Proceedings of the Zoological Institute RAS
Vol. 328, No. 2, 2024, pp. 298–307
10.31610/trudyzin/2024.328.2.298

UDC 591.543.43

The role of a non-native forest in the stopover ecology of migratory passerines

L. Bozó

Eötvös Loránd University, Department of Ecology and Systematic Zoology, 1117 Budapest, Pázmány Péter sétány 1/C; e-mail: bozolaszlo91@gmail.com

Submitted February 20, 2024; revised April 10, 2024; accepted April 20, 2024.

ABSTRACT

During their journey, migratory birds need stopover sites where they can replenish their energy stores. Mosaic forests of agricultural areas, often planted with non-native trees, can provide opportunities for birds to do this. In the present work, I sought to answer the question of the importance of these habitats for migratory birds. For this reason I studied the stopover ecology of 15 species of long- and short-distance migratory passerines. I calculated the minimum stopover duration and the extent of fat accumulation per species and by dividing species into different groups by habitat use and migration distance. For three species, I also estimated their possible flight ranges based on the accumulated fat, body mass and wing length. My results show that the planted oleaster forest has a different role in the stopover habits of the species studied. The body mass of the birds typically did not changed significantly during the time they spent in the area. Forest and farmland species spent the longest time in the area. Despite the possibly high rate of intra- and inter-specific competition, the area can provide sufficient food for birds throughout the whole period. Short-distance migrants stored less fat than long-distance migrants, probably due to the different migration strategies. Flight distances varied according to the migratory habits of the species. From a conservation biology point of view, the study highlighted the role of these habitats in bird migration.

Key words: flight range estimation, migration connectivity, oleaster, secondary habitats

---

Роль олеандровых рощ для остановок перелетных воробьиных птиц

Л. Бозо

Университет Этвёша Лоранда, факультет экологии и зоологии, Пазмани Петер Сетани 1/C, 1117 Будапешт, Венгрия; e-mail: bozolaszlo91@gmail.com

Представлена 20 февраля 2024; после доработки 10 апреля 2024; принята 20 апреля 2024.

РЕЗЮМЕ

Во время перелетов птицам необходимы места отдыха, где они могут восстановить силы. В сельскохозяйственных районах птицы могут использовать для этого лесопосадки, состоящие из чужеродных видов. В настоящей работе рассмотрен вопрос о значении олеандровых рощ для перелетных воробьиных птиц. Изучена экология птиц 15 видов, мигрирующих на дальние и ближние расстояния, в районах их остановок. Рассчитана минимальная продолжительность остановок и степень накопления жира для птиц каждого вида, с разделением их на группы по характеру используемых биотопов и протяженности миграций. Для трех видов оценен возможный диапазон дальности перелета, исходя из накопленного жира, массы тела и длины крыльев. Результаты показывают, что олеандровые лесопосадки используются птицами на остановках по-разному. За время, проведенное на отдыхе, масса тела птиц, как правило, существенно не меняется. Лесные виды и птицы сельскохозяйственных угодий проводят на остановках наибольшее время. Несмотря на возможно высокий уровень внутри- и межвидовой конкуренции, олеандровые рощи могут обеспечить птиц достаточным количеством корма в течение всего периода остановки. У мигрантов на короткие расстояния меньше жира, чем у птиц, осуществляющих дальние перелеты, что обусловлено, очевидно, различной стратегией их миграций. В зависимости от протяженности перелетов птиц варьирует их поведение на остановках. Исследования биологии птиц на местах их стоянок в ходе миграций важны с природоохранной точки зрения.

Ключевые слова: оценка дальности перелета, миграции птиц, олеандровые рощи, места остановок

INTRODUCTION

During migration, birds connect continents and different biomes (Hahn et al. 2009). This movement, known as migratory connectivity, involves not only breeding and wintering sites but also stopover sites along the migration route (Webster et al. 2002). Stopover sites play a prominent role during migration, as they provide for the birds the opportunity to replenish their energy stores, rest or simply wait for the best weather conditions to move on (Hutto 1998; Erni et al. 2002; Linscott and Senner 2021; Schmaljohann et al. 2022). Accordingly, birds spend a significant part of their migration at stopover sites (Schmaljohann et al. 2012; Lupi et al. 2016; Roques et al. 2020). The importance of a particular stopover site is determined by its location on the migration route, and also by the suitability of the habitat for the bird to replenish its energy stores or not (Mehlman et al. 2005; Domer et al. 2021). During migration, birds use a much wider range of habitats than in breeding time (Petit 2000), but the choice of stopover sites is not random (Moore and Aborne 2000). The rate of body mass gain is often positively correlated with the length of time spent at a stopover site (Schmaljohann and Eikenaar 2017; Collet and Heim 2022).

It is also a good question how far birds can fly with the energy stored at the stopover site. Nowadays, various technologies provide accurate and reliable data on stopover sites and migration routes of birds. However, these are very expensive and the number of methods that can be applied decreases with body size (Bozó et al. 2019). In the Carpathian Basin, only the migration of the smaller songbirds, as the House Martin *Delichon urbicum* (Linnaeus, 1758) and the Sand Martin *Riparia riparia* (Linnaeus, 1758) has been investigated using new generation methods (Szép et al. 2017). Fortunately, there are much more cost-effective methods for estimating migration distances based on biometric data (Delingat et al. 2008, Arizaga et al. 2013, Sander et al. 2017, Bozó et al. 2019, Fourcade et al. 2021, Gyurácz et al. 2023). As birds derive about 95% of the energy used during migration from fat (Jenni and Jenni-Eiermann 1998), calculations based on wing length, body mass and body fat can provide an accurate picture of migration distances.

