

Stopover Strategies of Lesser Whitethroat *Sylvia curruca* (Linnaeus, 1758) (Passeriformes: Sylviidae) during the Post-breeding Period in Western Hungary

József Gyurácz^{1*}, Péter Bánhidi², József Góczán², Péter Illés², Péter Koszorús², Sándor Kalmár¹, Zoltán Lukács¹, Csaba Németh², Péter Molnár¹ & László Varga²

¹ Department of Biology, Eötvös Lorand University, Savaria Campus, Károlyi Gáspár tér 4, H-9700 Szombathely, Hungary.

² Local Group of BirdLife Hungary, Károlyi Gáspár tér 4, H-9700 Szombathely, Hungary

Abstract: Stopover strategies of the lesser whitethroat *Sylvia curruca* during the post-breeding period were studied at Tömörd, western Hungary, between 1998 and 2017. Capture data of males and females were pooled for both juveniles and adults. Recapture rate, stopover length and fat deposition patterns were analysed. During stopover, juveniles and adults did not differ significantly either in stopover length, total change in body mass and fat score or in proportion and rate of body mass change. All recaptures showed an overall significant positive correlation between mass deposition rate (g/day) and departure body mass. According to the results, the lesser whitethroats used a time-minimisation migration strategy in autumn. The benefit of this strategy might be that it favoured early arrival in overwintering areas, prior to its competitors. The individuals arriving earlier at wintering sites might obtain higher-quality territories and achieve higher winter survival. This might be particularly important for populations of long-distance migrants such as the lesser whitethroat. The majority of lesser whitethroats used the site at Tömörd as a stopover area and only a part of them used it specifically as a site to fatten up.

Key words: Sylviidae, autumn migration, fuel deposition rate, Carpathian Basin

Introduction

Bird migration is a sequence of two main phases, a non-stop flight during which birds' energy reserves are depleted and stopovers during which migrants need to rest and refuel their fat stores (NEWTON 2011). Migratory birds spend about 90% of their whole migration time at stopovers and substantial mortality occurs during these periods (HEDENSTRÖM & ALERSTAM 1997, PAXTON et al. 2017). Therefore, much more research should focus on stopover strategies of birds and ringers should undertake more recapturing and reweighing of birds during their stopovers (HEDENSTRÖM & ALERSTAM 1997, BAIRLEIN 2003a). The migrant passerines need to accumulate sufficient fuel before undertaking energetically demanding migrations. In order to gain a better under-

standing of the birds' stopover strategy at the stopover sites and to protect these sites, more data on the relationship between fuel deposition rate and body mass at last recapture during migration are needed. The successful migration depends on strategies minimising time, energy or risk of predation (ALERSTAM & LINDSTRÖM 1990, CHERNETSOV 2012). At stopover sites, birds must find adequate food supplies that can be utilised for net energy gain; therefore, analysis of stopover has great importance for understanding the behaviour of migrant species (BIEBACH et al. 1986, ELLEGREN & FRANSSON 1992, BAIRLEIN 2003b). Survival of migrants may be affected by morphological and physiological characteristics, sex, age, social status or experience (MOORE et al. 2003,

*Corresponding author: gyuracz.jozsef@sek.elte.hu, ORCID ID 0000-0001-7407-1715

BULER et al. 2017). There are relationships between migration and social dominance among passerines, raptors and seabirds (CATRY et al. 2004, NEWTON 2011). According to some studies, many passerine species show age-dependent effects in energy stores carried during migration, in fat deposition rates at a stopover site and in foraging strategies (ELLEGREN 1991, WOODREY 2000, YOSEF & TRYJANOWSKI 2002, YOSEF & WINEMAN 2010). Food availability determines how fast and to what extent refuelling takes place (ELLEGREN 1991, FRANSSON 1998, DÄNHARDT & LINDSTRÖM 2001): when food is abundant, the effect of social status or scramble competition could be negligible (MOORE & YONG 1991). In addition, within a species, stopover duration can vary depending on year, site and fuel load (BIEBACH et al. 1986, MOORE & KERLINGER 1987, KUENZI et al. 1991, GANNES 2002). The analysis of fat deposition at stopover sites may explain how a species balances costs and benefits and can reveal the species' migration strategy (YOSEF & WINEMAN 2010, ZDUNIAK & YOSEF 2012). The effect of the factors that determine whether a certain habitat is appropriate or not is density dependent: in most cases, the suitability of the habitat decreases with increasing density of individuals in it (FRETWELL & LUCAS 1969).

The lesser whitethroat *Sylvia curruca* (Linnaeus, 1758) is a common passerine in Europe (CRAMP 1992) exhibiting an overall stability of the European populations (EBCC 2017). Northern and western populations are long-distance migrants but the southeastern populations are short-distance or partial migrants (SHIRIHAI et al. 2001). The European lesser whitethroat migrates in autumn in southeast direction to winter mainly in Sudan and Ethiopia. Previous studies have reported observations on its stopover ecology at ringing sites in Egypt (ARCILLA et al. 2016), Israel (FRANSSON et al. 2005, ZDUNIAK & YOSEF 2012) and Sweden (Åkesson et al. 1995). Stopover studies are particularly scarce in Central Europe, although this region plays an important role in "stopovering" lesser whitethroats due to its location at a few hundred kilometres from northern Italy where birds refuel before continuing their migration (BAKER 2002). Recaptured birds originally ringed in England, Germany, the Netherlands, Scandinavia and Poland show that a certain proportion of lesser whitethroats pass through the Carpathian Basin during the autumn migration. There are two subspecies found in Hungary: *S. c. curruca*, which is locally breeding and frequently passing, and *S. c. blythi*, which migrates in late autumn and probably originates from Siberia. Migration passage of the lesser whitethroat through Hungary starts in early August,

followed by one relatively high wave to mid-September and finishes in mid-October (GYURÁ CZ et al. 2017a). The Hungarian populations are migratory and the wintering areas are in Eritrea, Ethiopia, Sudan and Chad (CSÖRGŐ & GYURÁ CZ 2009).

The Trans-Saharan migrants exhibit four types of fattening patterns during migration (SCHAUB & JENNI 2000): (1) accumulate large fat stores and fly non-stop from the northern edge of the Sahara to sub-Saharan Africa (time minimisation model); (2) accumulate more fuel at each stopover site and fly from one site to the next; (3) migrate in short stages with accumulation of sufficient fat to fly to the next stopover site, and (4) similar strategy as the third but these birds stopover at desert oases or catch migrant insects. The patterns 2, 3 and 4 are energy and predation minimisation models. The lesser whitethroat alternates strategies during the course of migration. It is a time minimiser over the desert (YOHANNES et al. 2009), an energy maximiser at Eilat, Israel (ZDUNIAK & YOSEF 2012) and again a time minimiser between the wintering areas and the breeding grounds (TØTTRUP et al. 2008).

In this study, over 20 years of recapture data were analysed to improve our knowledge on stopover duration, body mass and fat-store changes. Based on our data and earlier European studies, we assume the time-minimisation model for the autumn migration of the lesser whitethroat age classes during post-breeding period in western Hungary. In this study, we asked the following questions: (1) What proportion of birds is re-trapped (non-transient individuals with stopover duration > 1 day) in the study area? (2) What is the average stopover length of re-trapped birds? (3) Does the average stopover length differ between age classes? (4) Do the amount and rate of body mass gain and fat deposition differ between juveniles and adults? (5) What factors determine the length of stopover period, rate of body mass gain and fat deposition?

Materials and Methods

Study site

The study was carried out at the Tömörd Bird Ringing Station in western Hungary (47°21'N 16°40'E), located 15 km from Szombathely. There were four natural habitat types around the station of Tömörd.

Shrubland: bushes and herbs forming compact, dense vegetation, which is dissected by small grass patches. Its characteristic plant is the blackthorn (*Prunus spinosa* L.).

