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Stopover strategies of Eurasian Blackcaps (*Sylvia atricapilla*) during the post-fledging period in western Hungary

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Stopover strategies of the Eurasian Blackcap (*Sylvia atricapilla*) during the post-fledging period were studied at Tömörd, western Hungary, between 1998 and 2015. Capture data of juveniles and adults were pooled for both sexes, and recapture rate, stopover length and fat deposition patterns were analyzed. During stopover, males and females did not differ significantly in stopover length, total change in body mass, proportion or rate of body mass change, or change in fat score. Among all recaptures, an overall significant positive correlation was recognized between mass deposition rate (g/day) and departure body mass. According to our results, both males and females use a time-minimization migration strategy in autumn. The benefit of this strategy might be that it favors early arrival in the overwintering areas, before competitors. The individuals arriving earlier at wintering sites might obtain higher-quality territories and achieve higher winter survival. This might be particularly important in populations that are increasing, which is the case for the Blackcap. Our data support the idea that most Blackcaps were using the study site at Tömörd as a stopover area, but only a small number of them were using it as a site specifically to fatten up.

1. Introduction

Migration of birds is divided into two main periods; non-stop flight during which their energy reserves are depleted, and stopovers during which they 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). Therefore, much more research should focus on stopover strategies of birds, and ringers should undertake more recapturing and reweighing of birds during their stopovers (Bairlein 2003a). There is a need to collect more data on the relationship between fuel-deposition rate and departure fuel load in retrapped birds during migration, because migrant passerines need to accumulate sufficient fuel before undertaking energetically demanding migrations. Successful migration depends on time, energy or risk of preda-

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tion minimizing strategies (Alerstam & Lindström 1990, Chernetsov 2012).

At stopover sites, birds must find adequate food supplies that can be utilized for net energy gain, therefore analysis of stopover has great importance for understanding the behavior of migrant species (Biebach *et al.* 1986, Ellegren & Fransson 1992, Bairlein 2003b). Survival of migrants may be affected by morphological and physiological quality, sex, age, social status or experience (Moore *et al.* 2003). There are frequent relationships between migration and social dominance among passerines, raptors and seabirds (Catry *et al.* 2004, Newton 2011). According to some studies, males often fatten more rapidly and stop over for a shorter time than subordinate females on stopover sites, which is due to the greater inedominance of males (Morris *et al.* 1994, Otahal 1995).

However, sex differences have not been observed in all passerines and at all stopover sites (Maitav & Izhaki 1994). Food availability determines how fast and to what extent refueling 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). Also, within a species, stopover duration can vary with 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 clearly reveal the species' migration strategy (Yosef & Wineman 2010).

The Eurasian Blackcap (*Sylvia atricapilla*) is a common passerine in Europe (Cramp 1992) and ringed in large numbers at European ringing sites (Berthold & Solenen 1997). Studies of its stopover ecology at some ringing sites in central Africa (Hjort *et al*. 1996), the Middle East (Maitav & Izhaki 1994, Izhaki & Maitav 1998, Gannes 2002, Erciyas *et al*. 2010, Yosef & Wineman 2010) and Europe (Lövei *et al.* 1985, Turrian & Jenni 1991, Ellegren & Fransson 1992, Grandío 1997, Arizaga *et al.* 2008) have already been reported. Studies are particularly scarce in Central Europe, although the region has a high interest for "stopovering" Blackcaps. Recaptured birds originally ringed in Scandinavia and Poland show that a certain proportion of Blackcaps, both during dispersal and in the migration periods, pass through the Carpathian Basin. The timing of their autumn migration shifted about two weeks later during the last 25 years in Hungary (Kovács *et al.* 2010). The Hungarian populations are migratory and the wintering areas are in the eastern and central Mediterranean territories (Csörgő & Gyurácz 2009).

The trans-Saharan migrants exhibit four types of fattening patterns during autumn 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 minimization 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, 4) similar strategy as the third, but these birds stopover at desert oases or catch migrant insects (2, 3 and 4 are energy and predation minimization models). Male Blackcaps follow a time-minimization strategy, while females place more importance on energy-maximization during spring migration (Yosef & Wineman 2010).

However, the positive relationship between departure body mass and mass deposition rate suggests a time-minimizing stopover strategy during autumn (Arizaga *et al.* 2008). In this study, over 18 years of recapture data were analyzed to improve knowledge on stopover duration, body mass and fat store changes. Considering types of migration strategy and earlier European studies, we suggest the time-minimization model for the autumn migration of the Blackcap sex classes during post-fledging period in western Hungary.