Given the high importance of stopover sites for migration, habitat degradation at these sites can have a significant impact on the survival of birds and even affect the population of the species (Weber et al. 1999). One of the main causes of habitat degradation is the increase in the proportion of farmland (Wilson et al. 2009; Şekercioğlu 2012), as well as the intensification of agriculture and the abandonment of old agricultural practices (Marini et al. 2011). A large number of studies have shown a loss of biodiversity in these areas, but most of them concern the bird species that nest there (Benton et al. 2003; Reif 2013). However, the role of these habitats in bird migration should be also highlighted, as they are often used as stopover sites by birds (Hutto 1998; Dänhardt et al. 2010; Schupkégel et al. 2020; Blount et al. 2021). The main problem is that most of the research on bird migration is done in protected natural habitats, but birds pass through largely unprotected, anthropogenic areas on their way between the breeding and wintering areas.

The aim of the present study was to provide data on the role of these secondary habitats in the migration of some short- and long-distance migratory songbird species. This could be done by using bird ringing data to investigate the stopover ecology of these species, which gives an indication of the importance of the stopover site. For this, I looked at the minimum stopover time of the birds and the rate of energy storage during this time. I also examined the analyses not only by species, but also by group based on migration distance and habitat use. Additionally, I also compared the migration timing of the species and estimated the flight ranges for three study species. I hypothesised that the study site play a different role in the migration of species using different habitats and characterised by different migratory strategies.

MATERIAL AND METHODS

Study site and data collection

The data were collected at a ringing station in a planted oleaster *Elaegnus angustifolia* (Elaeagnaceae) forest with a total area of 7 hectares in the outskirts of Kevermes, southeastern Hungary (46°26'N 21°12'E) (Fig. 1), during the period 2016–2023. The average height of the forest canopy is 3.5–4 m. In addition to the dominant oleaster, some taller elms (*Ulmus* spp.), black locusts (*Robinia pseudoacacia*) and European wild pears (*Pyrus pyraster*) can also be found. The shrub layer consists some black elderberries (*Sambucus nigra*) and sloes (*Prunus spinosa*), while dewberries (*Rubus caesius*) are the most common plant species in the lower levels. Vegetation is denser at the edge of the forest, with spots of reed (*Phragmites australis*) and weed next to the dominant sloe and black elderberry. Behind the forest, there is a drainage canal (Tulkán Canal) oriented southeast–northwest. Willows (*Salix* spp.), young walnuts (*Juglans regia*) and species of poplar trees (*Populus* spp.) grow on the bank, and the canal bed is covered with sparse reed. The average height of the plants in the canal was almost the same as in the forest. The canal was all the time dry without any water cover. The forest and the canal are bordered by farmland.

During the eight years of the study, the method of bird ringing was used for data collection; each bird was caught using mist nets and ringed with aluminium rings supplied by the Hungarian Bird Ringing Centre. I also collected biometric data from each bird (wing length, fat score and weight) and determined their age according to Svensson (1992) and Demongin (2016) before release. Wing-length was measured by the 'maximum flattened chord method' (Svensson 1992) to the nearest mm, while body mass was measured to the nearest 0.1 g. Fat scores followed Kaiser (1993) on a scale of 0 to 8. The work was conducted between the first week of August and the last week of October in every study years. I worked two days weekly and eight hours daily, with eight net checks daily, four in the morning and four in the afternoon. In each of the seven years, 13 mist nets were deployed. Of these, nine nets were placed in the oleaster forest and four along the canal. Windy and rainy days were avoided.

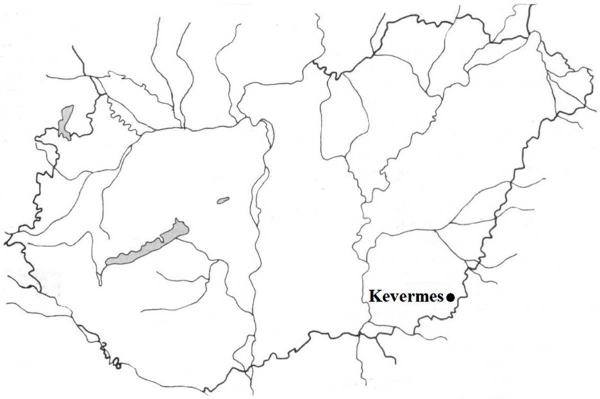

Fig. 1. The location of the study site within Hungary.