Forest: broadleaf trees and bushes forming compact, dense edge vegetation and an ecotone

community with Turkey oak (*Quercus cerris* L.) as the characteristic plant. There are dense shrubs and normal forestry management (e.g. periodic shrinkage of trees) in the forest.

Grassland with shrubs: this habitat type is a transition between the wet habitats of the swamp and the steppe communities that cover the croplands around the marsh. There are a few bushes in the grassland with two small patches of dwarf elder (*Sambucus ebulus* L.). The grassland is not managed.

Marsh: a small (6 ha), permanent and isolated wetland. The characteristic plant is reedmace (*Typha latifolia* L.).

Data collection and analysis

Birds were captured-marked-recaptured from 1998 to 2017 (Appendix 1). Bird ringing took place during the post-fledging period (dispersal and migration) between the last weekend of July and the first weekend of November. On average, the migration period of the lesser whitethroats in Hungary starts in early August (GYURÁ CZ et al. 2017a). We used 28 numbered Ecotone mist-nets (12 m long and 2.5 m high, with 5 shelves and a mesh size of 16 mm) for trapping. The nets were placed evenly in the four habitat types. Birds were captured from dawn to dusk, except on rainy and stormy days when the nets were closed. All birds were ringed, sexed and aged according to SVENSSON (1992). First-year birds that hatched in the year of ringing were defined as juveniles, while all older birds were defined as adults. Flattened maximum wing length was measured to the nearest mm using a graded wing-ruler. The birds were weighed to the nearest 0.1 g using a Pesola/digital balance. The fat reserves (fat score) were estimated visually according to the SE European Bird Migration Network protocol (BUSSE & MEISSNER 2015) – ranging from 0 (no fat) to 8 (bulging fat).

As adult lesser whitethroats were captured in small numbers, we pooled the data of age groups for both sexes. The “condition index” (CI) was calculated according to Swanson et al. (1999):

To avoid the effect of body mass changes in the diel cycles (WINKER et al. 1992), the data from birds captured during the morning and afternoon were treated separately for comparison of captures and recaptures or juveniles and adults. Biometric data were not available for all birds for every capture, resulting in a variation in sample sizes for the various analyses. The individual capture dates were not standardised to the mean arrival date for the given year (YOSEF & WINEMAN 2010).

In order to enable comparisons with other studies, minimum stopover length (MSL) of non-

transient individuals was defined as the period from the date of first capture to the date of last recapture (ELLEGREN 1991). It should be noted that this is often smaller than the real stopover length (RSL) as assessed by the Cormack-Jolly-Seber models (KAISER 1999, SCHAUB et al. 2001). Therefore, the ‘real’ stopover duration was also calculated using the CJS model in the capture-mark-recapture program MARK (COOCH & WHITE 2017). In these studies, ‘life-span’ has been transformed to give an estimate of RLS, using the formula $RSL = -I / \ln(I)$, as published in BROWNIE et al. (1985), where RSL is the mean estimated stopover length and (I) is the estimated daily ‘survival’ probability between two capture days.

The body mass at the first (arrival body mass, ABM) and last capture event (departure body mass, DBM) were available for each recaptured bird. Differences between DBM and ABM were used to assess the mass deposition rate (MDR). The departure fuel load was calculated as the percentage over lean body mass, LBM, i.e., mean body mass of individuals with zero fat score (ARIZAGA et al. 2008).

We analysed the following parameters according to YOSEF & WINEMAN (2010): 1) the factors (wing length, body mass, condition index, fat score distribution and date of first capture) which influenced the recapture of birds; we compared those birds that were captured only once and those that were recaptured; 2) the difference in juveniles and adults in aspects of stopover ecology: we compared the stopover attributes (for example length of stay, change in fat score) of ages; 3) the determinants of length of stopover: we analysed factors (see above) in relation to length of stay; 4) the effect of stopover length on energetic condition: we analysed the relationship between stopover length and other stopover attributes between first and last captures; and 5) the factors which influenced the proportion or rate of mass change: we analysed the body mass change in relation to several variables (date of first capture, initial weight and wing length). For the determination of the variables which influenced stopover length and stopover attributes, we applied a general linear model.

The Past computer program was used for the statistical analysis (HAMMER et al. 2006).

The general linear model (univariate GLM) was used for the determination of the effects of all independent factors. With the exception of the GLM, only non-parametric tests were used in the statistical analysis (Kruskal–Wallis, Spearman, Mann–Whitney U). The level of significance was set at 0.05.

Results

Comparison of recaptures and non-recaptures

The annual ratio of retraps in the study area (non-transient individuals with stopover duration > 1 day) was normally distributed and stationary between 1998 and 2017 ($mean = 0.15$, $SD = 0.14$, $p_{normal / Shapiro-Wilk} = 0.97 / 0.98$, 95% confidence interval $-0.78 - 0.36$, Fig. 1). Of all autumn captures (Table 1), 16.31% of juveniles and 14.73% of adults were recaptured at least once. Most recaptured lesser white-throats (39.31%) stayed at Tömörd for 2–4 days, while a few birds stayed for longer than one month (Fig. 2). Among all retraps, the average minimum length of stopover was 7.71 ± 6.17 days ($n = 349$), while the average calculated real stopover duration was 13.12 ± 3.03 days ($n = 349$). There were no significant differences in stopover duration between years (Kruskal-Wallis test, $H = 8.97$, $p > 0.05$). Morning and afternoon retraps and non-retraps did

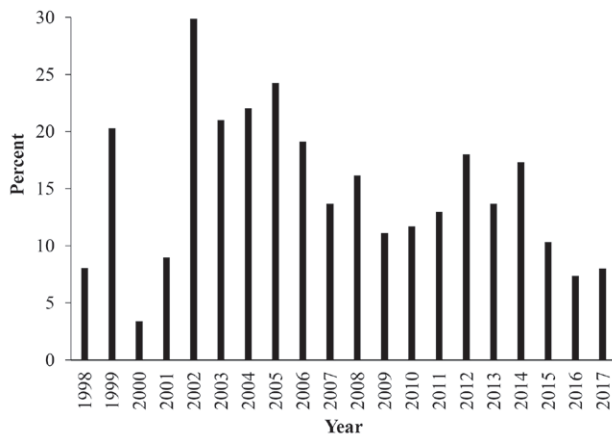


Fig. 1. Annual ratio of retrap (non-transient individuals with stopover duration more than 1 day in the study area) for the lesser whitethroats ($n=349$) at Tömörd, western Hungary.

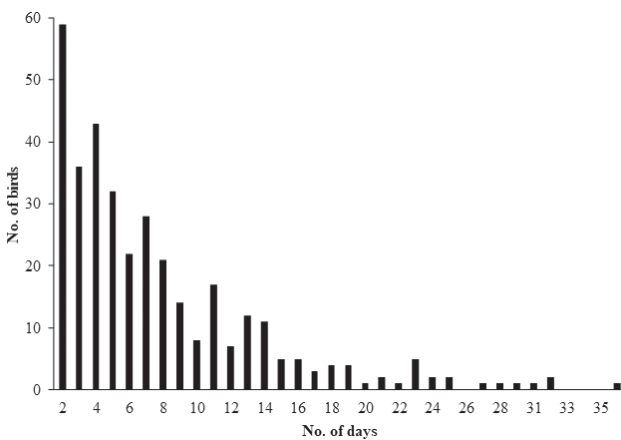


Fig. 2. Minimum length of stopover of recaptured lesser whitethroats ($n = 349$) at Tömörd, western Hungary.

Table 1. Ringing activity period, annual captures and recaptures of lesser whitethroats at the Tömörd Bird Ringing Station (1998–2017).

