio at stopovers may be biased towards juveniles as compared with the numbers aloft (coastal effect; Payevsky 1985, 1998, 2009). An increased proportion of individuals attracted by song playback from the flow of migrants (which includes proportionally more adults than found at stopovers) may cause an increased proportion of adults in tape-luring captures, reported in Eurasian reed warblers (Mukhin et al. 2005) and in bluethroats in northern Karelia (Panov and Chernetsov 2010b).

Response by first-autumn birds to the species-specific song in autumn, when *Acrocephalus* warblers are no longer singing, suggests an endogenous mechanism

Table 5.4 Numbers of birds tape-lured in the suboptimal habitat in the morning twilight in spring on the Courish Spit as compared with the numbers captured during daytime in the optimal habitat without song playback

Species	Tape-luring		Optimal habitat, day		χ^2	p
	n	%	n	%		n
Great reed warbler	4	1.90	1	0.26	2.73	0.0990
Marsh warbler	2	0.95	60	15.35	29.00	<0.0001
Sedge warbler	49	23.33	48	12.28	12.30	0.0004*
Eurasian reed warbler	116	55.24	122	31.20	27.40	<0.0001*
Tree pipit	1	0.48	1	0.26	0.09	0.7700
Bluethroat	1	0.48	1	0.26	0.09	0.7700
Icterine warbler	1	0.48	1	0.26	0.09	0.7700
Red-backed shrike	0	0.00	1	0.26	0.10	0.7500
Grasshopper warbler	6	2.86	15	3.84	0.15	0.7000
Pied flycatcher	2	0.95	15	3.84	3.15	0.7600
Spotted flycatcher	1	0.48	5	1.28	0.26	0.6100
Northern wheatear	0	0.00	1	0.26	0.10	0.7500
Common redstart	0	0.00	21	5.37	10.15	0.0014**
Willow warbler	4	1.90	5	1.28	0.06	0.8000
Whinchat	7	3.33	11	2.81	0.01	0.9200
Blackcap	1	0.48	35	8.95	15.90	0.0001**
Garden warbler	1	0.48	9	2.30	1.78	0.1800
Whitethroat	8	3.81	25	6.39	1.30	0.2500
Lesser whitethroat	6	2.86	14	3.58	0.05	0.8200
Barred warbler	0	0.00	0	0.00	–	–

*The proportion in tape-luring captures is significantly higher than in the optimal habitat
**The proportion in tape-luring captures is significantly lower
Habitat specialists are marked bold

of habitat recognition on the basis of acoustic stimuli. This mechanism that we have experimentally triggered in autumn normally functions during the spring migration. The song of adult males that are the first to arrive in spring (Payevsky 1985) is a marker of optimal habitat. We have hypothesised that this mechanism may be switched on already in wintering areas, where first-winter Eurasian reed warblers may use the singing of African reed warblers *Acrocephalus baeticatus* which is very similar to the song of the Eurasian species (Cramp 1992). A recent study of the process of the future breeding site selection in black-throated blue warblers *Dendroica caerulescens* showed that juveniles responded to the playback of adult song, i.e. use it as a cue to habitat suitability, already during the postfledging movements (Betts et al. 2008). This finding makes the use of acoustic stimuli during the autumn migration by *Acrocephalus* warblers for habitat recognition less astonishing.

Most interesting is the response to heterospecific song. A total of 17 species responded to the Eurasian reed warbler song during the four years of study (Mukhin et al. 2005). Most of these birds were other *Acrocephalus* warblers. The most obvious response was shown by the sedge warbler, both to its own song and to the Eurasian reed warbler song. On the other hand, playing back the redwing *Turdus iliacus* song on 7–25 May 2002 attracted as few as nine individuals: three lesser whitethroats, two red-backed shrikes, a marsh and a reed warbler, a European robin and a whinchat *Saxicola rubetra* (one individual of each species). Only three birds were captured before twilight. Not every bird song is attractive, but only that of species typical of certain habitats (wetlands in particular) which may be acoustic markers of such habitat (Mukhin et al. 2008). Distant markers that make indirect estimates of habitat quality possible may be more relevant for habitat specialists, especially those preferring fragmented habitats. However, birds with more general patterns of habitat use, like North American thrushes, also seem to be using distant cues. In the final phase of nocturnal flights thrushes change their flight direction and increase wingbeat frequency (Bowlin et al. 2005; Cochran et al. 2008), probably to decrease their ground speed. Most probably these (and maybe other) migrants visually explore the landscape and choose the site to land.

5.5 Search for Home Range and Settling

5.5.1 Range and Pattern of Morning Movements

After landing, migrants sample habitat quality at their new stopover site. Movements of newly grounded migrants often result in the morning peak of captures in standardised trapping projects, familiar to every bird ringer (Dolnik and Yablonkevich 1985; Brensing 1989; Berthold et al. 1991; Titov 1999b).