Stopover ecology

During the data analysis, 8258 first capture (ringing) and 1351 recapture data of 15 bird species were used: Red-backed Shrike *Lanius collurio*, Great Reed Warbler *Acrocephalus arundinaceus*, Marsh Warbler *A. palustris*, Eurasian Reed Warbler *A. scirpaceus*, Sedge Warbler *A. schoenobaenus*, Common Chiffchaff *Phylloscopus collybita*, Willow Warbler *Ph. trochilus*, Lesser Whitethroat *Curruca curruca*, Common Whitethroat *C. communis*, Eurasian Backcap *Sylvia atricapilla*, Common Nightingale *Luscinia megarhynchos*, Thrush Nightingale *L. luscinia*, European Robin *Erithacus rubecula*, Blue Tit *Cyanistes caeruleus*, Common Blackbird *Turdus merula* (Table 1). Two factors were analysed. The first was the minimum stopover duration of the recaptured birds, i.e. how long they spent in the area. The minimum stopover duration was calculated by subtracting the date that the individual was captured for the first time (ringing date) from the date that the individual was captured for the last time (Ellegren 1991). It is important to note that the minimum stopover duration calculated in this way is shorter than the real stopover time. Both methods are widely used in ornithological research (Schaub et al. 2001). I used this calculation because when comparing results, I have available literature that has calculated minimum stopover duration period in this way. Another factor was whether the birds' body weight had changed during the stopover time. To measure this, there was only considered data from individuals that had been recaptured. Since the data were not normally distributed ($p>0.05$), I used the Mann-Whitney U-test to determine whether the body weight values at first capture and recapture were different. Given that the 15 selected species differ in several aspects, these calculations were per-

Table 1. Results of analysis on body mass changes and minimum stopover duration of passerine birds in oleaster woodlands.

Species	Mean diff.		n	z	p	MSD, days
	gramm	%				
Lanius collurio (Linnaeus, 1758)	0.6	2.1	27	−0.242	0.810	7
Acrocephalus arundinaceus (Linnaeus, 1758)	2.1	5.7	17	−0.482	0.629	4
Acrocephalus palustris (Bechstein, 1798)	0.9	6.0	52	−1.700	0.089	4
Acrocephalus scirpaceus (Hermann, 1784)	0.1	0.8	27	−0.112	0.910	3
Acrocephalus schoenobaenus (Linnaeus, 1758)	0.8	5.4	13	−0.538	0.590	3
Phylloscopus collybita (Vieillot, 1818)	0.0	0.0	55	−1.448	0.147	7
Phylloscopus trochilus (Bechstein, 1793)	0.7	6.7	91	−2.630	**0.008**	4
Curruca curruca (Linnaeus, 1758)	−0.2	−1.6	38	−0.431	0.666	5
Curruca communis (Latham, 1787)	0.5	2.9	56	−0.753	0.450	7
Sylvia atricapilla (Linnaeus, 1758)	−0.2	−1.0	42	−0.630	0.528	7
Luscinia megarhynchos Brehm, 1831	1.3	5.4	61	−1.075	0.282	8
Luscinia luscinia (Linnaeus, 1758)	3.2	11.5	18	−2.500	**0.012**	8
Erithacus rubecula (Linnaeus, 1758)	0.2	1.2	140	−0.785	0.432	3
Cyanistes caeruleus (Linnaeus, 1758)	−0.4	−3.7	50	−2.721	**0.006**	6
Turdus merula Linnaeus, 1758	−0.8	−0.9	61	−1.024	0.306	21
Reedbed	0.9	5.0	109	−1.119	0.263	4
Farmland	0.5	2.4	83	−0.371	0.710	7
Forest	0.3	1.3	556	−0.385	0.700	7
LDM	0.6	3.6	497	−0.963	0.335	6
SDM	−0.2	0.6	251	−0.037	0.969	8

Abbreviations: LDM – long-distance migrant; Mean st. duration – mean stopover duration in days; MSD – minimum stopover duration; n – sample size; SDM – short-distance migrant. Significant values are in bold. Significant values are in bold.

formed not only per species but also per group as follows. Based on habitat use, they were classified into three different groups depending on the habitats they typically use. The four species of *Acrocephalus* were classified as “reedbed species”, the Red-backed Shrike and the Common Whitethroat as “farmland species”, while the other species were classified as „forest species”. Based on migration distance, two groups of short-distance migrants (European Robin, Blue Tit and Common Blackbird) and long-distance migrants (all other species) were identified. In order to estimate the importance of competition between species and individuals, I compared the median dates of daily captures of species and different groups using the Kruskal-Wallis test. I also provided the median dates of daily captures and the median dates of the annual last captures by species.

Estimated flight ranges

For estimating the flight ranges of the species re-fuelling at the study area, I selected three species with enough data represented all categories by habitat use and migration distance (Marsh Warbler, Common Whitethroat and European Robin). The methods used are similar to described in Bozó et al. (2019) (for more details see the cited reference). From the recorded biometric data, the wing length, body mass and fat score were used for this study. Because of the small sample size, in case of European Robin, I ommitted fat score ≥ 4, while the other species, I ommitted fat score 8.

First I calculate the lean body mass (m_0) for each individual of the selected species by using linear regression based on wing length measurements (dependent variable = body mass, explanatory = wing length). After that, I calculated the fat mass (body mass at capture – calculated lean body mass, $m-m_0$) and the relative fuel load (f) for each individual:

$$f=m-m0/m0$$

Flight range (Y) of passerines increases with the log-scaled relative fuel load (f) and flight speed (U) (60 km/h without wind profit) (Salewski et al. 2010):

$$Y=100\times \mathrm{U}\times \ln(1+f)$$

Flight ranges were calculated for each fat score value separately, and flight ranges with negative values were set to zero.

The mean flight ranges of species were compared by one-way ANOVA and Tukey tests.