We asked the following questions:

(1) What proportion of birds is retrapped in the study area?
(2) What is the average stopover length of retraps?
(3) Does the average stopover length differ between sex classes?
(4) Do the amounts and rate of body mass gain and fat deposition differ between males and females?
(5) What factors determine the length of stopover period and rate of body mass gain and fat deposition?

2. Materials and methods

2.1. Study site

The study was carried out at the Tömörd Bird Ringing Station in western Hungary (47°21'N 16°40'E), located 15 kilometers from Szombathely. There are four natural habitat types around the station of Tömörd. Bushes: bushes and herbs are made up of compact, dense vegetation, which is dissected by small grass patches. Its characteristic plant is the blackthorn (*Prunus spinosa* L.).Forest: broadleaf trees and bushes show compact, dense edge vegetation, forming an ecotone community with turkey oak *(Quercus cerris* L.) as the characteristic plant. There are plenty of crops and normal forestry management in the forest. Grassland with scrubs: this habitat type represents a transition between the wet habitats of the swamp and the steppe communities that used to 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.) in the marsh.

2.2. Data collection and analysis

The birds were captured-recaptured and ringed from 1998 to 2015 (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 Blackcaps started on the 20th of August (Gyurácz & Bánhidi 2008). We used 28 numbered Ecotone mist-nets (12 metrers long and 2.5 meters 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 millimeter using a graded wing-ruler, and birds were weighed to the nearest 0.1 g using a 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 Blackcaps 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):

CI = body mass/wing-length

To avoid the effect of body mass changes in the diel cycles (Winker *et al.* 1992), only data from birds captured during the morning period were used. The individual capture dates were not standardized to the mean arrival date for the given year (Yosef & Wineman 2010).

In order to enable comparisons with other studies, minimum stopover length 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 less than the stopover duration as assessed by Cormack-Jolly-Seber models (Kaiser 1999, Schaub *et al.* 2001). The body mass at the first (arrival body mass, ABM) and last capture event (departure body mass, DBM) were available for each recaptured bird. Difference between DBM and ABM was 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 analyzed 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 males and females in aspects of stopover ecology: we compared the stopover attributes (for example length of stay, change in fat score) of sexes, 3) the determinants of length of stopover: we analyzed factors (see above) in relation to length of stay, 4) the effect of stopover length on energetic condition: we analyzed the relationship between stopover length and other stopover attributes between first and last captures, 5) the factors which influenced the proportion or rate of mass change: we

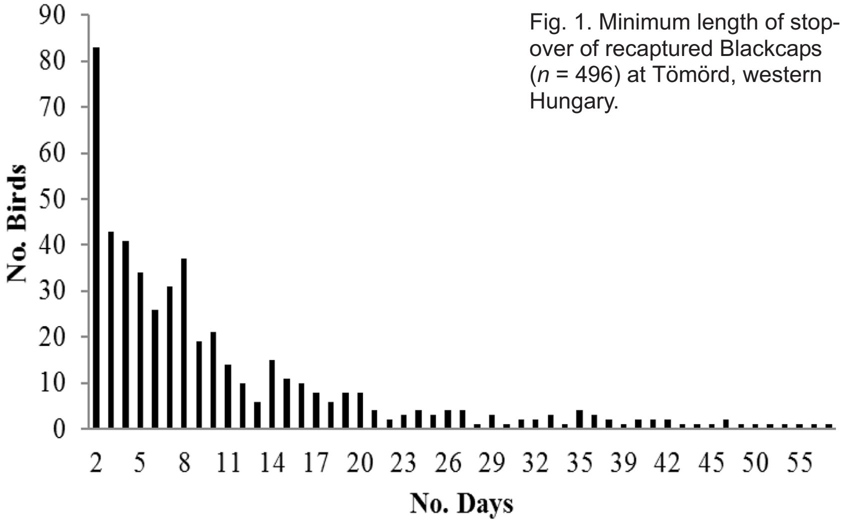

Fig. 1. Minimum length of stopover of recaptured Blackcaps (*n* = 496) at Tömörd, western Hungary.

analyzed the body mass change in relation to 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 (multivariate or univariate GLM) was used for the determination of the effects of all independent factors. With the exception of the GLM, non-parametric tests were used only in the statistical analysis (Kruskal–Wallis, Pearson, Mann–Whitney U). The level of probability for significance was set at 0.05.