It should be emphasized that ‘morning flights’ of nocturnal migrants (see the previous section) are not the morning peak of captures. Morning flights occur not everywhere and not all the time. They occur above the canopy and always higher than standard mist-nets are normally put up (usually their upper edge is 2–2.5 m above the ground). Birds that participate in morning flight are usually not captured in mist-nets. These flights most probably are performed to compensate wind drift or to move inland from the coast (Gauthreaux 1978; Bingman 1980), not to select optimal habitat. Conversely, the morning peak of movements within the canopy (and thus of captures) does suggest that fine-tuning of (micro)habitat selection in many passerine nocturnal migrants occurs during several hours after sunrise.

Some nocturnal migrants, e.g. European robins, perform longer movements (for 1–2 km), mainly within several hours after sunrise (Chernetsov 2005; Chernetsov and Mukhin 2006; Tsvey 2008). During the first day of stopover in spring and the first two days in autumn, radio-tagged European robins on the Courish Spit moved more broadly than in subsequent days, as shown by the daily values of the linearity index of their movements (Chernetsov and Mukhin 2006). Summer tanagers behave in a similar manner (Aborn and Moore 1997), and several other North American nocturnal migrants may also cover up to 2.0–2.5 km before they settle

(Taylor et al. 2011). However, other species, e.g. pied flycatchers, may perform relatively long movements (for several kilometres) during any day of stopover, also several days after their arrival (Chernetsov et al. 2004a). Such relatively long-distance movements of pied flycatchers and possibly other species should not be regarded as extended search. It seems more correct to say that in some species the exploitation of resources at stopover is based on broader movements than in others.

5.5.2 Search and Settling Time

As already mentioned, search and settling time varies between several hours (some individuals may occupy their home range very quickly, within minutes) and one, rarely two, days. European robins do not start to gain mass until they occupy a limited home range (Titov 1999a). The search/settling period apparently is usually characterised by negative FDR. Therefore time which a migrant is ready to invest into search and settling is an important parameter that influences its optimal migration strategy (Weber and Houston 1997a; Chernetsov et al. 2004b). Its value most probably depends on fuel stores at arrival (Chernetsov et al. 2004b). Time that a migrant is ready to spend exploring the stopover area should depend on temporal and energetic costs of exploration and on potential benefits that this information may bring (Aborn and Moore 1997). Both costs and benefits are likely condition-dependent. One can imagine that individuals with relatively large fuel stores may venture to be choosy, and maybe even to skip a site that cannot provide them with sufficiently high FDR and to depart during the next night. Continuing our metaphor of a human job seeker, someone with large personal means may choose to remain unemployed and continue looking for a perfect job for a longer time than someone who has bills that must be urgently paid. On the other hand, fatter birds may decide to continue flight in the next night anyway and not invest into looking for a good stopover site. In this case they should conserve energy and remain stationary. This was what fat Eurasian reed warblers tape-lured into a poor habitat on the Courish Spit did (Ktitorov et al. 2010).

Our radio-tagging study of stopover duration and stopover spatial behaviour of fat and lean European robins on the Courish Spit did not show any clear relationship between arrival fuel load and stopover behaviour (Chernetsov and Mukhin 2006). The area of the individual home range did not differ between robins that arrived fat ($n = 5$) and that arrived lean ($n = 8$; t-test, $t = 0.44$; $p = 0.67$). In the first two days of stopover, linearity of movements was not condition-related, either. It is especially interesting that the linearity index of movements on the first day upon arrival did not differ between the birds that departed after the first day and those that stopped over for a longer period (Chernetsov and Mukhin 2006). This means that the pattern of movements of a freshly arrived European robin does not allow prediction whether it is going to depart or to stay, i.e. whether it is a flyer or a feeder.

Table 5.5 Proportions of first-autumn birds among song thrushes and blackbirds captured on the Courish Spit in autumn (stationary funnel traps, passive and active trapping in mist-nest) and in the flow of nocturnal migrants in Denmark (Hansen 1954)

Species	Proportion of juveniles, %			
	Nocturnal flow	Stationary traps	Passive mist-netting	Active mist-netting
Song thrush	37.4	6.5 ± 0.7	3.5 (1.5–4.4 in various years)	15.7 (n = 51)
Blackbird			♂♂13.6; ♀♀ 15.1 (7.7–18.3 in various years)	50 (n = 30)

5.5.3 Coastal Effect: Are Movements of Migrants Age-Related?

Mobility of migrants immediately after landing may also depend on the age of birds. This is suggested by the analysis of the coastal effect, which is the abnormally high proportion of juveniles (first-autumn birds in autumn and second-year individuals in spring) among nocturnal migrants captured on the coasts of large water bodies (Ralph 1978, 1981; Dunn and Nol 1980; Payevsky 1998, 2009). The causes of this phenomenon remain unclear. It is usually assumed that the coastal effect is caused by differential behaviour of adults and juveniles when ceasing flight over large water bodies: juveniles go to the nearest land, whereas adults more often continue further inland where they may expect better-quality habitats (Payevsky 1985, 2009).