All statistical analyses were carried out in Past 4.14 and Microsoft Office Excel 2017.

RESULTS

Stopover ecology

In terms of body mass change, in all but three species, the body weight of the birds increased during the stopover. However, a significant increase was only found for the Thrush Nightingale and the Willow Warbler, a significant decrease only for the Blue Tit. When analysing the groups, similar results were obtained, with an increase in body weight for both habitat use and migration distance, but the increase was not significant in any of the cases (Table 1).

The minimum stopover duration was the longest for the Common Blackbird and the shortest for the Eurasian Reed Warbler, Sedge Warbler and European Robin. In terms of groups, reedbed species spent

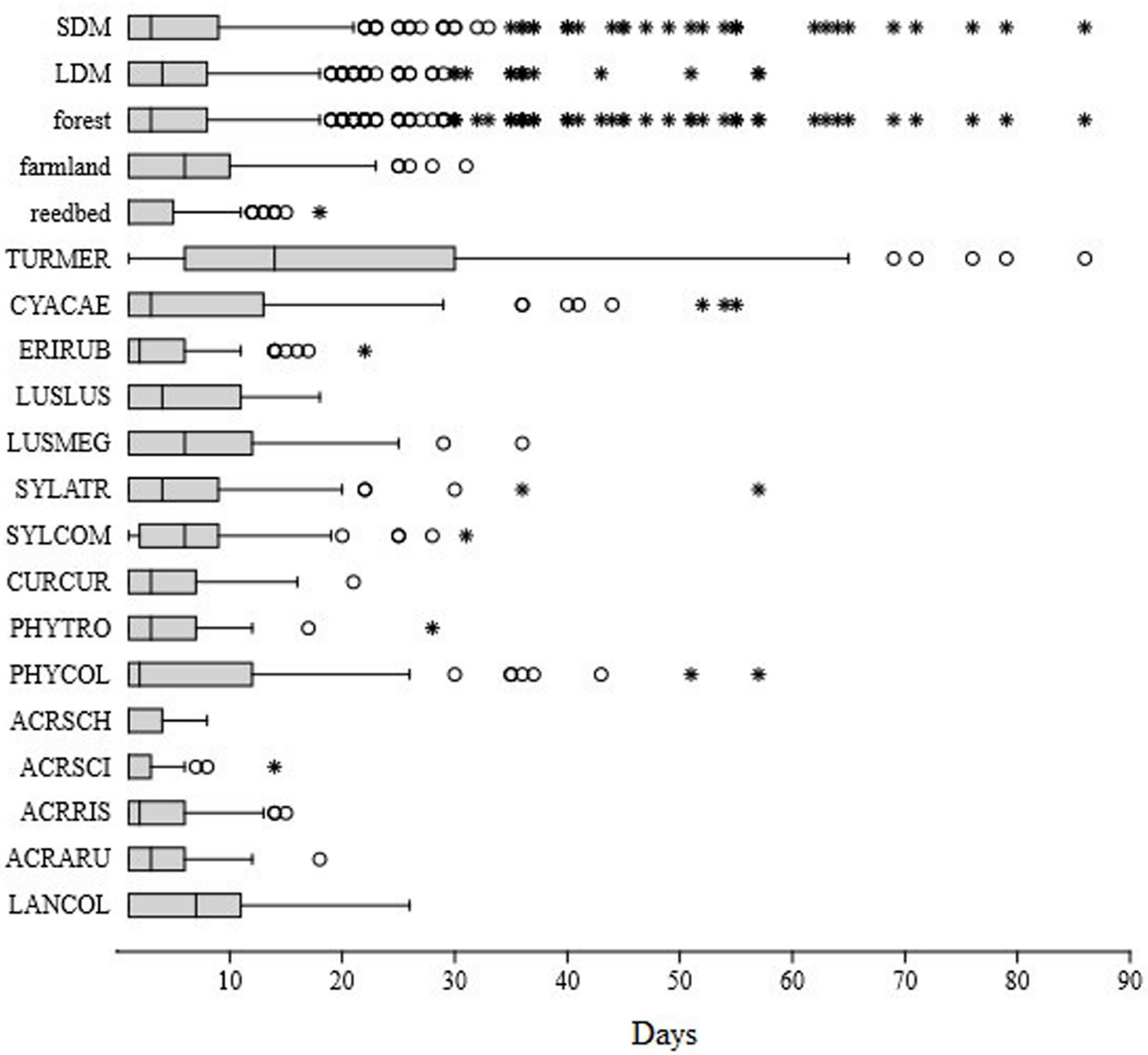

Fig. 2. Stopover duration of the study passerines by species, habitat use and migration distance. LANCOL – Red-backed Shrike; ACRARU – Great Reed Warbler; ACRRIS – Marsh Warbler; ACRSCI – Common Reed Warbler; ACRSCH – Sedge Warbler; PHYCOL – Common Chiffchaff; PHYTRO – Willow Warbler; CURCUR – Lesser Whitethroat; SYLCOM – Common Whitethroat; SYLATR – Blackcap; LUSMEG – Common Nightingale; LUSLUS – Thrush Nightingale; ERIRUB – European Robin; CYACAE – Blue Tit; TURMER – Common Blackbird; SDM – short-distance migrants; LDM – long-distance migrants.

the shortest time in the area, while stopover duration was about the same for forest and farmland species. On average, short-distance migratory species spent more time in the area than long-distance migrant species (Table 1, Fig. 2).