Year	No. Days	Capture			Recapture		
		All	Juvenile	Adult	All	Juvenile	Adult
1998	57	62	52	10	5	5	0
1999	71	69	42	27	14	10	4
2000	92	59	32	27	2	2	0
2001	106	78	51	27	7	2	5
2002	105	144	104	40	43	32	11
2003	105	119	82	37	25	19	6
2004	101	118	90	28	26	21	5
2005	98	169	122	47	41	31	10
2006	105	115	79	36	22	16	6
2007	104	95	58	37	13	8	5
2008	104	161	122	39	26	21	5
2009	98	153	117	36	17	13	4
2010	99	94	59	35	11	9	2
2011	100	108	78	30	14	7	7
2012	98	111	82	29	20	14	6
2013	99	95	81	14	13	9	4
2014	98	127	93	34	22	18	4
2015	101	126	102	24	13	12	1
2016	100	95	74	21	7	5	2
2017	101	100	74	26	8	6	2
Total	1741	2198	1594	604	349	260	89

not differ significantly in wing lengths, body mass, CI and fat score in the total population, among juveniles or adults (Tables 2 and 3). While 18% of the birds with fat score = 0 were recaptured, only less than 7% of the individual birds with fat score > 4 were recaptured (Fig. 3).

Comparison of juveniles and adults

Among all captures, adults had significantly longer wings than juveniles. Juvenile and adult lesser whitethroats did not differ significantly in body mass, CI and fat scores (Table 4). Among juveniles, the average minimal stopover length was 7.66 ± 5.7 days ($n = 260$), whereas it was 7.86 ± 7.26 days ($n = 89$) among adults. The age classes did not differ significantly with regard to stopover length (*Mann-Whitney U* = 11109, $p > 0.05$). Among non-transient juveniles, average DBM (11.79 ± 1.01 g, $n=246$) was significantly higher than average ABM (11.58 ± 0.99 g, $n = 214$, $U = 23393$, $p < 0.05$), whereas among non-transient adults average, DBM (11.76 ± 0.95 g, $n = 80$) and ABM (11.82 ± 1.02 g, $n=69$) did not differ significantly ($U=2705.5$, $p>0.05$). Among

juveniles with positive fat gain, average LBM was 10.94 ± 0.76 g ($n=54$), average DBM was 11.54 ± 0.89 g ($n = 59$). Among adults with positive fat gain, average LBM was 11.17 ± 0.95 g ($n = 19$) and average DBM was 11.79 ± 1.12 g ($n = 21$). Juveniles

and adults did not differ significantly in LBM ($U = 437.5$, $p > 0.05$, Fig. 4) and DBM ($U = 487.5$, $p > 0.05$). The departure fuel load of juveniles was 5.2%, and for adults 5.3%. Among all recaptures, the ages did not differ significantly with regard to any other variable tested (Table 5).

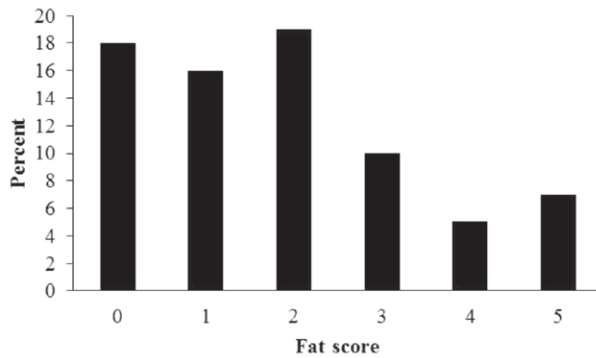


Fig. 3. Percentage of recaptures in each fat score category of recaptured lesser whitethroats ($n = 349$) at Tömörd, western Hungary. There were no birds captured with fat scores higher than 5.

Stopover ecology and patterns

Stopover length was not significantly associated with body mass, wing length or condition index among all captures, juveniles or adults (Table 6). The local birds and birds that arrived in the end of July and in August, stayed significantly longer than later arrivals (Fig. 5, Table 6). Juveniles that remained longer at Tömörd experienced a significantly greater body mass gain and gained a significantly higher proportion of their body mass, while in adults there was no such relationship observed (all captures: $F = 1.46$, $df = 2,323$, $p > 0.05$, juveniles: $F = 8.06$, $df = 2,242$, $p < 0.05$, adults: $F = 2.08$, $df = 2,78$, $p > 0.05$, Table 7). More than half

Table 2. Comparison of retrapped (R) and non-retrapped (NR) lesser whitethroats in the morning at Tömörd, western Hungary, all cap.= all captures (juveniles and adults together). Means \pm SD are shown.

	Wing	Body mass	CI	Fat score
R all cap.	65.44 ± 1.97	11.49 ± 0.85	0.17 ± 0.04	1.06 ± 0.95
NR all cap.	65.36 ± 1.85	11.58 ± 0.95	0.17 ± 0.02	1.29 ± 1.25
Mann-Whitney	$U_{1390,113}=75844$ $p=0.538$	$U_{1404,114}=79062$ $p=0.829$	$U_{1390,112}=72570$ $p=0.218$	$U_{1413,119}=78024$ $p=0.175$
R juveniles	65.15 ± 1.89	11.44 ± 0.81	0.17 ± 0.03	0.98 ± 0.95
NR juveniles	65.19 ± 1.81	11.57 ± 0.97	0.17 ± 0.03	1.27 ± 1.25
Mann-Whitney	$U_{1009,91}=45411$ $p=0.862$	$U_{1011,92}=45390$ $p=0.702$	$U_{1009,90}=43267$ $p=0.445$	$U_{1020,94}=42857$ $p=0.076$
R adults	66.64 ± 1.89	11.69 ± 0.99	0.15 ± 0.06	1.36 ± 0.91
NR adults	65.82 ± 1.88	11.60 ± 0.91	0.18 ± 0.02	1.35 ± 1.25
Mann-Whitney	$U_{377,22}=3250$ $p=0.620$	$U_{389,22}=4010$ $p=0.084$	$U_{376,22}=3448$ $p=0.176$	$U_{389,25}=4568$ $p=0.600$

Table 3. Comparison of retrapped (R) and non-retrapped (NR) lesser whitethroats in the afternoon at Tömörd, western Hungary, all cap.= all captures (juveniles and adults together). Means \pm SD are shown.

	Wing	Body mass	CI	Fat score
R all cap.	65.26 ± 1.67	11.97 ± 0.93	0.18 ± 0.03	1.54 ± 1.20
NR all cap.	65.28 ± 1.91	11.99 ± 1.05	0.18 ± 0.03	1.77 ± 1.24
Mann-Whitney	$U_{598,65}=19298$ $p=0.917$	$U_{1404,114}=27270$ $p=0.915$	$U_{598,65}=18871$ $p=0.693$	$U_{627,76}=21147$ $p=0.103$
R juveniles	65.20 ± 1.75	11.95 ± 0.92	0.18 ± 0.03	1.53 ± 1.22
NR juveniles	65.01 ± 1.87	11.90 ± 1.02	0.18 ± 0.02	1.72 ± 1.23
Mann-Whitney	$U_{429,55}=11202$ $p=0.536$	$U_{429,64}=13225$ $p=0.636$	$U_{429,55}=11603$ $p=0.838$	$U_{434,62}=12204$ $p=0.222$
R adults	65.60 ± 1.17	12.11 ± 0.97	0.18 ± 0.02	1.47 ± 1.19
NR adults	66.01 ± 1.85	12.25 ± 1.09	0.18 ± 0.03	1.88 ± 1.23
Mann-Whitney	$U_{162,10}=691$ $p=0.430$	$U_{183,16}=1389$ $p=0.735$	$U_{162,10}=706$ $p=0.487$	$U_{185,15}=1114$ $p=0.192$

(53.7%) of the birds recaptured at Tömörd either lost or did not gain body mass and most of these losses occurred among birds that stayed for a relatively short stopover period. On average, a bird would lose no more than 0.53 ± 0.99 g. Among all recaptures, birds that stayed for a longer period showed a greater positive change in fat score at Tömörd (Kruskal-Wallis test, $H = 34.65$, $p < 0.01$, $n = 315$) than those that stayed