Our trapping data on song thrushes and blackbirds *Turdus merula* at stopovers on the Courish Spit suggest that in these species the coastal effect may be partly explained by differential mobility of adults and juveniles. When the birds were flushed into the nets (so-called ‘active trapping’) the proportion of adults in capture was higher than during the routine ‘passive’ trapping (Table 5.5). One may expect that when stopover migrants are flushed into the nets, adults and juveniles should be captured proportionally to their occurrence in the vicinity of the nets, or at least that age-related bias should be substantially lower than when captures result from spontaneous movements only. The reason for the increased mobility of juveniles might be their subordinate social status (Gauthreaux 1978) which has also been recorded at stopovers (Woodrey 2000). Because of that juveniles may spend more time and move more before they finally manage to occupy their own home range.

It is however worth noting that during passive trapping of migrating song thrushes in the Dzhanybek oasis in the semi-desert of western Kazakhstan (an inland site), the proportion of adults in autumn 2004 was 18.4% (n = 103), i.e. it was very similar to the value found during active trapping on the Courish Spit (coastal site; Table 5.5: Yates-corrected $\chi^2 = 0.04$, $p = 0.84$). We did not do active trapping in Dzhanybek, but a significantly higher proportion of adult song thrushes there strongly suggests that age-related mobility of stopover migrants may be only a partial explanation of the coastal effect.

In the European robin on the Courish Spit, proportions of adults did not differ between active and passive trapping in mist-nets (spring: 14.3 and 13.3%, $n = 233$ and $n = 389$, respectively; $\chi^2 = 0.14$, $p = 0.70$; autumn: 5.1 and 5.0%, $n = 156$ and $n = 685$, respectively; $\chi^2 = 0.01$, $p = 0.93$). For comparison, at autumn stopovers in Dzhanybek the proportion of adults during passive trapping was 25.0% ($n = 280$). Thus, for the European robins we have no reason to assume the age-related level of mobility during search and settling at stopover. It may be mentioned that social status of migrants does not always depend on age, e.g. red-eyed vireos showed no age-related difference in status (Moore et al. 2003).

An explanation of coastal effect that does not involve differential mobility is age-related migration strategy. We have shown that first-autumn bluethroats in northern Karelia have lower FDR than the adults and make longer stopovers more often, whereas adults frequently stop over for one day only (Panov and Chernetsov 2010a). Adult bluethroats (and possibly other nocturnal migrants) may be underrepresented in captures because of their brief stopovers, whereas their proportion among migrants aloft may be significantly higher (e.g. Mukhin et al. 2005), representative of their actual population productivity. If and when age-related variation in the length of migratory flights and stopover duration is smaller (e.g. at some inland sites, for instance in western Kazakhstan), the coastal effect may be absent.

5.5.4 Broad Movements Throughout Stopover

Within species that move long distances (at the scales of several kilometres) during their migratory stopovers it probably makes little sense to speak of the search/settling period, for the simple reason that they never settle. Species that need to occupy a limited home range to start gaining mass, usually either settle or resume migration. Another possible option would be to perform a landscape-scale nocturnal flight for a distance of 5–30 km, as recently reported for Swainson's thrushes, hermit thrushes, black-throated blue warblers and white-throated sparrows *Zonotrichia albicollis* (Mills et al. 2011; Taylor et al. 2011). However, some species may exploit stopover resources when making relatively broad-scale daytime movements, as found in e.g. pied flycatchers on the Courish Spit (Chernetsov et al. 2004a), garden warblers (Fransson et al. 2008) and probably other species (Taylor et al. 2011). The overall distance that pied flycatchers covered during their daytime movements reached 4.0 km (Chernetsov et al. 2004a), and it should be emphasized that (1) this distance was not covered on the first day upon arrival; and (2) this is a minimum estimate, because the bird in question was lost when moving through dense forest. In reality they may have covered even longer distance (Table 5.6, Fig. 5.1). Garden warblers on Crete moved up to 5 km during stopover (Fransson et al. 2008).