The timing of migration differed significantly among species ($H=160.7$, $p<0.001$) and groups by habitat use ($H=39.14$, $p<0.001$), but not by migration distance ($H=0.762$, $p=0.368$). Reedbed and farmland species migrated significantly earlier than forest dwelling species (Table 2).

Table 2. The median dates of daily captures and the median dates of the annual last captures by passerine species.

Species	Median of migration	Median of last captures
Lanius collurio	18 August	23 September
Acrocephalus arundinaceus	13 August	1 September
Acrocephalus palustris	19 August	19 September
Acrocephalus scirpaceus	19 August	16 September
Acrocephalus schoenobaenus	2 September	8 October
Phylloscopus collybita	1 October	25 October
Phylloscopus trochilus	10 September	10 October
Curruca curruca	27 August	28 September
Curruca communis	24 August	28 September
Sylvia atricapilla	3 September	17 October
Luscinia megarhynchos	13 August	12 September
Luscinia luscinia	19 August	6 September
Erithacus rubecula	7 October	27 October
Cyanistes caeruleus	13 October	27 October
Turdus merula	25 September	27 October

Estimated flight ranges

The body mass of Marsh Warbler (ANOVA: $F_{7,\ 261}=108.8$, $p<0.001$), the Common Whitethroat (ANOVA: $F_{6,\ 379}=111.8$, $p<0.001$) and the European Robin (ANOVA: $F_{3,\ 806}=133.2$, $p<0.001$) differed significantly among individuals with different fat score classes, which increased strongly with body mass. The subset of birds with fat score 0 did not differ significantly in wing-length from birds with higher fat scores in any species (Marsh Warbler: $t=-0.8$, $p=0.424$; Common Whitethroat: $t=-1.23$, $p=0.218$; European Robin: $t=0.138$, $p=0.889$).

Table 3. Fuel load values and mean potential flight ranges by passerine species and fat score categories.

Species	Fat score	N	Fuel load			Mean potential flight range
			M	Min	Max	
Acrocephalus palustris	0	24	0.0004	−0.11	0.153	114.5
	1	15	0.005	−0.141	0.133	171.5
	2	39	0.057	−0.05	0.2	357.8
	3	60	0.129	−0.017	0.401	715
	4	32	0.175	−0.034	0.352	957.7
	5	27	0.191	0.043	0.456	1032.9
	6	37	0.32	0.094	0.564	1652
	7	35	0.506	0.342	0.798	2440
Curruca communis	0	79	−0.007	−0.12	0.166	11.7
	1	42	0.041	−0.086	0.172	86.2
	2	88	0.094	−0.027	0.287	286.2
	3	68	0.143	−0.013	0.322	596.1
	4	64	0.198	−0.03	0.407	974.7
	5	20	0.251	0.12	0.451	1226.2
	6	25	0.357	0.106	0.543	1788.7
Erithacus rubecula	0	367	−0.002	−0.224	0.276	161
	1	197	0.053	−0.166	0.362	358
	2	170	0.105	−0.132	0.385	602.5
	3	76	0.165	0	0.327	890.1

Abbreviations: M – mean; Min – minimum and Max – maximum values.

The mean potential flight range of all species was 534.7±458.9 km. However, the potential mean flight ranges of separate species were significantly different (ANOVA, F=109, df=2, p<0.001. European Robins have the shortest (379.2±275.1 km), Marsh Warblers the longest (996.2±332.6 km) potential migration distances, and the differences between species were significant for all species (Tukey test p<0.001) (Table 3).

DISCUSSION

The results show that the planted oleaster forest with the dry water canal has a different role for the migratory bird species. The reedbed species spent the least time here. Together with the fact, that the body mass of the recaptured individuals did not changed significantly, it can be concluded that mainly transient birds migrate here, and do not use the area to re-fuel. In contrast, farmland and forest species spent a long time in the area, which indicated that the study site provides suitable opportunities for them. A previous study has shown that planted berries in the area, including invasive non-native species such as the pokeberry (*Phytolacca americana*), provide excellent opportunities for them to replenish their energy stores (Schupkégel et al. 2020). As the migration timing of some species with similar type of food overlaps with each other, the possibility of competition arises, especially during migration peaks (Hansson and Pettersson 1989; Moore and Yong 1991; Petit 2000; Hardin et al. 2022). This competition could result in a reduction in body weight, as observed for example in the Eurasian Blackcap. However, for most species, this is not the case, so there is sufficient food in the forest throughout the whole period (Moore and Yong 1991). This indicates the importance of the stopover site for those species using the forest. The competition may also differ between age and sex groups, with juveniles and females being less dominant in a given habitat than adults and males (Ellegren 1991; Yong et al. 1998). However, I was unable to investigate this for any species due to the small sample size.

There were differences in fat accumulation: the short-distance migratory species accumulated less fat even if the results were not significant. Additionally, in the case of the Blue Tit, the amount of fat accumulated decreased significantly during the time spent in the area. In the case of this species, the most likely reason for this body mass change can be the so-called handling effect (Lindström 1995). As individuals of this species spent a short time in the area, it is possible that the handling effect is more pronounced than in other species. It is also possible that the difference is due to differences in the migration strategies of these species. While most long-distance migratory species need high fat reserves, this is less important for short-distance migrants, especially at the beginning of the migration season (Sandberg 1996). The migration of the Blue Tits is mainly restricted to the Carpathian Basin, but Common Blackbirds and European Robins migrate only to the Mediterranean at most, and do not need to fly over major barriers (Csörgő et al. 2009).

