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Comparative study of annual and daily capture-recapture and biometrics of two treecreeper species (*Certhia* spp.) in the post-breeding season over 23 years in western Hungary

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Abstract In this study, we detected and compared changes in the annual and daily captures of the Eurasian *(Certhia familiaris)* and Short-toed Treecreeper *(C. brachydactyla)* in the timing of their post-breeding movements, in the length of minimum stopover duration (MSD) in the area, and also in biometrics in western Hungary. The birds were captured and ringed, or recaptured from the end of July to the first weekend of November in all years from 2001 to 2023. The annual captures of both species indicated stable populations in this period, with milder February months having a positive effect on annual captures. There were similarities and differences in the movement strategies and habitat selection of the species. During the post-breeding season, the Eurasian Treecreeper was more strongly associated with the scrubland and forest edge than the Short-toed Treecreeper. There were two autumn capture waves in September and October for the Eurasian Treecreepers and just one in September for the Short-toed Treecreepers, which were primarily consisted of birds captured only once. There were no significant differences in wing length of the three capture intervals (July-August, September, October-November) in either species, which suggests that the dynamics of post-breeding movements cannot be explained on the bases of possible differences in the behavior of sexes, ages, or populations. The proportion of birds captured only once was about double of that of stopovers in both species each year. The average real length of stopover duration in the area for Eurasian Treecreepers was 94.25 days, and 84.31 days for Short-toed Treecreepers. The length of MSD in the area was not significantly associated with wing length and body mass in either species. Individuals of both species did not gain fat stores significantly during post-breeding season.

Keywords: post-breeding, migration, biometrics, Eurasian Treecreeper, Short-toed Treecreeper

Összefoglalás Jelen tanulmányban a hegyi fakusz *(Certhia familiaris)* és a rövidkarmú fakusz *(C. brachydactyla)* éves és napi fogásainak változásait, tartózkodási idejüket, szárnyhosszukat, testtömegüket és kondíciójukat hasonlítottuk össze. A madarakat 2001 és 2023 között, július végétől november első hétvégéig tartó időszakokban fogtuk be. Mindkét faj éves fogásai stabil populációkra utaltak, az enyhébb februári időjárást követő időszakokban több madarat fogtunk be. A két faj költés utáni diszperziós mozgása, vonulása és élőhelyválasztása között hasonlóságokat és különbségeket is kimutattunk. A költés utáni időszakban a hegyi fakuszt nagyobb arányban fogtuk be az erdős, cserjés élőhelyeken, mint a rövidkarmú fakuszt. A hegyi fakusz esetében két őszi fogási hullám volt szeptemberben és októberben, míg a rövidkarmú fakusz esetében csak egy szeptemberi, amelyben elsősorban az egyszer befogott madarak fordultak elő. A három fogási időszakban (július-augusztus, szeptember, október-november) befogott madarak szárnyhossza egyik faj esetében sem különbözött lényegesen, ami arra utal, hogy a költés utáni időszakban jellemző mozgások dinamikája nem magyarázható a nemek, a korcsoportok vagy a populációk különböző diszperziós vagy vonulási viselkedésével. A csak egyszer befogott madarak aránya mindkét faj esetében évente körülbelül kétszerese volt a visszafogott példányok arányának. A területen eltöltött valós idő átlagos hossza a hegyi fakusznál 94,25 nap, a rövidkarmú fakusznál 84,31 nap volt. A minimális tartózkodási idő egyik faj esetében sem függött a madarak szárnyhosszától és testtömegétől. Egyik faj egyedei sem növelték lényegesen zsírraktáraikat a költés utáni időszakban.

Kulcsszavak: költés utáni időszak, vonulás, biometria, hegyi fakusz, rövidkarmú fakusz

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Introduction

One consequence of the allopatric speciation during the last glacial period is the development of sibling treecreeper and other passerine species. In the postglacial period, the two treecreeper species maintained their independence, despite overlapping ranges (Moreau 1954). Both species are widespread in Europe, but the Eurasian Treecreeper *(Certhia familiaris)* is absent from the northernmost areas, the Mediterranean region and some parts of western Europe. The Short-toed Treecreeper *(C. brachydactyla)* also breeds in western Europe and the three large Mediterranean peninsulas (Berthold 1993, del Hoyo *et al*. 1992–2011). In central Europe, where their ranges overlap, the two species may occur in the same habitat and they may be in strong competition with each other (Clausel & Toft 1988, Moreno 1991, Gil 1997, Schepers & Török 1997).