This behaviour contrasts sharply with the behaviour of European robins that usually remain within a much more limited area (Fig. 5.1). Such a strategy of habitat exploitation by the pied flycatcher (and possibly by some other species) may result from relatively low costs of exploratory behaviour and/or high benefits

Table 5.6 Parameters of diurnal movements of radio-tagged pied flycatchers during their stopovers on the Courish Spit. For the individuals lost during their movements, minimum estimates are given

#	Tagging date	Tagging time	Stopover duration,days	Result of tracking	Location number	Overall distance moved (km)	Distance moved daily (km)	Linearity index of movements
006	28.04	7:50	≥1	Lost	8	3.80	3.80	0.910
013	29.04	9:50	≥3	Lost	20	4.00	3.04; 0.84; 1.02	0.589
021	30.04	14:50	2	Nocturnal departure	10	3.10	0.13; 3.10	0.730
027	02.05	11:50	1	Nocturnal departure	34	0.41	0.41	0.077
037	02.05	15:50	≥4	Lost	47	2.30	0.19; 0.17; 0.06; 2.30	0.108
041	08.05	14:10	1	Nocturnal departure	14	0.41	0.41	0.061
059	12.05	12:10	1	Nocturnal departure	8	0.27	0.27	0.474

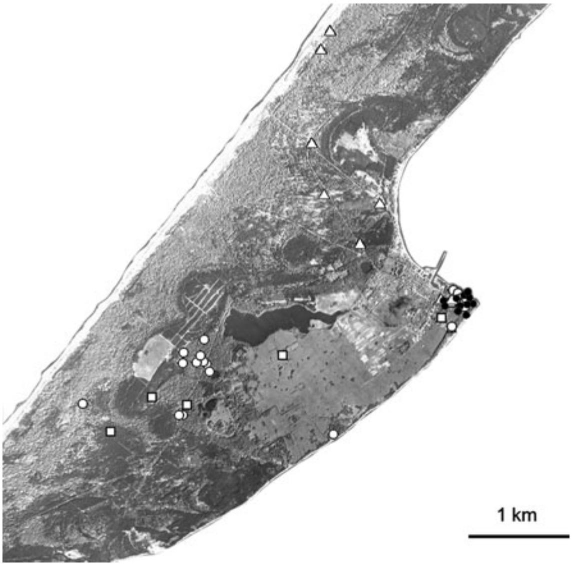

Fig. 5.1 The range of movements of pied flycatchers (*white* symbols) and European robins (*black dots*) during spring migratory stopovers. Different *white symbols* represent different pied flycatcher individuals in May 2003; black dots refer to the single European robin in April 2003. The stopover duration was 1–4 days in pied flycatchers and 3 days in the European robin

for exploring new areas, which is probably the case on the Courish Spit in spring. It is worth noting that during autumn stopovers in Portugal pied flycatchers reportedly occupy temporary territories, i.e. use a totally different strategy (Bibby and Green 1980). This contrasting stopover behaviour by the same species is most probably related to exploitation of different habitats, i.e. habitat dictates spatial strategy.

5.6 Habitat Exploitation

5.6.1 Non-Random Habitat Use

When migrants occupy a home range (if their spatial strategy includes this option), or during their broad movements across habitat, they apparently select and use habitats in a non-random manner (Bairlein 1981, 1983, 1992; Hutto 1985a, b; Ormerod 1990; Moore et al. 1990, 1993). As shown by capture results in different years at a standardised trapping site where the nets are located in exactly the same places year after year, the species-specific patterns of occurrence across habitats remain constant, even though the site is visited each year by different individuals (Bairlein 1981). This shows that the observed pattern is non-random and is typical of each species. First-autumn individuals usually utilise a broader spectrum of habitats than adults, which is usually explained by their less perfect ability to select the optimal habitat (Bairlein 1981, 1983). Another possible explanation of age-related difference in habitat use is that juvenile birds are displaced by adults into suboptimal habitats. Some songbird species alter their habitat preferences during the migratory period as compared to the breeding season. For instance, sedge warblers that usually do not breed in reedbeds, apparently prefer this habitat during their postbreeding and postfledging movements and during autumn and spring migration (Chernetsov 1998). Eurasian reed warblers redistribute within the reed stands: during the period of migration they start using loose stands that provide food but are poorly suitable for building nests (Chernetsov 1998). Migrating European robins and blue tits *Cyanistes caeruleus* during autumn passage spend much time and actively forage in reedbeds that are not used by these species during their breeding season.

The degree of habitat selectively varies between the species. Parnell (1969) found that some New World warblers used a broader array of habitats than others. Similarly, different European songbird migrants vary in their habitat selectivity (Bairlein 1983, Berthold et al. 1991). Whereas European robins occur within a very broad range of habitats, from different forest types through willow scrub on sandy dunes (Tsvey 2008) and even to reedbeds (see above), e.g. Eurasian reed warblers and sedge warblers normally only occur in reed stands during migration, and when tape-lured into other habitats invariably depart at the first opportunity (i.e. during the first night; Ktitorov et al. 2010).