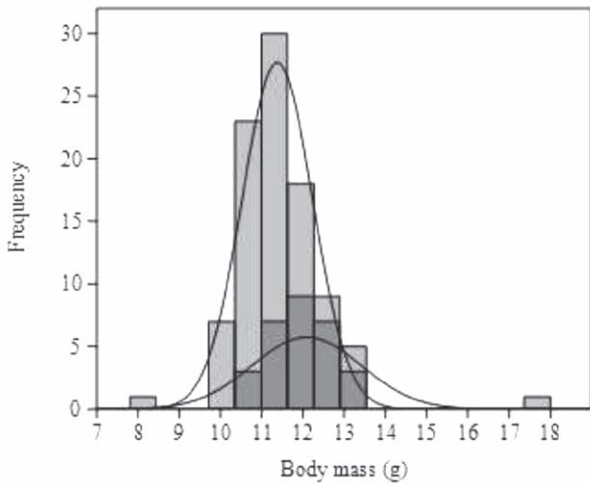


Fig. 4. Histogram of the body mass of juveniles (dark grey, $n = 54$) and adults (grey, $n = 19$) with zero fat score.

for a shorter period (Fig. 6). The maximum change of mass was observed in a juvenile that gained 7.1 g in 5 days. On average, a bird would gain no more than 1.24 ± 1.10 g. An overall significant positive correlation (Spearman) was observed between MDR and

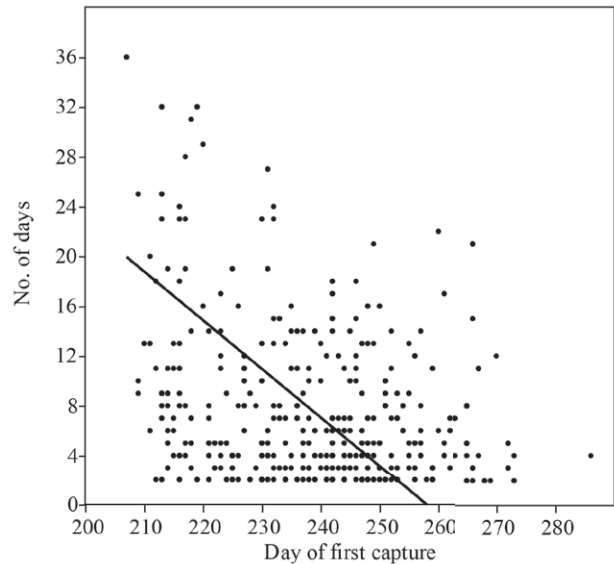


Fig. 5. Relationship between length of stopover and first capture day of recaptured lesser whitethroats ($n = 349$) at Tömörd, western Hungary. Date of first day ($n = 207$) = 28 July.

Table 4. Comparison of juvenile and adult (retrapped and non-retrapped together) lesser whitethroats at Tömörd, western Hungary. Means \pm SD are shown.

	Wing	Body mass (individuals with zero fat scores)	CI	Fat score
in the morning				
Juveniles	65.18 ± 1.81	11.56 ± 0.96	0.18 ± 0.02	1.25 ± 1.22
Adults	65.86 ± 1.89	11.60 ± 0.83	0.17 ± 0.02	1.34 ± 1.21
Mann-Whitney	$U_{1099,398} = 1.7E05$ $p < 0.001$	$U_{1100,410} = 2.14E05$ $p = 0.133$	$U_{1099,398} = 2.14E06$ $p = 0.520$	$U_{1111,413} = 2.1E05$ $p = 0.122$
in the afternoon				
Juveniles	65.03 ± 1.85	11.92 ± 1.03	0.18 ± 0.02	1.69 ± 1.23
Adults	65.99 ± 1.83	12.17 ± 1.04	0.18 ± 0.02	1.84 ± 1.23
Mann-Whitney	$U_{483,171} = 29583$ $p < 0.001$	$U_{484,196} = 40176$ $p = 0.001$	$U_{483,171} = 40094$ $p = 0.563$	$U_{487,198} = 44690$ $p = 0.122$

Table 5. Comparison of juvenile and adult retrapped lesser whitethroats at Tömörd, western Hungary

Parameters		Mann-Whitney U	p -value	Juvenile n	Adult n
Fat change	morning	3737.0	0.98	144	52
	afternoon	1391.0	0.68	101	29
Total change in body mass	morning	3473.5	0.44	144	52
	afternoon	1272.5	0.28	101	29
Proportion body mass change morning		3201.5	0.49	140	49
afternoon		1201.5	0.28	99	28
Body mass gain per day morning		3384.5	0.89	140	49
afternoon		1154.5	0.17	99	28

Table 6. Results of the general linear model (univariate) test with minimal stopover length of retrapped lesser white-throats as dependent variable and fat score, body mass, wing length, condition index at first capture and date of first capture as independent variables.

Group	Factors	Coeff.	SE	t	P value
All captures	Fat score	-0.61	0.33	-1.85	0.23
	Body mass	1.77	1.71	1.03	0.29
	Wing length	-0.03	0.34	-0.11	0.90
	Condition index	-68.78	111.75	-0.61	0.54
	First capture date	-0.11	0.02	-5.25	0.0001
Juveniles	Fat score	-0.60	0.37	-1.61	0.12
	Body mass	0.65	1.92	0.34	0.73
	Wing length	0.16	0.38	0.41	0.68
	Condition index	-14.07	123.9	-0.11	0.90
	First capture date	-0.09	0.02	-4.11	0.0001
Adults	Fat score	-0.39	0.72	-0.55	0.58
	Body mass	4.41	3.89	1.13	0.25
	Wing length	-0.61	0.82	-0.73	0.47
	Condition index	-218.94	261.19	-0.83	0.40
	First capture date	-0.14	0.05	-3.03	0.003

Table 7. Results of the general linear model (univariate) test with length of stay as dependent and total change in body mass (BMG) and proportion body mass change (PBM) of recaptured lesser whitethroats at Tömörd, western Hungary as independent variables. All captures (juveniles and adults together)

Group	Variables	Slope	SE	Intercept	SE	r_{Pearson}	p value
All captures	BMG	0.01	0.00	-1.33	1.15	0.08	0.13
	PBM	0.00	0.00	-0.10	0.10	0.08	0.16
Juveniles	BMG	0.01	0.01	-2.76	1.34	0.15	0.02
	PBM	0.00	0.00	-0.23	0.12	0.15	0.02
Adults	BMG	-0.01	0.01	2.38	2.20	-0.11	0.34
	PBM	0.00	0.00	0.23	0.18	-0.12	0.28

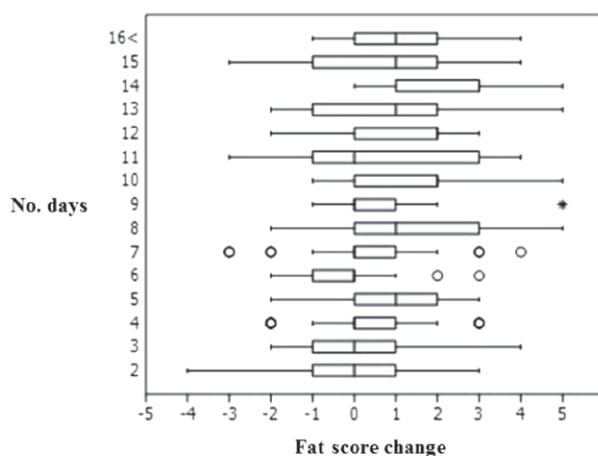


Fig. 6. Length of stopover and change in fat score of retrapped lesser whitethroats ($n = 349$) at Tömörd, western Hungary.