Most Eurasian Treecreeper populations are largely resident in Europe. The small sample size of distant recoveries show only short-distance, less than 500 kilometres movements. A bird from central Europe (Germany) appeared during winter in southern Spain. Birds from Fennoscandia winter around the Baltic Sea, in western and central Europe, as well as European Russia. Their movements are more intensive in irruption years (Spina *et al*. 2022). The Short-toed Treecreeper population is sedentary in Europe. Some altitudinal movements were locally recorded; post-breeding dispersal is rather limited (Harrap 2008). The 85% of the distant recoveries were less than 300 kilometres away from the ringing site. They showed only local and short-distance movements in Spain, Germany, Italy, Netherlands, Denmark, France, and Switzerland. There were two "long-distance" movements in Europe: (1) bird ringed in Belgium was recoveried during winter in southern Portugal; (2) bird ringed in early spring in northern Spain was encountered during breeding season in western Africa (Mali) (Spina *et al*. 2022). Both species are partial migrants and strongly territorial and can be observed all year round in Hungary (Bauer & Kaiser 1991, del Hoyo *et al*. 2008, Gyurácz 2022a, 2022b). The Eurasian Treecreepers breeding in Hungary are resident, whereas the northern, probably mainly Slovakian migrants arrive during autumn, and may overwinter in Hungary. The Hungarian breeding population of the Short-toed Treecreeper is also resident, but there are some passing through in September-October. The origin of possible migrants is not known (Csörgő & Karcza 2000, Török 2009a, 2009b). Their breeding period is more extensively studied (Kuitunen 1985, 1986, Kuitunen & Aleknonis 1992, Suorsa *et al*. 2005, Jäntti *et al*. 2007, Haraszthy 2019), but little is known about their post-breeding occurrence, movement dynamics and habitat selection (Török 2009a, 2009b).

In the present study, 23 post-breeding seasons of capture data were processed. The aim of our study was to analyze annual and daily variation in the number of captures and duration of time spent in the area of the Eurasian and Short-toed Treecreepers at a study site in western Hungary and to identify changes in biometric parameters. We asked the following questions: (1) Do the annual and daily capture – recapture dynamics differ between species? (2) Is there a relationship between winter temperature, precipitation and the annual captures of bird species? (3) Do the minimum stopover duration (MSD) and real length of stopover duration in the area and habitat selection of birds differ between species? (4) Does the rate of change in body mass differ between species? (5) What biometrics determine the MSD and rate of change in body mass?

Material and Methods

Study area

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. The climate is continental with cold winters and warm summers. There are four natural habitat types in the 15 ha study area. (1) Bushes: bushes and herbs make up compact, dense vegetation, which is dissected by small grass patches; its characteristic plant is the blackthorn *(Prunus spinosa)*. (2) Forest: broadleaf trees and bushes form a compact, dense edge, making up an ecotone community with the Turkey oak *(Quercus cerris)* as the characteristic plant. There is plenty of felling and normal forestry management in the forest. (3) Grassland with shrubs: this unmanaged habitat type represents a transition between the wet habitats of the swamp and the steppe communities that used to cover the surrounding agricultural land; there are a few bushes in the grassland, with two small patches of dwarf elder *(Sambucus ebulus)*. (4) Marsh: a small (6 ha), permanent, and isolated wetland; the characteristic plant is the broadleaf cattail *(Typha latifolia) (Figure 1)*.

Data collection and analysis

The birds were captured and ringed, or recaptured during the post-breeding season between the end of July and the first weekend of November in all years from 2001 to 2023. This time period was the same every year (Gyurácz *et al.* 2017).