5.6.2 Factors that Govern Habitat Selection by Migrants

The pattern of habitat exploitation is defined by a combination of several factors: endogenous preferences and functional morphology (Bairlein 1983, 1992), foraging strategy and the spatial distribution of food (Hutto 1985a; Martin and Karr 1986; Chernetsov 1998; Titov 2000; Chernetsov and Titov 2003), habitat carrying capacity and density of competitors (Hutto 1985b). Besides, predation risk is another important habitat characteristic which significantly influences the appeal of a habitat to stopover migrants (Alerstam and Lindström 1990; Dierschke 2003; Lank and Ydenberg 2003; Sapir et al. 2004).

These factors deserve special attention. Endogenous habitat preferences based on morphology during migration probably do not differ much from other parts of the annual cycle. At least, no data suggests it. Apparently, species morphologically adapted e.g. to reedbeds with their vertical structure, e.g. Eurasian reed warblers and great reed warblers *Acrocephalus arundinaceus* (Winkler and Leisler 1985; Leisler et al. 1989), will use such habitats also during migration. Moreover, such species have special behavioural adaptations that make it easier for them to locate the patches of this specific and highly fragmented habitat (Sect. 5.4).

It should not be assumed, however, that all migrating songbirds must use the same habitats during migration and wintering that they utilise during the breeding season. I have just mentioned the use of reedbeds by European robins and blue tits. Our stomach flushing data suggest that during autumn passage on the Courish Spit, willow warblers actively feed on plum aphids that they collect in the reedbeds.

Wintering European robins often use habitats that are very much unlike deciduous and coniferous forests where they prefer to breed (Malchevsky and Pukinsky 1983). In the Iberian Peninsula these birds may spend their winter in thin savannah-like cork oak plantations, and in the coastal areas of Abkhazia, where the density of wintering European robins may be very high, they occupy literally all the available habitats, including stony slopes near the Black Sea coast (Chernetsov, unpubl.). Generally speaking, habitat requirements in winter quarters may or may not be similar to the habitat requirements in the breeding range, with habitat specialists showing the strongest correspondence between breeding and winter habitats (Leisler and Schulze-Hagen 2011). Thus, the role of endogenous habitat preferences based on ecomorphological adaptations (that have been experimentally shown to exist, Ley 1988; Grünberger and Leisler 1990, 1993) in habitat selection during migration should not be overestimated.

The pattern of spatial distribution of food resources significantly influences the spatial behaviour of migrants at stopover (see Chap. 6). The same species may utilise different habitats, and even the same habitat, differently: pied flycatchers remain within a limited area and even reportedly occupy territories at stopovers during autumn passage in Portugal (Bibby and Green 1980), but move broadly in spring on the Courish Spit (Fig. 5.1). Rufous hummingbirds *Selasphorus rufus* at stopovers may defend territories, but also may behave as non-territorial roamers depending on their social status (Carpenter et al. 1993b). Apparently, if habitat shows fine-scale variation, the scale of movements will significantly influence habitat use by stopover migrants.

Besides, habitat quality strongly depends on the quality of cover it provides. It has been experimentally shown that blackcaps in migratory disposition started to forage more intensively when they were shown a stuffed sparrowhawk (Fransson and Weber 1997). The authors suggest that blackcaps did it to reach the departure threshold fuel stores sooner and to spend less time at a dangerous site. It is difficult to understand why blackcaps did not try to reach the highest possible FDR anyway (especially if they were time minimising migrants), but irrespectively of interpretations, this study has shown that migrating passerines may adjust their stopover behaviour in respect to predation situation. A field study of behaviour of northern wheatears during autumn stopovers on Helgoland, conversely, showed that migrants significantly decreased their FDR when predation danger (measured as the rate of real raptors flying over) was high (Schmaljohann and Dierschke 2005). The data on relationship between FDR and predation danger is thus equivocal, but a significant influence seems to be a fact. Another thing is that the claim of the authors that 'wheatears do not directly minimise predation risk during migration' should be treated with caution. We have seen in Chap. 4 that the optimal migration theory is very sensitive to *a priori* assumptions that are often made implicitly. By playing with assumptions, one can 'prove' a lot of things in the framework of this theory.

5.6.3 The Importance of Landscape Context

Apart from the immediate local habitat environment, the more general landscape context may play an important role. The response of birds to the general landscape structure is well known for breeding individuals (Hinsley et al. 1995), but in the studies of songbird stopover ecology the importance of landscape context is underestimated (Freemark et al. 1995). It is intuitively clear that when migrating birds are crossing areas with restricted stopover opportunities, like large water bodies or deserts, they should use different criteria of habitat selection than when flying over ecologically hospitable areas. It has been shown that on the Great Plains in North America the density of songbird migrants in spring was inversely proportional to the area of forest patches (Martin 1980). Territoriality of some passerines at stopovers (Rappole and Warner 1976; Kordic-Brown and Brown 1978; Bibby and Green 1980, 1981; Carpenter et al. 1983, 1993a, b; see Chap. 6 for more details) and density-dependent occupation of home ranges (Veiga 1986; Hansson and Pettersson 1989; Moore and Wang 1991; Shochat et al. 2002; Kelly et al. 2002; Ottich and Dierschke 2003) suggest inter- and intraspecific competition between migrants at stopovers. Direct evidence for interference competition is scarce (e.g. Salewski et al. 2007), but the reason is the methodological difficulty to demonstrate competition formally, rather than scarcity of this event in the wild.