3. Results

3.1. Comparison of recaptures and non-recaptures

Of all autumn captures, 3.76% of males and 6.33% of females were recaptured at least once (Appendix 1). Most recaptured Blackcaps stayed at Tömörd for 2–4 days, while a few birds stayed for longer than one month (Fig. 1). Among all retraps, the average length of stopover was 10.73 ± 10.74 days (*n* = 496). Retraps had significantly shorter wing lengths and lower body mass than non-retraps in the total population, among males and

Table 1. Comparison of retrap (R) and non-retrap (NR) Blackcaps at Tömörd, western Hungary, all cap.= all captures (males and females together). Means ± SD are shown.

	Wing	Body mass	CI	Fat score
R all cap.	73.13 ± 1.94	17.73 ± 1.45	0.24 ± 0.02	0.95 ± 1.18
NR all cap.	73.65 ± 2.01	18.14 ± 1.41	0.25 ± 0.02	1.82 ± 1.35
Mann-Whitney	$U_{8176,446}$ = 1.5E06 p<0.001	$U_{8981,497}$ = 1.9E06 p<0.001	$U_{8848,389}$ = 1.6E06 p = 0.195	$U_{9094,497}$ = 1.7E06 p<0.001
R males	73.13 ± 1.89	17.64 ± 1.22	0.24 ± 0.01	0.85 ± 1.12
NR males	73.70 ± 1.98	18.10 ± 1.37	0.25 ± 0.02	1.73 ± 1.30
Mann-Whitney	$U_{4450,161}$ = 3.0E05 p<0.001	$U_{4482,180}$ = 3.2E05 p<0.001	$U_{4418,161}$ = 3.2E05 p<0.05	$U_{4418,161}$ = 3.2E05 p<0.05
R females	73.32 ± 1.95	18.07 ± 1.37	0.25 ± 0.02	1.18 ± 1.23
NR females	73.58 ± 2.04	18.32 ± 1.41	0.25 ± 0.02	1.78 ± 1.39
Mann-Whitney	$U_{3726,229}$ = 3.8E05 p<0.05	$U_{3757,253}$ = 4.4E05 p<0.05	$U_{3697,228}$ = 4.0E05 p = 0.191	$U_{2935,254}$ = 2.7E05 p<0.001

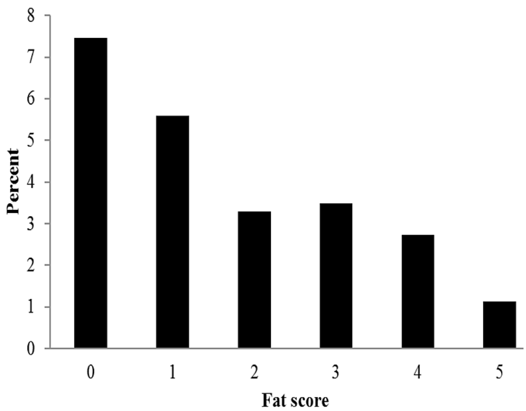

Fig. 2. Percentage of recaptures in each fat score category of recaptured Blackcaps (n = 496) at Tömörd, western Hungary.

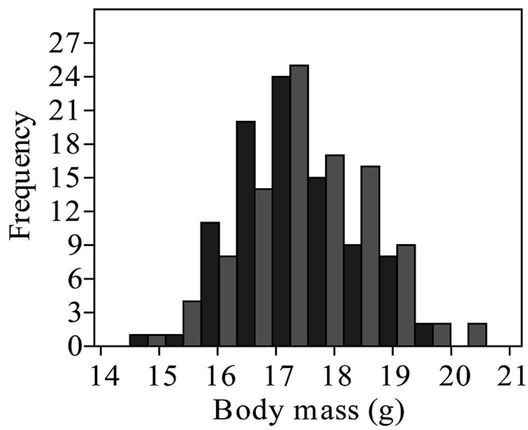

Fig. 3. Histogram of the body mass of males (black, n = 91) and females (gray, n = 98) with zero fat score.

also among females. Retraps and non-retraps did not differ significantly in CI in the total population and among females but the difference was significant among males. Retraps had significantly lower fat score than non-retraps in the total population, among males and also among females (Table 1). While 7% of birds with fat score zero were recaptured, only less than 2% of the individuals birds with more than fat score four were recaptured (Fig. 2).