DBM (all recaptures: $r_s = 0.72$, $p < 0.001$, $n = 326$ (Fig. 7); juveniles: $r_s = 0.76$, $p < 0.001$, $n = 245$; adults: $r_s = 0.65$, $p < 0.001$, $n = 80$), so birds with lower MDR tended to depart with less fuel. The positive correlation between MDR and DBM was also significant among individuals with a negative refuelling rate ($r_s = 0.58$, $p < 0.01$, $n = 154$). Individuals with lower fat score (i.e. thinner birds) upon arrival gained a significantly higher proportion of their body mass than fatter individuals but it was not significant among adults. There were no significant relationships between body mass, wing length, condition index at first capture and proportion of body mass change among all captures, juveniles or adults. Individuals with later date of first capture gained a slightly higher proportion of their body mass than early-arrived birds, but it was not significant among adults (Table 8). Individuals

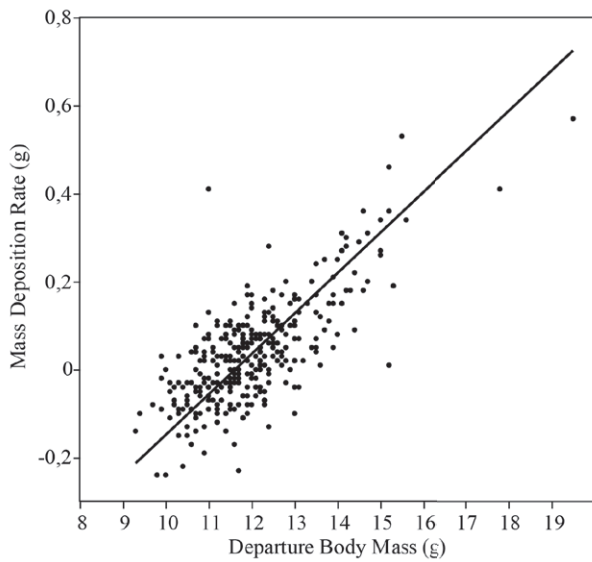


Fig. 7. Departure body mass and body mass gain (g/day) for migrating lesser whitethroats ($n = 326$) at Tömörd, western Hungary.

Table 8. Results of the general linear model (univariate) test with proportion of body mass change (PBM) as dependent and fat score, body mass, wing length, condition index at first capture, date of first capture of recaptured lesser whitethroats at Tömörd, western Hungary as independent variables.

All captures (juveniles and adults together) ANOVA: $F=17.58$, $df=5,305$, $p<0.001$				
Factors	r	SE	t	p -value
Fat score	-0.02	0.01	-3.04	0.002
Body mass	-0.04	0.03	-1.21	0.22
Wing length	0.00	0.01	0.69	0.48
Condition index	-0.65	2.17	-0.29	0.76
First capture date	0.001	0.00	0.02	0.002
Juveniles, ANOVA: $F=17.49$, $df=5,241$, $p<0.05$				
Fat score	-0.02	0.01	-2.81	0.005
Body mass	-0.09	0.04	-2.33	0.02
Wing length	0.01	0.01	1.72	0.08
Condition index	2.05	2.46	0.84	0.40
First capture date	0.001	0.001	3.56	0.001
Adults, ANOVA: $F=4.32$, $df=5,64$, $p<0.01$				
Fat score	-0.01	0.01	-1.22	0.22
Body mass	0.08	0.06	1.34	0.18
Wing length	-0.16	0.01	-1.36	0.18
Condition index	-7.62	4.22	-1.81	0.08
First capture date	-0.001	0.001	-1.98	0.05

with lower body mass upon arrival gained body mass at a significantly faster rate than heavier individuals (all captures: $slope = -0.23$, $r = -0.41$, $SE = 0.001$, $t = -8.17$, $p < 0.001$, $n = 326$; juveniles: $slope = -0.025$, $r = -0.38$, $SE = 0.001$, $t = -6.51$, $p < 0.001$, $n = 246$; adults: $slope = -0.021$, $r = -0.49$, $SE = 0.002$, $t = -5.01$, $p < 0.001$, $n = 80$).

Discussion

Probability of recapture

Stopover duration of migratory passerines usually varies between 1 and 15 days but a significant proportion of migrants stop over for one day only and continue their migration on the first night after arrival (CHERNETSOV 2012). Similarly, we can assume that the majority of the lesser whitethroats captured only once in our study also stayed for only one day during post-fledging period. Small proportions of birds (mean 15%) remained longer than one day (minimum about 7 days on average and realistically about 13 days on average) at Tömörd. A different average retrap rate ($2.6 \pm 2.2\%$) and different stopover duration of the recaptured lesser whitethroats (4.8 ± 0.2 days) was described during a similar period of autumn at the Eilat Ringing Station in Israel (ZDUNIAK & YOSEF 2012). Recapture rates showed that more juveniles than adults stayed longer than one day at Tömörd. This was also observed at Eilat, where the adults also migrated earlier than juveniles during autumn (ZDUNIAK & YOSEF 2012), suggesting that adults use a time-minimisation migration strategy in autumn and also in spring (YOHANNES et al. 2009). The adults can suspend their moult during autumn migration (HALL 2002) and they are more efficient at foraging and/or dominant over juveniles, which may allow adults to fuel up and migrate faster than juveniles (WOODREY 2000). However, there was no significant difference in stopover length of retrapped juveniles and adults at Tömörd. Wing length, body mass and fat score of individuals that were retrapped and those that were captured only once did not differ significantly. In contrast to the locations of the studies performed during the autumn migration close to or in Sahara Desert, our study site is far from this barrier, which could be the reason for the lack of differences between our retrapped birds and transients in body mass and fat score. Similarly to our results, retrapped migrating Eurasian blackcaps (*Sylvia atricapilla*) did not differ from non-retraps in body-mass and CI during spring at Eilat, Israel (YOSEF & WINEMAN 2010). However, in this case the birds were captured during spring migration at capturing sites located after Sahara Desert and not before an

ecological barrier, which might explain the lack of difference in these cases. In other studies, Eurasian blackcaps and individuals of other species caught only once showed a higher body mass than those captured more than once during both autumn (BAIRLEIN 1985, PETERSSON & HASSELQUIST 1985, BIEBACH et al. 1986, ARIZAGA et al. 2008) and spring migrations (MOORE & KERLINGER 1987, KUENZI et al. 1991). A similar result was also obtained for American redstarts (*Setophaga ruticilla*), in which loss of body mass was the cause of the increased probability of recapture (MORRIS 1996). Contrary to our results on the lesser whitethroat, the retrapped Eurasian blackcaps had slightly but significantly shorter wings than non-recaptured birds and this was true for both sexes at Tömörd and Eilat. Smaller, subordinate birds are likely to be less successful in migration, but it seems that wing size is not an important factor in the determination of whether a bird is recaptured or not (YOSEF & WINEMAN 2010). Some lighter lesser whitethroats, that stayed for more weeks, were late-fledging immatures or late breeding/late moulting adults (pers. obs.), which had less time to fatten than earlier birds.