When habitats are strongly fragmented, which is commonplace in the areas under much anthropogenic pressure (i.e., sadly, across most of the globe), patch size and the degree of their isolation significantly influence migrant density and thus the severity of competition. It should be expected that FDR will be related to habitat structure. At a stopover in Israel *Sylvia* warblers were less common in an optimal habitat than in a suboptimal one (Shochat et al. 2002). The pattern observed was different from the ideal free distribution. The authors concluded that the observed pattern of distribution of stopover migrants was due to isolation of the suitable habitat patches. The distance between habitat patches was about one kilometre (Shochat et al. 2002).

Our data on energy condition of songbird migrants in different habitats in an oasis in western Kazakhstan suggest that this interpretation should be treated with caution. In autumn 2004 we captured passerines in two habitats in Dzhanybek (49°24′ N, 46°48′ E). One habitat was a plantation of various trees and shrubs, including those fruit-bearing ones: the rowan *Sorbus aucuparia*, single-seeded hawthorn *Crataegus monogyna*, common barberry *Berberis vulgaris*, hedge cotoneaster *Cotoneaster lucidus* etc. (for a more detailed description see Karandina and Erpert 1972). In the diet of garden warblers these berries played a significant role, as shown by inspection of their faeces. Another habitat was the belt of windbreak forest which consisted of Siberian elms *Ulmus pumila*. Even though the former plantation was apparently a rich, and windbreak forest a poor habitat (especially for garden warblers, but also for other species), only two songbirds out of the six analysed showed habitat-related variation in body mass: the common redstart and the chiffchaff *Phylloscopus*

Table 5.7 The habitat-related difference in body mass of migrants captured in Dzhanybek (western Kazakhstan) in autumn 2004

Species	Forest plantation	Windbreak belt	Body mass difference	Wing length difference
Garden warbler	357	68	t = 0.69, p = 0.49	t = 0.08, p = 0.94
Common redstart	288	172	t = 2.02, p = 0.044	t = 0.15, p = 0.88
Chiffchaff	290	25	t = 2.31, p = 0.028	t = 1.73, p = 0.09
Willow warbler	192	31	t = 1.26, p = 0.21	t = 0.09, p = 0.93
European robin	193	18	t = 0.98, p = 0.34	t = 0.57, p = 0.58
Red-breasted flycatcher	483	83	t = 0.27, p = 0.78	t = 1.08, p = 0.28

collybita (Table 5.7). Common redstarts were predictably heavier in the plantation than in windbreak forest belt (15.22 g [SE = 0.099, n = 288] vs. 13.91 g [SE = 0.115, n = 172]). Chiffchaffs, conversely, were lighter in the apparently optimal habitat (7.69 g [SE = 0.051, n = 290] vs. 8.10 g [SE = 0.167, n = 25]), but because of size difference condition index (size-corrected body mass) did not differ between the habitats: t = 1.78, p = 0.086.

We can conclude that the body condition of birds in an apparently poor habitat (windbreak forest belt) was generally not poorer than in an apparently optimal habitat (forest plantation with fruit-carrying shrubs), and the difference was not significant even in such frugivorous migrants as the garden warbler (Table 5.7). This example suggests that before claiming that some habitat is suboptimal for stopover migrants because of food availability, shelter, or physical structure, it is necessary to show by analysing the diet, foraging intensity, FDR etc. that this is indeed the case.

On the other hand, Ktitorov et al. (2008) showed that the proportion of forest habitat within 2–5 km from a trapping site significantly influences FDR of willow warblers and common redstarts during autumn passage throughout Europe. This study showed that landscape context indeed had an impact on stopover site quality in addition to the local habitat situation. Landscape context was shown to influence not the density of stopover migrants, but directly the FDR of those individuals that stopped over at certain sites. FDR, as we have seen in Chap. 3, is one of the principal characteristics of stopover. Buler (2006) who used the density of migrants as a dependent variable, obtained a similar scale of influence of landscape characteristics: 4.9 km.