3.2. Comparison of males and females

Among all captures, males had significantly longer wings, but lower body mass than females. Males had significantly lower CI than females. Male and female Blackcaps did not differ significantly in fat scores (Table 2). Among males, the average stopover length was 11.98 ± 11.90 days (n = 177), whereas this was 10.41 ± 10.62 days (n = 253) among females. The sexes did not differ significantly with regard to stopover length. Among males with positive mass gain, LBM was 17.40 ± 0.86 g (n = 78), DBM was 18.48 ± 1.55 g (n = 84), and among females with positive mass gain, LBM was 17.63 ± 0.94 g (n = 78) and DBM was 19.05 ± 1.83 g (n = 96). Males and females did not differ significantly in LBM (U = 2560, p>0.05, Fig. 3), but males had significantly lower DBM than females (U = 3126.5, p<0.05). The departure fuel load of males was 6.2%, and for females 9.0%. Among all recaptures, the sexes did not differ significantly with regard to any other variable tested (Table 3).

3.3. Stopover ecology and patterns

Among indicators of energetic condition and body size, fat score was found to be correlated with stopover length at first capture. Stopover length was not significantly associated with body mass, wing length or condition index among all captures, males or females (Table 4). The local birds, and

Table 2. Comparison of male and female Blackcaps at Tömörd, western Hungary.

	Wing mean ± SD	Body mass (individuals with zero fat scores) mean ± SD	CI mean ± SD	Fat score mean ± SD
Males	73.68 ± 1.98	18.08 ± 1.37	0.24 ± 0.02	1.68 ± 1.31
Females	73.57 ± 2.03	18.30 ± 1.41	0.25 ± 0.02	1.73 ± 1.39
Mann-Whitney	$U_{4611,3955}$ = 8.8E06 p<0.01	$U_{4662,4010}$ = 8.4E06 p<0.001	$U_{4579,3925}$ = 8.0E06 p<0.001	$U_{3359,3189}$ = 5.3E06 p>0.05

Table 3. Comparison of male and female retrap Blackcaps at Tömörd, western Hungary.

Parameters	Mann-Whitney *U*	*p*-value	Male *n*	Female *n*
Fat change	1.994E04	0.25	177	241
Total change in body mass	1.905E04	0.06	174	246
Proportion body mass change	1.906E04	0.06	174	246
Body mass gain per day	1.92E04	0.07	174	246

Table 4. Results of the general linear model (univariate) test with length of stay of retrapped Blackcaps at Tömörd, western Hungary 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	–2.03	0.47	–4.33	0.0001
	Body mass	–1.02	0.92	–1.10	0.27
	Wing length	–0.31	0.36	–0.84	0.39
	Condition index	28.53	73.58	0.38	0.69
	First capture date	–0.21	0.02	–10.03	0.00001
Males	Fat score	–1.93	0.82	–2.35	0.02
	Body mass	220.38	283.87	0.77	0.44
	Wing length	–4.37	3.96	–1.10	0.27
	Condition index	–0.15	1.07	–0.14	0.88
	First capture date	–0.22	0.03	–6.42	0.00001
Females	Fat score	–1.41	0.56	–2.51	0.01
	Body mass	–90.86	208.29	–0.43	0.66
	Wing length	0.56	2.83	0.19	0.84
	Condition index	–0.22	0.77	–0.29	0.76
	First capture date	–0.17	0.02	–6.27	0.00001

Table 5. Results of the general linear model (multivariate) test with length of stay as dependent and total change in body mass (BMG) and proportion body mass change (PBM) of recaptured Blackcaps at Tömörd, western Hungary as independent variables. All captures (males and females together).

Group	Variables	*Slope*	*SE*	*Intercept*	*SE*	*r*	*p-value*
All captures	BMG	0.04	0.01	–0.27	0.09	0.30	0.0001
	PBM	0.01	0.00	0.14	0.01	0.31	0.0001
Males	BMG	0.04	0.01	–0.24	0.14	0.34	0.0001
	PBM	0.002	0.001	–0.01	0.01	0.35	0.0001
Females	BMG	0.05	0.01	–0.43	0.13	0.32	0.0001
	PBM	0.002	0.001	–0.015	0.01	0.23	0.001

birds that arrived in the end of July and in August, stayed significantly longer than later arrivals (Fig. 4, Table 4). Individuals that remained longer at Tömörd experienced a significantly greater body mass gain and gained a significantly higher proportion of their body mass (all captures: $F = 27.47$, $df = 2{,}429$, $p<0.0001$, males: $F = 12.03$, $df = 2{,}153$, $p<0.001$, females: $F = 12.39$, $df = 2{,}211$, $p<0.0001$, Table 5). 43.8% of the birds recaptured at Tömörd either lost or did not gain body mass,