Stopover ecology of juveniles and adults

In our study, juveniles and adults did not differ significantly in total change in body mass, rate of body mass change or change in fat score during stopover. In both age classes, the retrapped birds were in better body condition at the last than at the first capture. Such pattern in the body condition of the lesser whitethroat was also recognised by ZDUNIAK & YOSEF (2012) at Eilat, Israel. In contrast, in many other species of passerines, juveniles and adults show differences in energy stores carried during their migration, in the foraging strategies and rates of fuel deposition at a stopover site (ELLEGREN 1991, WOODREY 2000, YOSEF & TRYJANOWSKI 2002, YOSEF & WINEMAN 2010). The age classes of the lesser whitethroat in our study and the sexes of the Eurasian blackcap, at the same study site (GYURÁCZ et al. 2017b) did not differ significantly with regard to fat deposition rate. This could be explained by the possibility that juveniles and adults or males and females avoid intraspecific resource competition by foraging in different microhabitats at stopover sites. In the absence of competition, stopover features and fat deposition rate may not differ between ages and sexes (ELLEGREN 1991). Another possible explanation for lack of significant differences in fuel management among age and sex classes is that food availability at Tömörd in the post-fledging period is very high, due to the ripening of abundant blackberries and elderberries, a highly preferred food of migrating lesser whitethroats and Eurasian

blackcaps (JORDANO & HERRERA 1981, JORDANO 1985, GYURÁCZ et al. 2017b). When the food abundance is high, the competition for food among age or sex classes might be negligible (MOORE & YONG 1991). This is probably the case at our study site.

Stopover ecology patterns

In this study, the stopover length was not negatively correlated with the fat score at first capture. YOSEF & WINEMAN (2010) did not find a significant relationship between energetic condition at first capture and stopover length of the Eurasian blackcaps during spring migration at Eilat, Israel. A different result was obtained in northern Spain during autumn migration, where birds arriving with less fuel had longer stopover duration; stopover times were 3.6 and 13.6 days for the fattest and the leanest individuals, respectively (ARIZAGA et al. 2008). A possible explanation is that the birds do not need to reach high fat and body mass at Tömörd for their further migration. If a stopover site is not used for fat accumulation, birds of lower energetic condition may actually stay for a shorter duration in order to more quickly reach a refuelling site (WINKER et al. 1992). In other studies, Eurasian blackcaps often remained for several days and put on up to 45% of lean body mass at stopover sites with berries, which are preferred by this species. In contrast, they stopped over for shorter periods at other sites without berries (PHILLIPS 1994). Among all captures, wing length was not a significant determinant of stopover duration of the lesser whitethroats at Tömörd. The larger birds with longer wings were not competitively dominant at this stopover site; they probably did not forage more efficiently and did not spend a shorter period at Tömörd. Another possible explanation is that longer-winged birds are more likely to be transient individuals originating from breeding grounds located to the north of the study site.

There was a significant negative correlation between first capture date and stopover length among all captures; juveniles and adults. This could be in part related to local immature lesser whitethroats being captured at the end of July and early August. They might need more time to prepare for migration because of their late moulting. Like migratory Eurasian blackcaps in southern England (PHILLIPS 1994) and Tömörd (GYURÁCZ et al. 2017b), earlier-arriving lesser whitethroats stayed longer at the stopover site than later migrants at Tömörd. This could be explained with the territorial behaviour of the lesser whitethroats in the wintering area (Baker 2002). The birds that arrived earlier had time to stopover, while birds that arrived later attempted to reach the wintering grounds

as soon as possible (YOSEF & WINEMAN 2010). The individuals arriving earlier at wintering sites might obtain higher-quality territories and achieve higher winter survival (SALEWSKI et al. 2002, OŻAROWSKA & ZANIEWICZ 2015). Successful winter survival may be one reason for the stable annual ratio of transient birds at Tömörd and the stable breeding population of the lesser whitethroat in Europe (EBCC 2017).

Based on the study of WOJCIECHOWSKI et al. (2014) concerning the pattern of body mass change of migratory lesser whitethroats, we can assume that in birds with a body mass below 10.94g (juvenile) or 11.17g (adult), weight increased almost exclusively due to an increase in lean body mass. Above LBM, increasing fat mass was responsible for increasing weight. When lesser whitethroats were first captured at Tömörd during the post-fledging period, they showed a mean weight of 11.58 g (juveniles) and 11.82 g (adults) (about 5.5% above their lean body mass) and after stopover they reached a mean body mass of 11.79 g and 11.76 g (about 7.2% and 5.0% above their lean body mass). The maximum fat scores for age groups were five, both in Tömörd and the southern Baltic coast in Poland (SCILOWSKA & BUSSE 2005). The mean fat scores of juveniles (1.81) and adults (1.86) in Poland were also very similar to the mean fat scores of birds ringed in Tömörd. A significantly higher mean fuel load during autumn migration was reported by ELLEGREN & FRANSSON (1992) and ARIZAGA et al. (2008) for lesser whitethroats (9.3%) and Eurasian blackcaps (about 15%) in Scandinavia and Spain, respectively. These two European stopover sites are located adjacent to ecological barriers (the Baltic and Mediterranean Seas, respectively), which necessitate more energy investment by migratory birds for non-stop flight. The comparatively lower fat loads observed in the lesser whitethroat at Tömörd may be because they probably commence their autumn migration in Europe before the post-juvenile moult is completed and the lack of the ecological barriers in the region of the study area. When migrating over more benign areas, like western Hungary, they usually have low or moderate fat reserves.

The pre-migratory fuel deposition rate of birds varies according to the length of their non-stop flights and this variation is evident even for different populations of the same species (RUBOLINI et al. 2002, NEWTON 2011). McCABE et al. (2018) showed that variation in wind selectivity at departure could produce migratory behaviours that mimic the classic “time-minimiser” and “energy-minimiser” strategies developed in birds. In general, migrants with higher MDR are leaving the stopover site with higher body mass, suggesting a time-minimising strategy

(ALERSTAM & LINDSTRÖM 1990). Such a strategy could be a selective advantage in the occupation of favourable territories. The lesser whitethroats appear to maintain a strategy of time minimisation at Eilat, Israel (ZDUNIAK & YOSEF 2012) and Tömörd. It was reported from a number of localities in Spain that winter site fidelity in Eurasian blackcaps is relatively high (about 30–40%; CANTOS & TELLERÍA 1994, CUADRADO et al. 1995, BELDA et al. 2007), a fact that might be attributed to the arrival in these wintering areas before their competitors. Our results indicated that the change of body mass was positively correlated with stopover length for juveniles. We did not detect such relationships among adults because of the substantially lower sample size. Longer stopover duration is beneficial for a bird’s energetic condition, although such advantages are not always gained immediately. A similar pattern was observed in Eurasian blackcaps during spring migration at Eilat, Israel (YOSEF & WINEMAN 2010). Usually, birds are captured in lower energetic condition in degraded environments but Tömörd, with bushes providing a lot of berries, is a relatively good stopover site for lesser whitethroats.

Body mass of birds in a favourable habitat shows diurnal fluctuations. The mass increases during the day due to the nutrition and decreases by nocturnal metabolism at night (MORRIS & GLASGOW 2001). Thus, a bird recaptured the next morning will have lost weight, but will regain it during the day. A similar phenomenon has been reported in other small passerines, such as European robins (*Erithacus rubecula*), that lost body mass during the first day or two after arrival in Britain (DAVIS 1962), Norway (MEHLUM 1983) and Hungary (GYIMÓTHY et al. 2011). This suggests that energy assimilation may be limited by reduced digestive organs (TRACY et al. 2010). Explanations for the initial mass loss of recaptured individuals may include the effects of capture and handling (NISBET & MEDWAY 1972), the inefficient foraging due to the unknown stopover site (YONG & MOORE 1997), as well as a common mechanism of gaining/losing fat reserves in migrating birds (ALERSTAM & LINDSTRÖM 1990).

Thirty-nine percent of the lesser whitethroats recaptured at Tömörd lost or did not gain body mass but most lesser whitethroats stopping over at Tömörd gained mass by the departure day. Similar rates (ca. 40%) were encountered in Eurasian blackcaps at Losa, Spain (ARIZAGA et al. 2008) and Tömörd (GYURÁČZ et al. 2017b). This could in part be related to costs of stopover, though some birds seem unable to gain mass over several days. The significant positive correlation between MDR and DBM among Lesser Whitethroats with a negative refuelling rate at

Tömörd likely suggests that weight loss was regularly occurring. The explanation of these results is not clear. It is possible that unlike the short- and long-distance migrating Eurasian blackcaps (ARIZAGA et al. 2008, GYURÁCZ et al. 2017b) with a decreasing mass gain close to their departure (KLAASEN & LINDSTRÖM 1996, FRANSSON 1998), the lesser whitethroats follow a simple linear strategy when accumulating fat (CARPENTER et al. 1983). Our data support the idea that most lesser whitethroats were using the study site as a stopover area but only a part of them were using Tömörd as a site to fatten up. As migration strategy of birds is changing over time, particularly in association with environmental factors such as climate change and light pollution, long-term bird ringing is important even for common species.