The results of flight range estimations also supported these statements. Short-distance migrant European Robins had the least fat, and individuals of this species potentially covered the shortest flight distances (<400 km on average). European Robins re-fuelled in the study area with at least fat score 2 and 3 may be able to fly 600–900 km. The species' migration strategy is characterised by flying up to 700 km in two night flights, after which its fat reserves are completely depleted and it takes an average of 10 days to replenish them (Pettersson and Hasselquist 1985). The number of lean individuals (fat score 0) was very high compared to other species, so it is likely that the study area is an important resting site for the birds coming from the north-northeast. From here, it can reach the wintering grounds with a further two nights of continuous flight. The Common Whitethroat migrate typically with low fat reserves as far as the Mediterranean. They are flying about 300 km in one night, and birds in the best condition can fly for two nights (Fransson 1998). Birds stopping at Kevermes suggest that they can fly an average of 541 km, which fits this pattern. Marsh Warblers, on the other hand, can fly almost double this, about 1000 km on average, thanks to their large fat stores. The species is generally migrate with high fat reserves, especially in front of geographical barriers (Csörgő et al. 2009).

All of these results suggest that the study site can play a completely different role in species using different migration strategies. However, from a conservation biology perspective, the results highlights a problem that is currently unresolved, namely the protection of non-natural, secondary planted forests. A previous study on the Europen Robin in the same place has shown that the area plays a similar role in the migration of the species as the natural habitats

(Bozó and Bozóné Borbáth 2020). The role of farmlands in migration has been highlighted by several studies, but most studies have focused on larger species such as geese, cranes or other waterbirds (Galle et al. 2009; Pearse et al. 2011; Krapu et al. 2014). Our knowledge on songbirds is incomplete in this respect, but the results suggest that planted forests in farmlands are key habitats for some species. Ktitorov et al. (2007) highlighted the role of the habitat cover of the landscape. They found for the Willow Warbler, that the body mass of the birds tend to lose or gain mass at a lower rate if the cover of the woody habitats is less than 10%.

In general, of the species studied, European populations of forest species are increasing, while those nesting in reedbeds and agricultural areas are declining (Keller et al. 2020). Negative changes in wintering areas or migration routes are often cited as a cause of decline, one element of which may be precisely the fact that planted forests and other non-natural habitats are not protected by law, can be cut down at any time and their sites can be brought under cultivation. An important task for the future would be to ensure that these habitats also receive some level of legal protection, such as the timing of their clear-cuttings and an immediate re-plantation after clear-cutting.

CONCLUSION

In agricultural areas, degradation of natural habitats has left only planted forests and other anthropogenic habitats available for migratory birds. As a significant part of the migration route passes through such areas, their presence is of paramount importance for the replenishment of the birds' energy stores. The results of my study suggest that this is not universal for all bird species, but is certainly the case for forest- and farmland-associated species. The length of time spent in the area also depended on the type of habitat to which the bird species was basically related. With the amount of fat accumulated, birds are able to cover similar distances as they would if resting at a stopover site in a natural habitat. The protection of these habitats is therefore important, but not yet a solved problem.

ACKNOWLEDGEMENTS

The study was supported by the ÚNKP-23-4 New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund. The author is grateful for Nikolett Olajos for the English language review of the manuscript as well as for József Gyurácz and another anonymous reviewer for their helpful comments and suggestions.

REFERENCES

Arizaga J., Maggini I., Hama F., Crespo A. and Gargallo G. 2013. Site- and species-specific fuel load of European-Afrotropical passerines on arrival at three oases of southeast Morocco during spring migration. *Bird Study*, **60**: 11–21. https://doi.org/10.1080/00063657.2012.735222

Benton T.G., Vickery J.A. and Wilson J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**: 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Blount J.D., Horns J.J., Kittelberger K.D., Neate-Clegg M.H. and Şekercioğlu Ç.H. 2021. Avian use of agricultural areas as migration stopover sites: A review of crop management practices and ecological correlates. *Frontiers in Ecology and Evolution*, **9**: 650641. https://doi.org/10.3389/fevo.2021.650641

Bozó L. and Bozóné Borbáth E. 2020. Migration and stopover ecology of European Robins *Erithacus rubecula* in an oleaster forest in southeastern Hungary. *Ringing & Migration*, **35**: 24–31. https://doi.org/10.1080/03078698.2021.2001676

Bozó L., Csörgő T. and Anisimov Y. 2019. Estimation of flight range of migrant leaf-warblers at Lake Baikal. *Ardeola*, **67**: 57–67. https://doi.org/10.13157/arla.67.1.2020.sc1

Collet L. and Heim W. 2022. Differences in stopover duration and body mass change among *Emberiza* buntings during autumn migration in the Russian Far East. *Journal of Ornithology*, **163**: 779–789. https://doi.org/10.1007/s10336-022-01976-3

Csörgő T., Karcza Zs., Halmos G., Magyar G., Gyurácz J., Szép T., Bankovics A., Schmidt A. and Schmidt E. 2009. Magyar Madárvonulási Atlasz. Kossuth Kiadó Zrt., Budapest, 672 p.