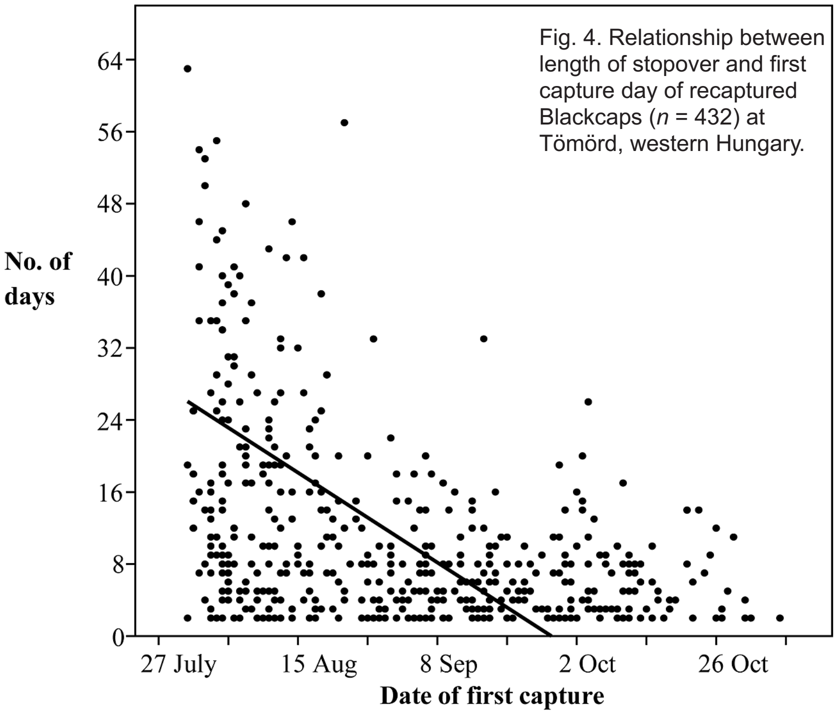

Fig. 4. Relationship between length of stopover and first capture day of recaptured Blackcaps (n = 432) at Tömörd, western Hungary.

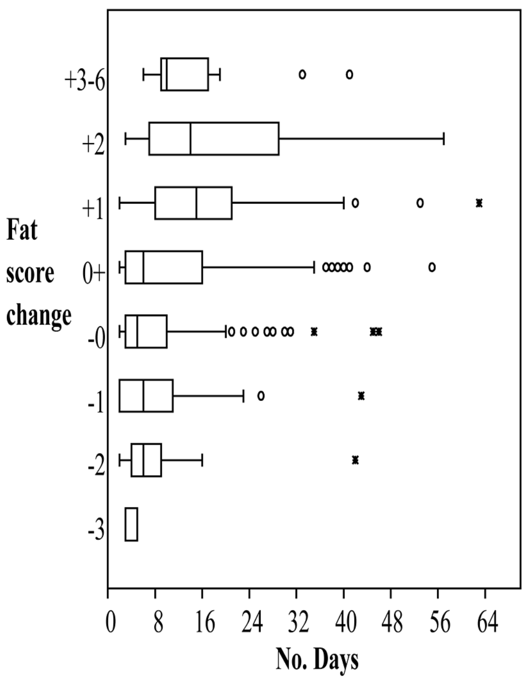

Fig. 5. Length of stopover and change in fat score of retrapped Blackcaps (n = 496) at Tömörd, western Hungary.