Acknowledgements: We would like to thank all who took part in the fieldwork and the members of Birdlife Hungary for the bird ringing and the data collecting work. We are also grateful to anonymous reviewers and the editors for their detailed critiques of the earlier manuscript, which helped to greatly improve the manuscript. The project was supported by the European Union and co-financed by the European Social Fund (Grant no. EFOP-3.6.2-16-2017-00014 *Development of international research environment for light pollution studies*). This paper is part of the South-East Bird Migration Research Network and Actio Hungarica publications.

Ethical approval: All procedures performed in the studies involving animals were in accordance with the ethical standards and practices of the Savaria Campus.

References

- Åkesson S., HEDENSTRÖM A. & HASSELQUIST D. 1995. Stopover and fat accumulation in passerine birds in autumn at Ottenby, southeastern Sweden. *Ornis Svecica* 5:81-91.
- ALERSTAM T. & LINDSTRÖM A. 1990. Optimal bird migration, the relative importance of time, energy, and safety. In: GWINNER E. (Ed.): *Bird Migration, Physiology and Ecophysiology*. Heidelberg: Springer, pp. 331-349.
- ARCILLA N., SOULTAN A. E. & ZALAT S. 2016. Advanced autumn stopover dates of Palearctic passage migrants in South Sinai, Egypt. *International Journal of Avian and Wildlife Biology* 1(1): 00003. DOI: 10.15406/ijawb.2016.01.00003
- ARIZAGA J., BARBA E. & BELDA E. J. 2008. Fuel management and stopover duration of Blackcaps *Sylvia atricapilla* stopping over in northern Spain during autumn migration period. *Bird Study* 55 (1): 124-134.
- BAIRLEIN F. 1985. Body weights and fat deposition of Palearctic passerine migrants in the central Sahara. *Oecologia* 66: 141-146.
- BAIRLEIN F. 2003a. The study of bird migrations – some future perspectives. *Bird Study* 50(3): 243-253.
- BAIRLEIN F. 2003b. Nutritional strategies in migratory birds. In: BERTHOLD P., GWINNER E., SONNENSCHNEIN E. (Eds.): *Avian migration*. Berlin: Springer, pp. 321-332.
- BAKER J. 2002. Lesser Whitethroat *Sylvia curruca*. In: WERNHAM C.V., TOMS M.P., MARCHANT J.H., CLARK J.A., SIRIWARDENA G.M. & BAILLIE S.R. (Eds.) *The Migration Atlas: movements of the birds of Britain and Ireland*. London: T. and A.D. Poyser, pp. 552-554.
- BELDA E.J., BARBA E. & MONRÓS J.S. 2007. Resident and transient dynamics, site fidelity and survival in wintering Blackcaps: evidence from capture–recapture analyses. *Ibis* 149: 396-404.
- BIEBACH H., FRIEDRICH W. & HEINE G. 1986. Interaction of body mass, fat, foraging and stopover period in trans-Saharan migrating passerine birds. *Oecologia* 69: 370-379.
- BULER J. J., LYON R. L., SMOLINSKY J. A., ZENZAL T. J. Jr. & MOORE F. R. 2017. Body mass and wing shape explain variability in broad-scale bird species distributions of migratory passerines along an ecological barrier during stopover. *Oecologia* 185 (2): 205-212.
- BUSSE P. & MEISSNER W. 2015. *Bird Station Manual*. SE European Bird Migration Network, Bird Migration Research Station, University of Gdansk. Gdansk.
- BROWNE C., ANDERSON D. R., BURNHAM K. P. & ROBSON D. S. 1985. *Statistical Inference from Band-Recovery Data – A Handbook*. 2nd Edition. Resource Publication No. 156. Washington, D.C.: Fish & Wildlife Service, U.S. Department of the Interior.
- CANTOS F. & TELLERIA J. L. 1994. Stopover site fidelity of four migrant warblers in the Iberian Peninsula. *Journal of Avian Biology* 25: 131-134.
- CARPENTER F. L., PATON D. C. & HIXON M. A. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proceedings of the National Academy of Sciences of the United States* 80: 7259-7263.
- CATRY P., CAMPOS A., ALMADA V. & CRESSWELL W. 2004. Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology* 35: 204-209.
- CHERNETSOV N. 2012. *Passerine Migration, Stopovers and Flight*. Berlin – Heidelberg: Springer-Verlag.
- COOCH E. G. & WHITE G. C. 2017. Program MARK. A Gentle Introduction. <http://www.phidot.org>. dx.doi.org/10.3996/122012-JFWM-110R1.S8
- CRAMP S. 1992. *Handbook of the Birds of the Europe, the Middle East and North Africa*. Vol. 6. New York: Oxford University Press.
- CSÖRGŐ T. & GYURÁCZ J. 2009. Lesser Whitethroat – *Sylvia curruca*. In: CSÖRGŐ T., KARCZA Zs., HALMOS G., MAGYAR G., GYURÁCZ J., SZÉP T., BANKOVICS A., SCHMIDT A. & SCHMIDT E. (Eds.): *Hungarian bird migration atlas*. Budapest: Kossuth Kiadó, pp. 511-512 (in Hungarian with English Summary).
- CUADRADO M., SENAR J. C. & COPETE J. L. 1995. Do all blackcaps *Sylvia atricapilla* show winter site fidelity? *Ibis* 137: 70-75.
- DAVIS P. 1962. Robin recaptures on Fair Isle. *British Birds* 55: 225-229.
- DÄNHARDT J. & LINDSTRÖM A. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behavior* 62: 235-243.
- EUROPEAN BIRD CENSUS COUNCIL 2017. Trends of common birds in Europe, update 2017. <https://www.ebcc.info/index.php?ID=631>. Accessed 30 May 2018
- ELLEGREN H. 1991. Stopover ecology of autumn migrating bluethroats (*Luscinia s. svecica*) in relation to age and sex. *Ornis Scandinavica* 22: 340-348.
- ELLEGREN H. & FRANSSON T. 1992. Fat loads and estimated flight ranges in four *Sylvia* species analysed during autumn migration at Gorland, South-East Sweden. *Ring and Migration* 13: 1-12.
- FRANSSON T. 1998. Patterns of migratory fuelling in Whitethroats *Sylvia communis* in relation to departure. *Journal of Avian Biology* 29: 569-573.
- FRANSSON T., JAKOBSSON S. & KULLBERG C. 2005. Non-random distribution of ring recoveries from Trans-Saharan migrants indicates species-specific stopover areas. *Journal of Avian Biology* 36: 6-11.
- FRETWELL S. D. & LUCAS H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.