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 distributed in the four habitat types *(Figure 1)*. Throughout the study period the number of nets and their location did not change. Birds were captured from dawn to dusk, except on rainy and stormy days. All birds were ringed according to Svensson (1992). First-year and older birds were examined together, because ageing is uncertain. Flattened maximum wing length was measured to the nearest

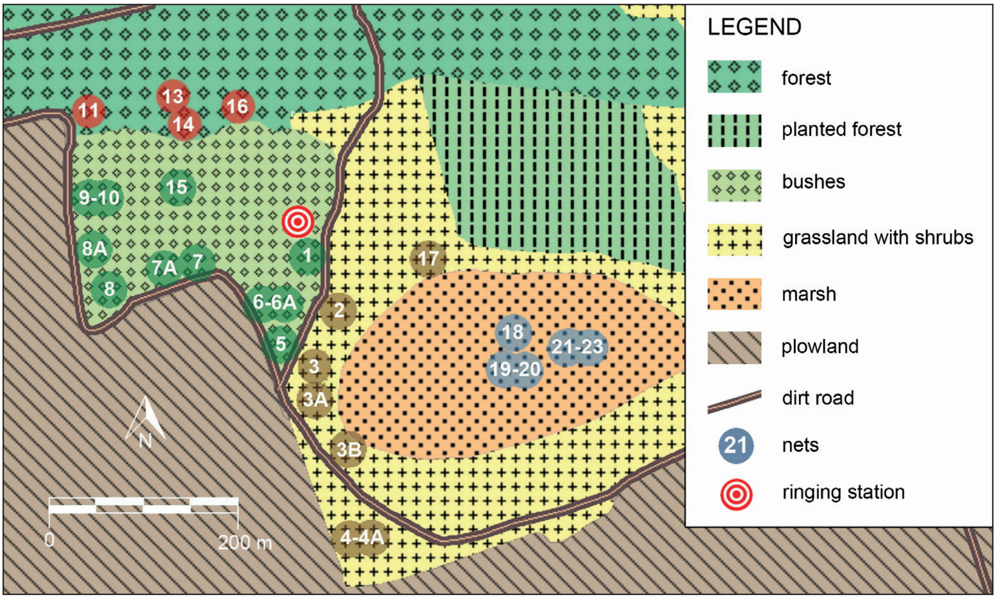

Figure 1. Habitat map of the study area with locations of mist-nets
1. ábra A vizsgálati terület élőhely-térképe a függönyhálók helyeivel

millimeter using a graded wing ruler, and birds were weighed to the nearest 0.1 g. Fat scores were estimated visually according to the SE European Bird Migration Network protocol, zero is the lowest value, eight is the highest (Busse & Meissner 2015).

The total annual capture of the first year (2001) was set as 100% and the population index of change in captures was calculated with the following formula (Greenwood *et al.* 1993):

$$I_x = \frac{N_x}{N_{x-1}} \times I_{x-1}$$

where I_x is the chain index of the specific year, I_{x-1} is the chain index of the previous year, N_x is the annual number of captures of species in the specific year, N_{x-1} is the annual number of captures of species in the previous year. Daily changes in the number of birds captured only once and individuals recaptured (birds captured at least twice in the same season) were analyzed separately. Generalized linear modelling (GLM) with identity link function was used to determine trends in the chain indices, timing of first captures and minimum stopover duration (MSD). The significance level was set at $P < 0.05$. GLM was also used to determine the effects of monthly mean temperatures, maximum and minimum daily mean temperatures and monthly precipitation totals during the winter months (December-March) preceding the breeding season and autumn migration on the annual captures. We used temperature and precipitation data from the Szombathely Meteorological Station, 15 km from the ringing station (NNDC 2023). GLM analyses were conducted using the Past program version 4.03 (Hammer *et al.* 2001). For some analyses, calendar dates were transformed to ordinal dates.

The length of MSD in the area of individuals recaptured was defined as the period from the date of first capture to the date of last recapture (Ellegren 1991). The real length of stopover duration (RSD) in the area was also calculated using the Cormack-Jolly-Seber model (Kaiser 1999, Schaub *et al*. 2001) in the capture-mark-recapture program MARK (Cooch & White 2017) as this is often longer than the length of MSD. In these studies, "lifespan" has been transformed to give an estimate of RSD using the formula RSD = −I / ln (I), as published in Brownie *et al.* (1985) where RSD is the mean estimated length of time spent in the area and I is the estimated daily survival probability between two capture days. These analyses were performed using MARK software, version 10.X (White & Burnham 1999).