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 0.96 ± 0.63 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 = 59.90, p<0.001, n = 482) than those that had stayed for a shorter period (Fig. 5). The maximum change of mass was observed in a juvenile male that gained 6.4 g in 33 days. On average, a bird would gain no more than 1.16 ± 1.14 g. An overall significant positive correlation (Pearson) was observed between MDR and DBM (all recaptures: r = 0.44, p<0.001, n = 370 (Fig. 6); males: r = 0.40, p<0.001, n = 156; females: r = 0.46, p<0.001, n = 214), so birds with lower MDR tended to depart with less fuel. However, the correlation between MDR and DBM was not significant among individuals with a negative refueling rate (r = 0.46, p>0.05). Individuals with lower body mass upon arrival gained a significantly higher proportion of their body mass than heavier individuals, but it was not significant among males. Individuals with longer wing lengths (i.e., larger birds) gained a slightly higher proportion of their body mass than

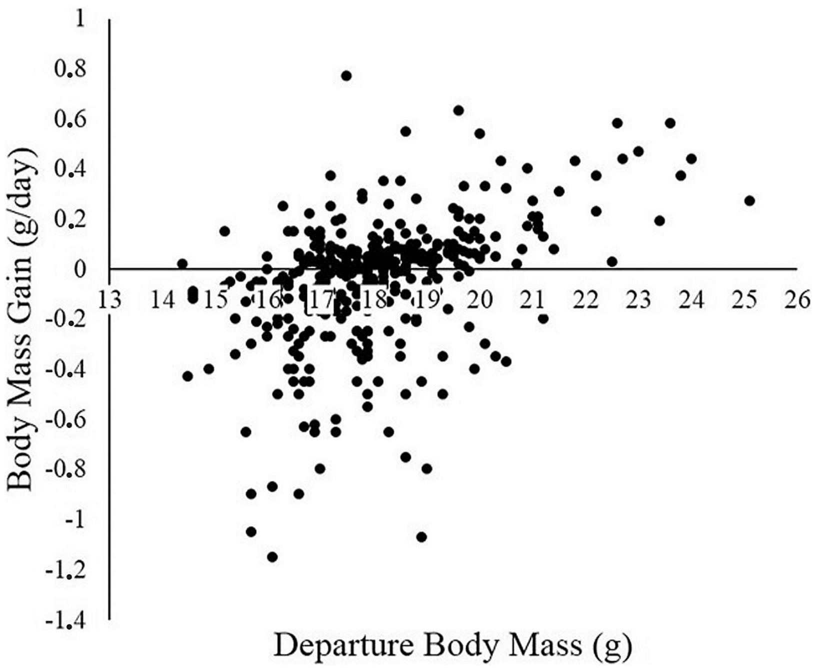

Fig. 6. Departure body mass and mass deposition rate for migrating Blackcaps (n = 370) at Tömörd, western Hungary.

birds with shorter wings, but it was not significant among males.

There were no significant relationships between fat score, condition index at first capture, date of first capture and proportion of body mass change among all captures; males and females (Table 6). Individuals with lower body mass upon arrival gained body mass at a significantly faster rate than heavier individuals (all captures: slope = –0.004, r = –0.25, SE = 0.001, t = –5.43, p<0.001, n = 432; males: slope = –0.003, r = –0.28, SE = 0.001, t = –3.60, p<0.001, n{plain = 156; females: slope = –0.003, r = –0.25, SE = 0.001, t = –3.71, p<0.001, n = 214).

4. Discussion

4.1. Probability of recapture

Stopover duration of migratory passerines usually varies between1 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 Blackcaps captured only once in our study also stayed for only one day during post-fledging period. Small proportions of birds (3–7%) remained longer than one day (10–11 days on average) at Tömörd. A similar retrap rate (3%), but quite different stopover duration of recaptured birds (5.6 ± 5.2 days), was described during a similar period of autumn at the Cernek Ringing Station in Turkey (Erciyas *et al.* 2010). Recapture rates showed that more females than males stayed longer than one day at Tömörd. This observation is supported by data obtained on a Mediterranean island where the males migrated earlier than females during autumn (Lövei *et al.* 1985), suggesting that males also operate a time-minimization migration strategy in autumn and spring (Yosef & Wineman 2010).

However, there was no significant difference in stopover length of retrapped males and females at Tömörd. When comparing wing length, body mass and fat score of individuals that were retrapped and those that were captured only once, the former were siginificantly smaller and leaner. One possible explanation is that smaller birds are less successful migrants, thus they require longer stopover. It is also possible that retrapped Blackcaps are in worse energetic condition than non-

Table 6. 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 Blackcaps at Tömörd, western Hungary as independent variables.