It should be mentioned that Ktitorov et al. (2008) used a rather simplistic binary classification of habitats: forest habitats were tested against all other types of habitat. The proportion of forest habitats explained a considerable proportion of variation in FDR when forest did not occupy more than 10% of the area in the surroundings. Ten percent was the threshold after exceeding which the proportion of forest habitats in the landscape did not influence FDR of migrants any more (Ktitorov et al. 2008). This means that landscape context is mostly important when the optimal habitat is scarce, i.e. its availability is a limiting factor. This situation is driven to extreme in the case of island habitats and physical offshore islands.

5.7 Fuel Deposition in Oases

Stopovers in small islands and in oases in deserts are an extreme case of contrasting habitat quality between small patches of the optimal (or at least somehow suitable) habitat and very large areas of low-quality matrix. The possibility to select a suitable stopover habitat are strongly limited. One may expect that in such situations low values of FDR should occur more frequently that when migrating over suitable continental areas, because stopover migrants have to accept sites with low FDR: in the matrix habitat, stopover is either completely impossible (water) or there is no chance to achieve a positive FDR (desert). Variation of FDR values recorded in oases should also be higher because of frequent occurrence of low values.

Dolnik (1990) summarised the results of earlier studies of stopover ecology and behaviour of passerines in Central Asia (Dolnik 1982, 1985a, b, 1987). He concluded that among songbirds that stopped over in oases, body mass change was positive in 40% in autumn and in 48% in spring. The proportion of birds gaining mass was inversely related to their mean initial body mass in the given oasis. Generally Dolnik (1990) concluded that small oases in Central Asia did not give small passerines an adequate opportunity to refuel. Because of competition between migrants, the mean FDR in oases in this region was not significantly higher than in open desert.

We studied refuelling in several species of long-distance migrants in a large oasis in Eilat (Israel) on the northernmost tip of the Red Sea (Yosef and Chernetsov 2004, 2005) and in a small oasis in Dzhanybek on the border between Volgograd Region of Russia and Western Kazakhstan Region of Kazakhstan (Chernetsov et al. 2007). In Eilat the FDR of Eurasian reed warblers varied between –1.00 and 1.25 g day^{-1}, on average 0.117 g day^{-1} ± SE = 0.011 (n = 429). The difference between spring values, when the birds were recovering after the flight across the Arabian Desert, and autumn, when they were fuelling up to cross the desert, were non-significant ($t_{230,197} = 0.26$, $p = 0.80$). In the sedge warbler in the same area, FDR varied between -1.50 and 2.40 g day^{-1}, on average 0.140 g day^{-1} ± SE = 0.016 (n = 366). Like in the former species, season-related variation in FDR was not significant ($t_{315,49} = 1.32$, $p = 0.19$). The difference between these two species was not significant, either: $t_{365,428} = 1.16$, $p = 0.25$.

On the Courish Spit which is not located at the edge of an ecological barrier, FDR in the Eurasian reed warbler did not vary between the seasons, either ($t_{747,111} = 1.50$, $p = 0.13$) and was on average 0.037 g day^{-1} ± SE = 0.008 (n = 829). The mean FDR was significantly lower than in Eilat ($t_{858,428} = 5.70$, $p < 0.001$), but dispersions of values did not differ (Fisher's test: $F_{858,428} = 1.07$, $p = 0.21$). In the sedge warbler on the Courish Spit season-related variation was not significant, either ($t_{97,380} = 0.37$, $p = 0.71$), and the mean FDR was 0.065 g day^{-1} ± SE = 0.011 (n = 479). Like the Eurasian reed warbler, the mean FDR in the sedge warbler was significantly lower than in Eilat ($t_{478,365} = 3.81$, $p < 0.001$), but the dispersion of values was significantly lower on the Courish Spit than in Eilat (Fisher's test: $F_{478,365} = 1.62$, $p < 0.001$). The coefficient of variation of FDR values on the

Table 5.8 The body mass change in songbird migrants in Dzhanybek (western Kazakhstan) in autumn

Species	Mean body mass change (g ± SE)	Mean rate of body mass change (g day^{-1} ± SE)	Coefficient of variation of body mass change rate	n	Threshold stopover duration (days)	Threshold initial mass (g)
Garden warbler	0.20 ± 0.202	−0.11 ± 0.065	5.01	72	1.3	20.3
Common redstart	0.16 ± 0.136	0.10 ± 0.082	6.56	64	0	15.7
Chiffchaff	−0.02 ± 0.115	−0.02 ± 0.041	11.04	29	2.6	7.8
Willow warbler	0.08 ± 0.202	0.09 ± 0.107	3.94	11	–	–
European robin	−0.19 ± 0.090	−0.08 ± 0.047	4.24	52	–	–
Red-breasted flycatcher	0.04 ± 0.048	0.03 ± 0.032	11.82	123	–	9.5

In the species which showed a relationship between body mass change and stopover duration and initial body mass, the threshold values of the latter two parameters are given. The birds gain body mass when stopover duration above the threshold and body mass below the threshold

Courish Spit was 6.34 in the Eurasian reed warbler and 3.70 in the sedge warbler. In Eilat the respective values were 1.95 and 2.19.