Based on daily captures, three capture intervals were identified (July-August, September, October-November) for the comparison of the temporal changes in wing length, body mass and fat score of birds captured only once and birds recaptured. The body mass at the first arrival and last capture event were available for each recaptured individual. The difference between the two body mass values was used to assess the total body mass gain, expressed as a percentage of the initial body mass value (PBM). To determine the effects of the variables which influenced the length of MSD in the area and body mass change (PBM), we applied a multiple linear model (Yosef & Wineman 2010). Otherwise, non-parametric tests were used exclusively in the statistical analysis of biometrics (Kruskal-Wallis test, Wilcoxon's test, Spearman correlation). Based on the distribution of captured birds by habitat, the habitat diversity of the two species were compared using the Shannon formula and t test (Magurran 2004). All analyses were performed using R 3.6.0. (R Core Team 2015).

Results

Annual, daily captures, time spent and spatial distribution

We used the records of 267 Eurasian Treecreepers (173 birds captured only once, 94 birds recaptured) and 312 (202 birds captured only once, 110 birds recaptured) Short-toed Treecreepers captured and ringed from the end of July to early November within the study period of 2001–2023 *(Appendix 1)*.

There were no long-term trends in the chain index of annual captures, recaptures or recapture ratios between 2001 and 2023 in either species except for an increasing trend in Short-toed Treecreeper recaptures *(Figure 2, 3, 4)*. Annual captures and recaptures were positively correlated in both species (Eurasian Treecreeper: r_{Sp} = 0.67, P = 0.01, Short-toed Treecreeper: r_{Sp} = 0.75, P = 0.01), but the annual captures and recaptures of the two species were not correlated (capture: r_{Sp} = 0.06, P = 0.78, recapture: r_{Sp} = 0.17, P = 0.44). Among the environmental factors, the mean monthly temperature in February of the previous year was found to be correlated with annual capture of the Short-toed Treecreeper (GLM: slope = 0.22, SE = 0.07, G = 9.71, P = 0.01).

There was no significant trend in daily captures of Short-toed Treecreepers captured only once, but the daily captures of Eurasian Treecreepers captured only once showed a significant increasing trend and the daily captures of birds recaptured of both species a

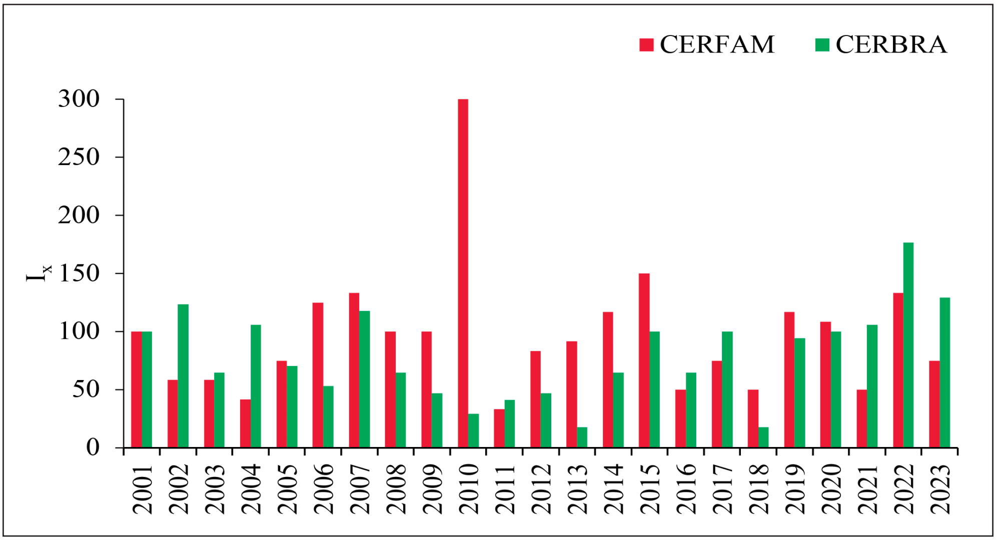

Figure 2. Capture indices at the study site calculated for 2001–2023. CERFAM: Eurasian Treecreeper GLM: slope = 0.12, SE = 1.77, G = 0.01, P = 0.94. CERBRA: Short-toed Treecreeper GLM: slope = 0.21, SE = 1.23, G = 0.97, P = 0.32