Factors	*r*	*SE*	*t*	*p*-value
All captures (males and females together) ANOVA: $F = 10.63$, $df = 5,426$, $p < 0.001$				
Fat score	–0.01	0.001	–1.43	0.15
Body mass	–0.02	0.01	–2.81	0.005
Wing length	0.01	0.002	3.39	0.0007
Condition index	0.14	0.49	0.27	0.78
First capture date	0.001	0.001	1.31	0.19
Males, ANOVA: $F = 3.07$, $df = 5,150$, $p < 0.05$				
Fat score	–0.01	0.01	–1.28	0.20
Body mass	–0.04	0.02	–1.28	0.20
Wing length	0.01	0.003	1.68	0.09
Condition index	1.51	1.99	0.75	0.44
First capture date	0.001	0.001	0.19	0.85
Females, ANOVA: $F = 6.60$, $df = 5,208$, $p < 0.0001$				
Fat score	0.01	0.01	0.80	0.42
Body mass	0.03	0.03	1.10	0.27
Wing length	–0.01	0.01	–0.52	0.60
Condition index	–4.61	2.24	–2.05	0.04
First capture date	0.001	0.002	1.63	0.10

retraps, thus leaner birds would require a longer refuel time.

In other studies, 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, Pettersson & 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, in which loss of body mass was the cause of the increased probability of recapture (Morris 1996). In contrast, retrapped Blackcaps did not differ from non-retraps in body-mass and CI during spring at Eilat, Israel (Yosef & Wineman 2010).

However, similarly to our results, there was a tendency for retraps to have lower fat scores than non-retraps. Retraps 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 light birds that stayed for more weeks were perhaps late-fledging immatures or late breeding/late moulting adults, which would have had less time to fatten than earlier birds.

4.2. Stopover ecology of males and females

In our study, males and females did not differ significantly in total change in body mass, rate of body mass change, or change in fat score during stopover. Such similarity in body condition was also recognized by other researchers during spring and autumn migration (Turrian & Jenni 1991, Ellegren & Fransson 1992, Arizaga *et al*. 2008, Yosef & Wineman 2010). This similarity in the stopover ecology of sexes has been shown to occur in other species (Otahal 1995, Morris & Glasgow 2001). The sexes did not differ significantly with regard to fat deposition rate. This could be explained by the possibility that 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 sexes (Ellegren 1991). Another possible explanation for lack of significant differences in fuel management among 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 Blackcaps (Jordano & Herrera 1981, Jordano 1985). Thus, because of food abundance, there may be less competition for food at Tömörd (Moore & Yong 1991).

4.3. Stopover ecology patterns

In this study, the stopover length was negatively correlated with fat score at first capture. A similar result was obtained in northern Spain during autumn migration period, 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). Yosef & Wineman (2010) did not find a significant relationship between energetic condition at first capture and stopover length of Blackcaps during spring migration at Eilat, Israel.

A possible explanation for the negative correlation between stopover length and fat load at first capture is that Tömörd serves as a refueling site for some of the Blackcaps. The greatest rate of change in mass was observed in a male Blackcap that gained 37% of its lean body mass in 33 days at Tömörd. 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, Blackcaps often remained for several days and put on up to 45% of lean body mass at stopover sites with a supply of berries 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 a significant determinant of stopover duration at Tömörd. If the larger birds with longer wings were competitively dominant at stopover sites, they probably forage more efficiently and spent 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; males and females. This could in part be related to local immature birds 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 Blackcaps in southern England (Phillips 1994), earlier-arriving birds stayed longer at the stopover site than later migrants at Tömörd. This could be explained by territorial behavior of Blackcaps in the wintering area. 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 increasing number of Blackcaps in Central Europe (Zaniewicz & Busse 2010, Gyurácz & Puskás 2011, Szép *et al.* 2012, Ożarowska *et al.* 2016).

The pattern of body mass change of migratory Blackcaps indicates that in birds with a body mass below 17.8 g, weight increased almost exclusively due to an increase in lean body mass. Above 17.8 g, increasing fat mass was responsible for increasing weight (Wojciechowski *et al*. 2014). When Blackcaps landed at Tömörd during the post-fledging period, they showed a mean weight of 17.64 g (males) and 18.07 g (females) (about 1.4% and 2.5% above their lean body mass), and after stopover they reached a mean body mass of 18.48 g and 19.05 g (about 6.2% and 9.0% above their lean body mass). Significantly higher mean fuel load during autumn migration was reported by Ellegren & Fransson (1992) and Arizaga *et al.* (2008) for populations of Blackcaps in Scandinavia (about 15%) and Spain (about 9.5 and 17.8%), respectively.