- GANNES L. Z. 2002. Mass change pattern of blackcaps refueling during spring migration: evidence for physiological limitations to food assimilation. *Condor* 104: 231–239.
- GYIMÓTHY ZS., GYURÁC J., BANK L., BÁNHIDI P., FARKAS R., NÉMETH Á. & CSÖRGŐ T. 2011. Wing-length, body mass and fat reserves of Robins (*Erithacus rubecula*) during autumn migration in Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae* 57 (2): 203–218.
- GYURÁC J., BÁNHIDI P., GÓCZÁN J., ILLÉS P., KALMÁR S., KOSZORÚS P., LUKÁCS Z., NÉMETH Cs. & VARGA L. 2017a. Bird number dynamics during the post-breeding period at the Tömörd Bird Ringing Station, Western Hungary. *The Ring* 39: 23–60.
- GYURÁC J., BÁNHIDI P., GÓCZÁN J., ILLÉS P., KALMÁR S., LUKÁCS Z., NÉMETH Cs. & VARGA L. 2017b. Stopover strategies of Eurasian Blackcaps (*Sylvia atricapilla*) during the post-fledging period in western Hungary. *Ornis Fennica* 71/11: 1298–1303. DOI: 10.1515/biolog-2016-0149
- HALL K. S. 2002. Lesser Whitethroats *Sylvia curruca* under time constraint do not interrupt moult. *Avian Science* 2: 33–37.
- HAMMER O., HARPER D. A. T. & RYAN P. D. 2006. PAST (Paleontological Statistics Version 1.38), Oslo.
- HEDENSTRÖM A. & ALERSTAM T. 1997. Optimal fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189: 227–234.
- JORDANO P. 1985. The annual cycle of frugivorous passerines in Southern Spanish Mediterranean shrub land: the wintering season and between-year variations. *Ardeola* 32: 69–94 (in Spanish).
- JORDANO P. & HERRERA C. M. 1981. The frugivorous diet of Blackcap populations *Sylvia atricapilla* wintering in southern Spain. *Ibis* 123: 502–507.
- KLAASEN M. & LINDSTRÖM A. 1996. Departure fuel loads in time minimizing migrating birds can be explained by the energy costs of being heavy. *Journal of Theoretical Biology* 183: 29–34.
- KUENZI A. J., MOORE F. R. & SIMONS T. R. 1991. Stopover of Neotropical land bird migrants on East Ship Island following trans-Gulf migration. *Condor* 93: 869–883.
- MCCABE J. D., OLSEN B. J., OSTI B. & KOONSC P. O. 2018. The influence of wind selectivity on migratory behavioral strategies. *Behavioral Ecology* 29(1): 160–168. DOI:10.1093/beheco/axx141
- MEHLUM F. 1983. Weight changes in migratory robins (*Erithacus rubecula*) during stop-over at the island of Store Faerder, Outer Oslofjord, Norway. *Fauna Norvegica. Ser. C. Cinclus* 6: 57–61.
- MOORE F. R. & KERLINGER P. 1987. Stopover and fat deposition by North American wood-warblers (*Parulinae*) following spring migration over the Gulf of Mexico. *Oecologia* 74: 47–54.
- MOORE F. R. & YONG W. 1991. Evidence of food based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28: 85–90.
- MOORE F. R., MABEY S. & WOODREY M. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. In: BERTHOLD P., GWINNER E. & SONNENSCHNEIN E. (Eds.): *Avian Migration*. Berlin: Springer, pp. 281–292.
- MORRIS S. R. 1996. Mass loss and probability of stopover by migrant warblers during spring and fall migration. *Journal of Field Ornithology* 67: 456–462.
- MORRIS S. R. & GLASGOW J. L. 2001. Comparison of spring and fall migration of American Redstarts on Appledore Island, Maine. *Wilson Bulletin* 113: 202–210.
- NISBET I. C. T. & MEDWAY L. 1972. Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114: 451–494.
- NEWTON I. 2011. *The migration ecology of birds*. Elsevier, London.
- OŻAROWSKA A. & ZANIEWICZ G. 2015. Temporal trends in the timing of autumn migration of short- and long-distance migrating Blackcaps (*Sylvia atricapilla*). *Ornis Fennica* 94: 144–152.
- PAXTON E. B., DZRSZ S. L., SOGGE M. K., KORONKIEWICZ T. J. & PAXTON K. L. 2017. Survivorship across the annual cycle of a migratory passerine, the willow flycatcher. *Journal of Avian Biology* 48(8): 1126–1131
- PETTERSSON J. & HASSELIQUIST D. 1985. Fat deposition and migration capacity of Robins *Erithacus rubecula* and Goldcrest *Regulus regulus* at Ottenby, Sweden. *Ringling & Migration* 6: 66–75.
- PHILLIPS N. J. 1994. Autumn migration and weights of Blackcaps *Sylvia atricapilla* and garden Warblers *S. borin* at an inland site in southern England. *Ringling & Migration* 15: 17–26.
- RUBOLINI D., PASTOR A. G., PILASTRA A. & SPINA F. 2002. Ecological barriers shaping fuel stores in Barn Swallows *Hirundo rustica* following the central and western Mediterranean flyways. *Journal of Avian Biology* 33: 15–22.
- SALEVSKI M., BAIRLEIN F. & LEISLER B. 2002. Different wintering strategies of two Palearctic migrants in West Africa – a consequence of foraging strategies? *Ibis* 144: 85–93.
- SCHAUB M. & JENNI L. 2000. Body mass of six long-distance migrant passerine species along the autumn migration route. *Journal of Ornithology* 141: 441–460.
- SCHAUB M., PRADEL R., JENNI L. & LEBRETON J. D. 2001. Migrating birds stop over longer than usually thought: an improved capture–recapture analysis. *Ecology* 82: 852–859.
- SHIRIHAI H., GARGALLO G. & HELBIG A. J. 2001. *Sylvia* Warblers – Identification, Taxonomy and Phylogeny of the Genus *Sylvia*. London: Christopher Helm. Helm Identification Guides.
- SWANSON D. L., LIKNES E. T. & DEAN K. T. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant ruby-crowned kinglets. *Wilson Bulletin* 111: 61–69.
- SVENSSON L. 1992. *Identification guide to European Passerines*. 4th ed., Stockholm.
- TØTTRUP A. P., THORUP K., RAINIO K., YOSEF R., LEHIKONEN E. & RAHBEK C. 2008. Avian migrants adjust migration in response to environmental conditions en route. *Biology Letters* 4: 685–688.
- TRACY C. R., MCWHORTER T. J., WOJCIECHOWSKI M. S., PINSHOW B. & KARASOV W. H. 2010. Carbohydrate absorption by blackcap warblers (*Sylvia atricapilla*) changes during migratory refuelling stopovers. *The Journal of Experimental Biology* 213: 380–385.
- WINKER K., WARNER D. W. & WEISBROD A. R. 1992. Daily mass gains among woodland migrants at an inland stopover site. *Auk* 109: 853–862.
- WOODREY M. S. 2000. Age-dependent aspects of stopover biology of passerine migrants. *Studies in Avian Biology* 20: 43–52.
- WOJCIECHOWSKI M. S., YOSEF R. & PINSHOW B. 2014. Body composition of north and southbound migratory blackcaps is influenced by the lay-of-the-land ahead. *Journal of Avian Biology* 45: 264–272.
- YOHANNES E., BIEBACH H., NIKOLAUS G. & PEARSON D. J. 2009. Migration speeds among eleven species of long-distance migrating passerines across Europe, the desert and eastern Africa. *Journal of Avian Biology* 40: 126–134.
- YONG W. & MOORE F. R. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. *Auk* 114: 263–278.
- YOSEF R. & TRYJANOWSKI P. 2002. Avian species saturation at a long-term ringing station – a never-ending story? *Journal of Yamashina Institute of Ornithology* 34: 89–95.
- YOSEF R. & WINEMAN A. 2010. Differential stopover of blackcap (*Sylvia atricapilla*) by sex and age at Eilat, Israel. *Journal of Arid Environments* 74: 360–367.
- ZANIEWICZ G. & BUSSE P. 2010. Like a phoenix from the ashes. *The Ring* 32: 17–30.
- ZDUNIAK P. & YOSEF R. 2012. Crossing the desert barrier: Migration ecology of the Lesser Whitethroat (*Sylvia curruca*) at Eilat, Israel. *Journal of Arid Environments* 77: 32–38.

Received: 13.08.2018
Accepted: 24.09.2018