2. ábra A 2001 és 2023 közötti éves fogásokból számított fogási indexek Tömördön. CERFAM: hegyi fakusz GLM: meredekség = 0,12, SE = 1,77, G = 0,01, P = 0,94. CERBRA: rövidkarmú fakusz GLM: meredekség = 0,21, SE = 1,23, G = 0,97, P = 0,32

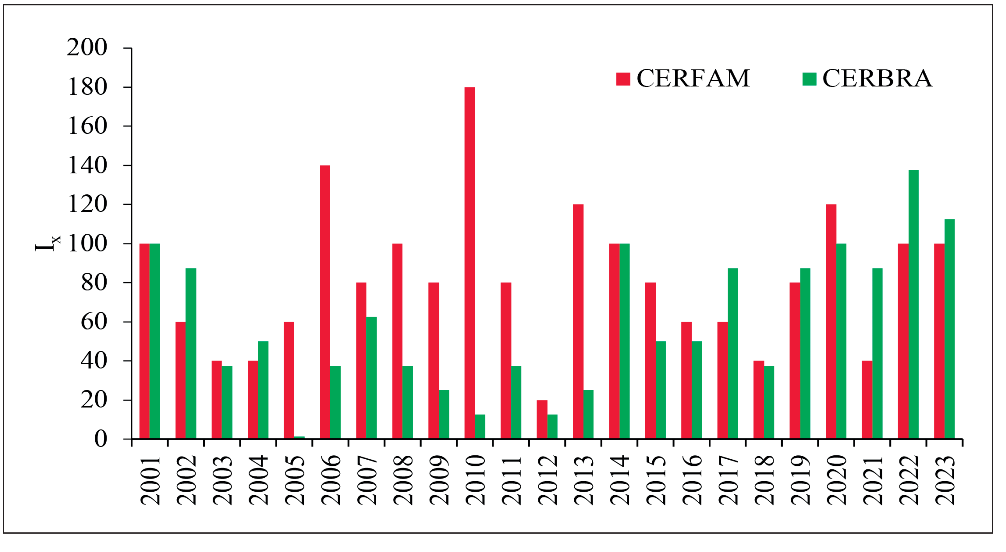

Figure 3. Recapture indices at the study site calculated for 2001–2023. CERFAM: Eurasian Treecreeper GLM: slope = 0.18, SE = 1.19, G = 0.03, P = 0.87. CERBRA: Short-toed Treecreeper GLM: slope = 0.25, SE = 1.05, G = 5.52, P = 0.02

3. ábra A 2001 és 2023 közötti éves visszafogásokból számított visszafogási indexek Tömördön. CERFAM: hegyi fakusz GLM: meredekség = 0,18, SE = 1.19, G = 0,03, P = 0,87. CERBRA: rövidkarmú fakusz GLM: meredekség = 0,25, SE = 1,05, G = 5,52, P = 0,02