Both these European stopover sites are located adjacent to ecological barriers (the Baltic and Mediterranean Seas, respectively), which necessitates more energy investment by migratory birds for non-stop flight. 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). In general, migrants with higher MDR left the stopover site with higher body mass, suggesting a time-minimizing strategy (Alerstam & Lindström 1990). Such a strategy could have a selective advantage in the occupancy of favorable territories. It was reported from a number of localities in Spain that winter site fidelity in 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 arrival in these wintering areas before competitors.Our results indicate that change of body mass was positively correlated with stopover length for both males and females. Longer stopover duration is beneficial for a bird's energetic condition, although such advantages are not always gained immediately. A similar pattern was observed during spring migration in 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 Blackcaps.

However, body mass of birds in a favorable habitat shows diurnal fluctuation. The mass increases during the day due to the nutrition and decreases by nocturnal metabolism at night (Morris & Glasgow 2001). So, 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 Robins, 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 (Young & Moore 1997), as well as a common mechanism of gaining/losing fat reserves in migrating birds.

More than 40% of Blackcaps recaptured at Tömörd and Eilat had either lost or not gained body mass, but most Blackcaps stopping over at Tömörd and Losa, Spain (Arizaga *et al*. 2008) gained mass by the departure day. This could in part be related to costs of stopover, though some birds seem unable to gain mass over several days. The lack of a significant correlation between MDR and DBM among individuals with a negative refueling rate at Tömörd and Losa might suggest that weight loss was not systematic. The reasons for these results are not clear. It is possible that Blackcaps do not follow a simple linear strategy when accumulating fat (Carpenter *et al*. 1983). For example, according to other studies, the mass gain in migrants tends to decrease close to their departure (Klaasen & Lindström 1996, Fransson 1998). It is also possible that under natural environments, when access to food is more restricted, some Blackcaps are unable to reach the level of fuel deposition which could allow them to decrease the rate of refueling close to the departure (Arizaga *et al.* 2008). Our data support the idea that most Blackcaps were using the study site as a stopover area, but only a small number of them were using Tömörd as a site specifically to fatten up.

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Mustapääkertun (*Sylvia atricapilla*) syysmuuttostrategioista Unkarissa

Tutkimuksessa selvitettiin mustapääkertun syksyistä muuttokäyttäytymistä ja välilaskuja Unkarin Tömördissa vuosina 1998–2015. Koiraiden ja naaraiden välillä ei havaittu eroja välilaskujen pituudessa tai painon tai rasvaindeksin muutoksissa. Välilaskun aikainen painonlisäys (g/pv) korreloi positiivisesti muuton jatkamispäivän painon kanssa. Tulokset viittaavat siihen että sekä naaraat että koiraat pyrkivät minimoimaan välilaskuun käytetyn ajan. Tämä strategia voi auttaa saavuttamaan talvehtimisalueet ennen kilpailijoita. Aikaiset saapujat pystyvät luultavasti valtaamaan paremmat reviirit ja selviävät paremmin talven yli. Tämä voi olla erityisen tärkeää lajeilla, joiden populaaatiot

ovat kasvussa, kuten mustapääkertulla. Tutkimuksemme mukaan mustapääkertut siis käyttävät Tömördin aluetta muutonaikaisena välilaskualueena, mutta vain harvat yksilöt keräävät rasvavarastoja siellä.

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Appendix 1. Annual captures and recaptures of Blackcaps at Tömörd Bird Ringing Station (1998–2015).

Year	No. Days	Capture			Recapture		
		All	Male	Female	All	Male	Female
1998	57	208	108	79	6	0	6
1999	71	275	142	95	9	3	5
2000	92	189	82	86	2	0	2
2001	106	271	141	108	9	4	5
2002	105	320	138	103	14	7	3
2003	105	430	192	192	16	5	11
2004	101	471	210	214	18	4	11
2005	98	502	263	189	28	14	11
2006	105	493	225	197	31	7	15
2007	104	503	240	231	28	12	14
2008	104	633	301	282	38	13	23
2009	98	878	446	351	51	15	30
2010	99	507	250	239	33	14	17
2011	100	1,176	612	485	75	24	33
2012	98	642	320	275	25	11	12
2013	99	460	238	177	35	13	16
2014	98	767	391	341	14	6	7
2015	101	840	399	398	64	25	35
In total	1,741	9,565	4,698	4,042	496	177	256