Dänhardt J., Green M., Lindström Å., Rundlöf M. and Smith H.G. 2010. Farmland as stopover habitat for migrating birds – effects of organic farming and landscape structure. *Oikos*, **119**: 1114–1125. https://doi.org/10.1111/j.1600-0706.2009.18106.x

Delingat J., Bairlein F. and Hedenström A. 2008. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern wheatears (*Oenanthe oenanthe*). *Behaviour Ecology and Sociobiology*, **62**: 1069–1078. https://doi.org/ 10.1007/s00265-007-0534-8

Demongin L. 2016. Identification guide to birds in the hand. Beauregard-Vendon, France, 392 p.

Domer A., Vinepinsky E., Bouskila A., Shochat E. and Ovadia O. 2021. Optimal stopover model: A state-dependent habitat selection model for staging passerines. *Journal of Animal Ecology*, **90**: 2793–2805. https://doi.org/10.1111/1365-2656.13581

Ellegren H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia scvecica* in relation to age and sex. *Ornis Scandinavica*, **22**: 340–348. https://doi.org/10.2307/3676506

Erni B., Liechti F. and Bruderer B. 2002. Stopover strategies in passerine bird migration: a simulation study. *Journal of Theoretical Biology*, **219**: 479–493. https://doi.org/10.1006/jtbi.2002.3138

Fourcade J.M., Fontanilles P. and Demongin L. 2021. Fuel management, stopover duration and potential flight range of pied flycatcher Ficedula hypoleuca staying in South-West France during autumn migration. *Journal of Ornithology*, **163**(1): 61–70. https://doi.org/10.1007/s10336-021-01941-6

Fransson T. 1998. Patterns of migratory fuelling in whitethroats *Sylvia communis* in relation to departure. *Journal of Avian Biology*, **29**: 569–573. https://doi.org/10.2307/3677177

Galle A.M., Linz G.M., Homan J.H. and Bleier W.J. 2009. Avian use of harvested crop fields in North Dakota during spring migration. *Western North American Naturalist*, **69**: 491–500. https://doi.org/10.3398/064.069.0409

Gyurácz J., Bánhidi P., Góczán J., Illés P., Kalmár S., Koszorús P. and Varga L. 2023. Fuel load and flight range estimation of migrating passerines in the western part of the Carpathian Basin during the autumn migration. *Acta Zoologica Academiae Scientiarum Hungaricae*, **69**: 47–61. https://doi.org/10.17109/AZH.69.1.47.2023

Hahn S., Bauer S. and Liechti F. 2009. The natural link between Europe and Africa – 2.1 billion birds on migration. *Oikos*, **118**: 624–626. https://doi.org/10.1111/j.1600-0706.2008.17309.x

Hansson M. and Pettersson J. 1989. Competition and fat deposition in Goldcrests (*Regulus regulus*) at a migration stop-over site. *Vogelwarte*, **35**: 21–31.

Hardin F.O., Beckman A.K., Earl A.D. and Grace J.K. 2022. Optimizing and competing for resources. In: Proppe D.S. (Ed). Songbird Behavior and Conservation in the Anthropocene. CRC Press, Taylor & Francis Group: 155–190. https://doi.org/10.1201/9780429299568-7

Hutto R.L. 1998. On the importance of stopover sites to migrating birds. *Auk*, **115**: 823–825. https://doi.org/10.2307/4089500

Jenni L. and Jenni-Eiermann S. 1998. Fuel supply and metabolic constraints in migrating birds. *Journal of Avian Biology*, **29**: 521–528. https://doi.org/10.1016/S0305-0491(00)80104-2

Kaiser A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology*, **64**: 246–255.

Keller V., Herrando S., Voríšek P., Franch M., Kipson M., Milanesi P., Martí D., Anton M., Klvanová A., Kalyakin M.V., Bauer H.-G. and Foppen R.P.B. 2020. European Breeding Bird Atlas 2. Distribution, Abundance and Change. European Bird Census Council & Lynx Edicions, Barcelona, 967 p.

Krapu G.L., Brandt D.A., Kinzel P.J. and Pearse A.T. 2014. Spring migration ecology of the mid-continent sandhill crane population with an emphasis on use of the Central Platte River Valley, Nebraska. *Wildlife Monographs*, **189**: 1–41. https://doi.org/10.1002/wmon.1013

Ktitorov P., Bairlein F. and Dubinin M. 2007. The importance of landscape context for songbirds on migration: body mass gain is related to habitat cover. *Landscape Ecology*, **23**: 169–179. https://doi.org/10.1007/s10980-007-9177-4

Lindström Å. 1995. Stopover ecology of migrating birds: some unsolved questions. *Israel Journal of Zoology*, **41**: 407–416.