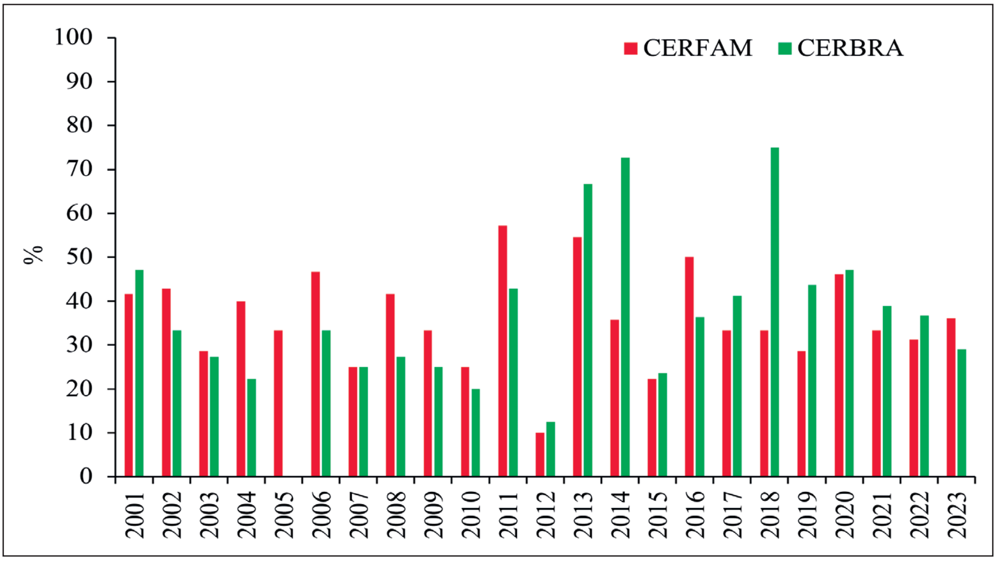

Figure 4. Recapture ratios at the study site calculated for 2001–2023. CERFAM: Eurasian Treecreeper GLM: slope = -0.15, SE = 0.35, G = 0.19, P = 0.66. CERBRA: Short-toed Treecreeper GLM: slope = 0.94, SE = 0.54, G = 3.02, P = 0.08

4. ábra A 2001 és 2023 közötti éves visszafogási arányok Tömördön. CERFAM: hegyi fakusz GLM: meredekség = -0,15, SE = 0,35, G = 0,19, P = 0,66. CERBRA: rövidkarmú fakusz GLM: meredekség = 0,94, SE = 0,54, G = 3,02, P = 0,08

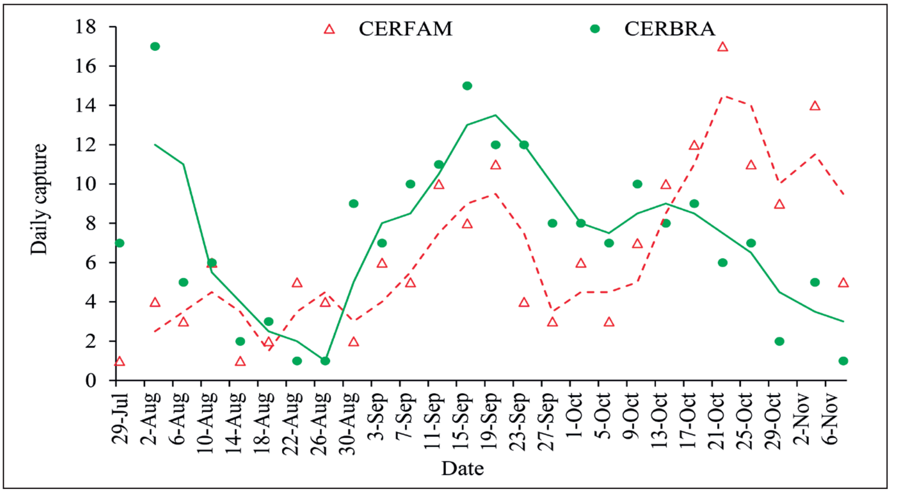

Figure 5. Total capture numbers of the birds captured only once (transients) per four days in the studied period. Lines – smoothed by 2-section moving mean. CERFAM: Eurasian Treecreeper GLM: slope = 0.09, SE = 0.02, G = 18.72, P = 0.01. CERBRA: Short-toed Treecreeper GLM: slope = -0.01, SE = 0.03, G = 0.19, P = 0.66

5. ábra Az egyes években négynaponként egyszer befogott madarak összegyedszáma a vizsgált időszakban Tömördön. Grafikonok – 2 négynapos időszakonkénti mozgóátlag. CERFAM: hegyi fakusz GLM: meredekség = 0,09, SE = 0,02, G = 18,72, P = 0,01. CERBRA: rövidkarmú fakusz GLM: meredekség = -0,01, SE = 0,03, G = 0,19, P = 0,66