In a small oasis at the edge of clay semi-desert in Dzhanybek the mean FDR varied between −0.11 g day^{-1} in the garden warbler and 0.10 g day^{-1} in the common redstart (Table 5.8). The coefficient of variation of FDR values varied between 3.94 in the willow warbler and 11.82 in the red-breasted flycatcher. In Rybachy in the same species, except for the red-breasted flycatcher which is rare on the Courish Spit, the respective values ranged from 10.6 in the chiffchaff to 32.5 in the European robin (Table 5.9).

In four species out of five (the only exception was the chiffchaff) the coefficients of variation of FDR were higher in Dzhanybek than on the Courish Spit, and in the European robin the difference was by an order of magnitude. Mass gain rate did not differ between the two sites in four out of five species (t-test, $t > 0.05$), and only in the garden warbler it was significantly different ($t = 1.99$, $p = 0.045$). It should be noted that FDR in this species in Rybachy was close to zero, 0.03 g day^{-1} (SE = 0.024), whereas in Dzhanybek garden warblers were losing mass with the average rate of 0.11 g day^{-1} (SE = 0.065, Tables 5.8, 5.9). However, the mean change of body mass during a stopover in this oasis was positive. The cause of this apparent paradox was that garden warblers that made short stopovers were quickly losing mass, whereas those birds that stopped over for a longer period of time (more than 1.3 days on average, Table 5.8) gained mass (Chernetsov et al. 2007).

During spring migration across the Sahara in several passerine nocturnal migrants in Mauritania body mass and fuel stores of birds that stopped in an oasis were higher than in their conspecifics found in the desert. Moreover, most birds were gaining mass in an oasis in Ouadâne (Salewski et al. 2010b). This data is in contrast with the findings of Biebach et al. (1986) who argued that mainly lean birds were found in oases where they tried to refuel and Dolnik (1990) who added that they mainly failed to do so. However, the data from Mauritania agree with our

Table 5.9 The mean mass change rate in passerine migrants in autumn in Rybachy (Courish Spit)

Вид	Mean rate of body mass change (g day^{-1} ± SE)	Coefficient of variation of body mass change rate	n
Garden warbler	0.03 ± 0.024	14.56	391
Common redstart	0.02 ± 0.038	18.83	76
Chiffchaff	0.02 ± 0.014	10.68	171
Willow warbler	0.03 ± 0.028	12.23	173
European robin	−0.01 ± 0.004	32.54	6365

findings (Yosef and Chernetsov 2004, 2005; Chernetsov et al. 2007) that transient migrants refuel in oases, both large and small ones. FDR in oases did not differ from the sites located in areas with continuous stopover opportunity or was higher at the edge of barriers.

5.8 Fuel Deposition on Islands

Fuel deposition rate of European robins during autumn passage on Helgoland in the North Sea (0.04–0.11 g day^{-1} depending on the progress of the season (Ottich and Dierschke 2003) did not differ from the respective values recorded on the Courish Spit (on average 0.064 g day^{-1}; Tsvey 2008). The mean body mass change of European robins initially captured during a strong fallout of migrants in autumn on the island of Greifswalder Oie in the western Baltic was 0.26 g ($n = 175$), which together with the mean stopover duration of 2.67 days gives a mean estimate of 0.097 g day^{-1} (Mädlow 1997). This value is by 50% higher than on the Courish Spit. At both sites birds recaptured on the first and second day of stopovers lost mass, and started to regain it since the third day upon arrival (Mädlow 1997; Titov 1999a, c). Fuel deposition rates of garden warblers during autumn migration on Greifswalder Oie and on Helgoland were among the highest values recorded at European sites (Schaub and Jenni 2000).

In conclusion, the hypothesis of low mean FDR in songbird migrants and of high variation of this parameter in oases and on islands is not supported by the data, either from large or from small oases. Apparently, the oases where passerines regularly stop over for more than one day normally offer them adequate refuelling opportunities. At sites where such opportunity is lacking (e.g. in open desert), only one-day stopovers are made (see also Biebach et al. 1986; Salewski et al. 2010). The idea that oases are 'black holes' [or, in current terminology, ecological traps (Schlaepfer et al. 2002)] for emaciated passerine migrants where they stop but cannot refuel (Dolnik 1990) is not supported by the data. It cannot be ruled out that situations of overcrowding do occur in small oases in the centre of large deserts or on small isolated offshore islands, when the small patches of suitable habitat cannot support the large numbers of grounded migrants. However, such situations that likely result in catastrophic mortality of migrating birds are probably uncommon (Payevsky 1999).

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