Linscott J.A. and Senner N.R. 2021. Beyond refueling: Investigating the diversity of functions of migratory stopover events. *Condor*, **123**: duaa074. https://doi.org/10.1093/ornithapp/duaa074

Lupi S., Goymann W., Cardinale M. and Fusani L. 2016. Physiological conditions influence stopover behaviour of short-distance migratory passerines. *Journal of Ornithology*, **157**: 583–589. https://doi.org/10.1007/s10336-015-1303-5

Marini L., Klimek S. and Battisti A. 2011. Mitigating the impacts of the decline of traditional farming on mountain landscapes and biodiversity: a case study in the European Alps. *Environmental Science & Policy*, **14**: 258–267. https://doi.org/10.1016/j.envsci.2010.12.003

Mehlman D., Mabey S., Ewert D., Duncan C., Abel B., Cimprich D., Sutter R. and Woodrey M. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. *Auk*, **122**: 1281–1290. https://doi.org/10.1093/auk/122.4.1281

Moore F.R. and Aborn D.A. 2000. Mechanisms of en route habitat selection: How do migrants make habitat decisions during stopover? *Studies in Avian Biology*, **20**: 34–42

Moore F.R. and Yong W. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behaviour Ecology and Sociobiology*, **28**: 85–90. https://doi.org/10.1007/BF00180984

Pearse A.T., Krapu G.L., Cox R.R. and Bruce E. 2011. Spring-migration ecology of Northern Pintails in south-central Nebraska. *Waterbirds*, **34**: 10–18. https://doi.org/10.1675/063.034.0102

Petit D.R. 2000. Habitat use by landbirds along Neartic-Neotropical migration routes: Implications for conservation of stopover habitats. *Studies in Avian Biology*, **20**: 15–33. https://doi.org/10.2307/3802919

Pettersson J. and Hasselquist D. 1985. Fat deposition and migration capacity of robins *Erithacus rubecula* and goldcrests *Regulus regulus* at Ottenby, Sweden. *Ringing & Migration*, **6**: 66–76. https://doi.org/10.1080/03078698.1985.9673859

Reif J. 2013. Long-term trends in bird populations: a review of patterns and potential drivers in North America and Europe. *Acta Ornithologica*, **48**: 1–16. https://doi.org/10.3161/000164513X669955

Roques S., Henry P.Y., Guyot G., Bargain B., Cam E. and Pradel R. 2020. When to depart from a stopover site? Time-since-arrival matters more than weather conditions. *Auk*, **139**: ukab057. https://doi.org/10.1093/ornithology/ukab057

Salewski V., Schmaljohann H. and Liechti F. 2010. Spring passerine migrants stopping over in the Sahara are not fall-outs. *Journal of Ornithology*, **151**: 371–378. https://doi.org/10.1007/s10336-009-0464-5

Sandberg R. 1996. Fat reserves of migrating passerines at arrival on the breeding grounds in Swedish Lapland. *Ibis*, **138**: 514–524. https://doi.org/10.1111/j.1474-919X.1996.tb08072.x

Sander M.M., Eccard J.A. and Heim W. 2017. Flight range estimation of migrant Yellow-browed Warblers *Phylloscopus inornatus* on the East Asian flyway. *Bird Study*, **64**: 569–572. https://doi.org/10.1080/00063657.2017.1409696

Schaub M., Pradel R., Jenni L. and Lebreton J.D. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. *Ecology*, **82**(3): 852–859. https://doi.org/10.1890/0012-9658(2001)082[0852:MBSOLT]2.0.CO;2

Schmaljohann H. and Eikenaar C. 2017. How do energy stores and changes in these affect departure decisions by migratory birds? A critical view on stopover ecology studies and some future perspectives. *Journal of Comparative Physiology*, **203**: 411–429. https://doi.org/10.1007/s00359-017-1166-8

Schmaljohann H., Fox J.W. and Bairlein F. 2012. Phenotypic response to environmental cues, orientation and migration costs in songbirds flying halfway around the world. *Animal Behaviour*, **84**: 623–640. https://doi.org/10.1016/j.anbehav.2012.06.018

Schmaljohann H., Eikenaar C. and Sapir N. 2022. Understanding the ecological and evolutionary function of stopover in migrating birds. *Biological Reviews*, **97**(4): 1231–1252. https://doi.org/10.1111/brv.12839

Schupkégel B., Bozó L. and Tölgyesi Cs. 2020. The role of a water canal and secondary forest for migrants. *Ring*, **42**: 3–13. https://doi.org/10.2478/ring-2020-0001

Şekercioğlu C.H. 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *Journal of Ornithology*, **153**: 153–161. https://doi.org/10.1007/s10336-012-0869-4

Svensson L. 1992. Identification guide to European passerines. Svensson, Stockholm, 375 p.

Szép T., Liechti F., Nagy K., Nagy Zs. and Hahn S. 2017. Discovering the migration and non-breeding areas of sand martins and house martins breeding in the Pannonian basin (central-eastern Europe). *Journal of Avian Biology*, **48**: 114–122. https://doi.org/10.1111/jav.01339

Weber T.P., Houston A.I. and Ens B.J. 1999. Consequences of habitat loss at migratory stopover sites: a theoretical investigation. *Journal of Avian Biology*, **30**: 416–426. https://doi.org/10.2307/3677014

Webster M.S., Marra P.P., Haig S.M., Bensch S. and Holmes R.T. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution*, **17**: 76–83. https://doi.org/10.1016/S0169-5347(01)02380-1

Wilson J.D., Evans A.D. and Grice P.V. 2009. Bird conservation and agriculture. Cambridge University Press, Cambridge, 394 p.

Yong W., Finch D.M., Moore F.R. and Kelly J.F. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *The Auk*, **115**(4): 829–842. https://doi.org/10.2307/4089502