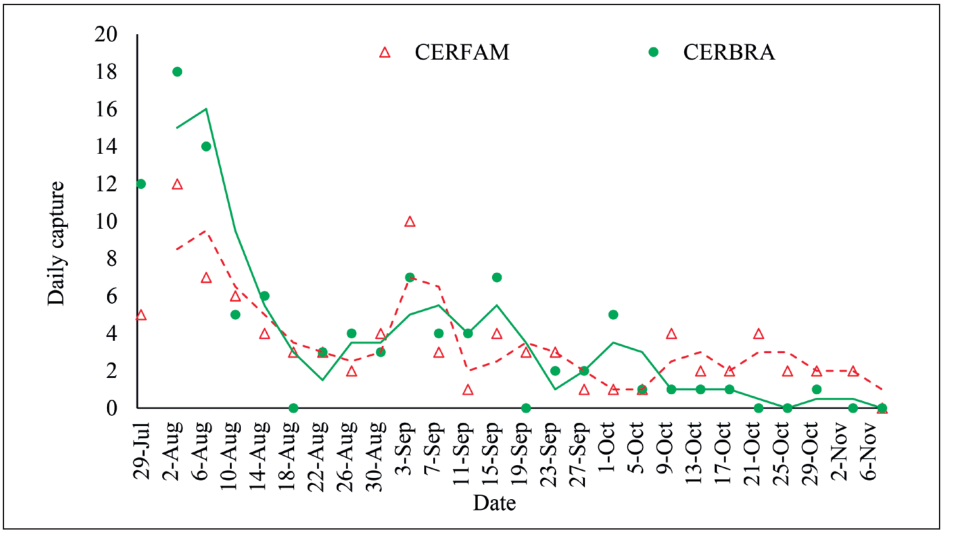

Figure 6. Total capture numbers of the birds recaptured per four days in the studied period. Lines – smoothed by 2-section moving mean, CERFAM: Eurasian Treecreeper GLM: slope = -0.05, SE = 0.01, G = 13.93, P = 0.01., CERBRA: Short-toed Treecreeper GLM: slope = -0.11, SE = 0.02, G = 26.77, P = 0.01

6. ábra Az egyes években négynaponként befogott és legalább egyszer visszafogott madarak összegyedszáma a vizsgált időszakban Tömördön. Grafikonok – 2 négynapos időszakonkénti mozgóátlag. CERFAM: hegyi fakusz GLM: meredekség = -0,05, SE = 0,01, 13,93, P = 0,01. CERBRA: rövidkarmú fakusz GLM: meredekség = -0,11, SE = 0,02, G = 26,77, P = 0,01

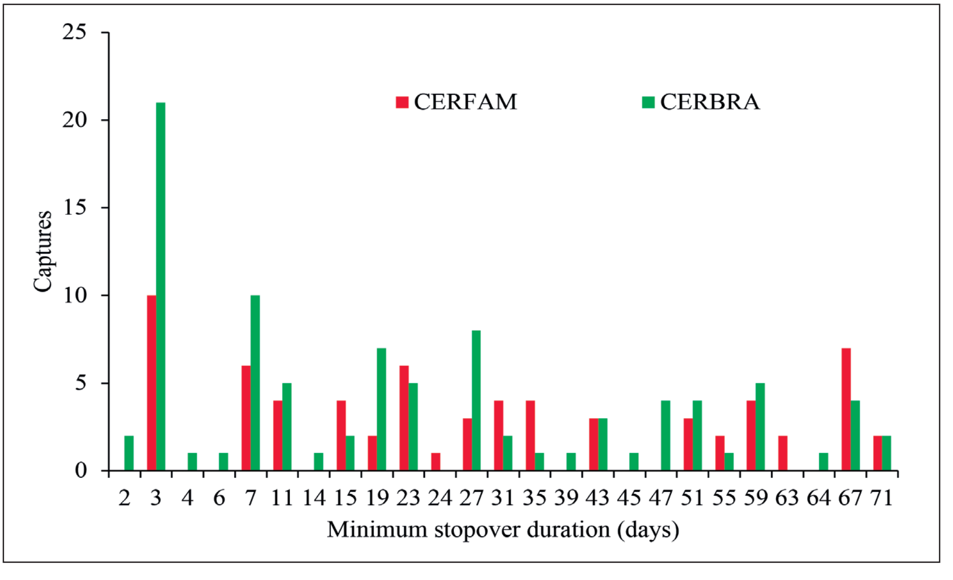

Figure 7. Length of MSD of birds recaptured at Tömörd, western Hungary, 2001–2023. CERFAM: Eurasian Treecreeper, CERBRA: Short-toed Treecreeper

7. ábra A visszafogott madarak minimum tartózkodási ideje Tömördön, 2001–2023. CERFAM: hegyi fakusz, CERBRA: rövidkarmú fakusz

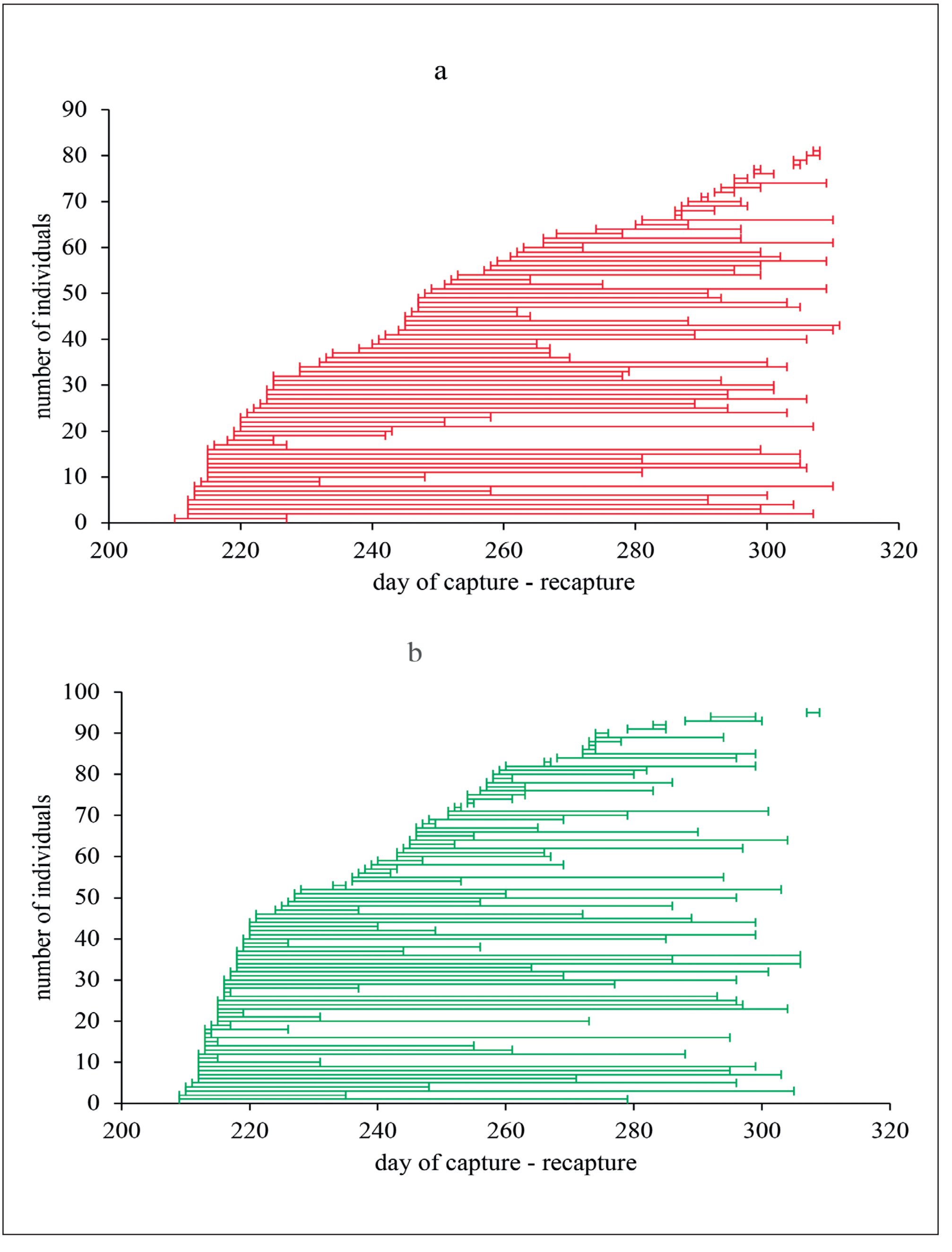

Figure 8. Individual capture-recapture histories of treecreepers at Tömörd, western Hungary. (a) Eurasian Treecreeper; (b) Short-toed Treecreeper. Horizontal lines: length of MSD in the area. Day 210 is 29 July.

8. ábra A visszafogott (a) hegyi és (b) rövidkarmú fakuszok első befogási idejének kumulatív eloszlása a vizsgált időszakban Tömördön. Vízszintes vonalak: minimum tartózkodási idők hossza a vizsgálati területen. A 210. nap július 29.

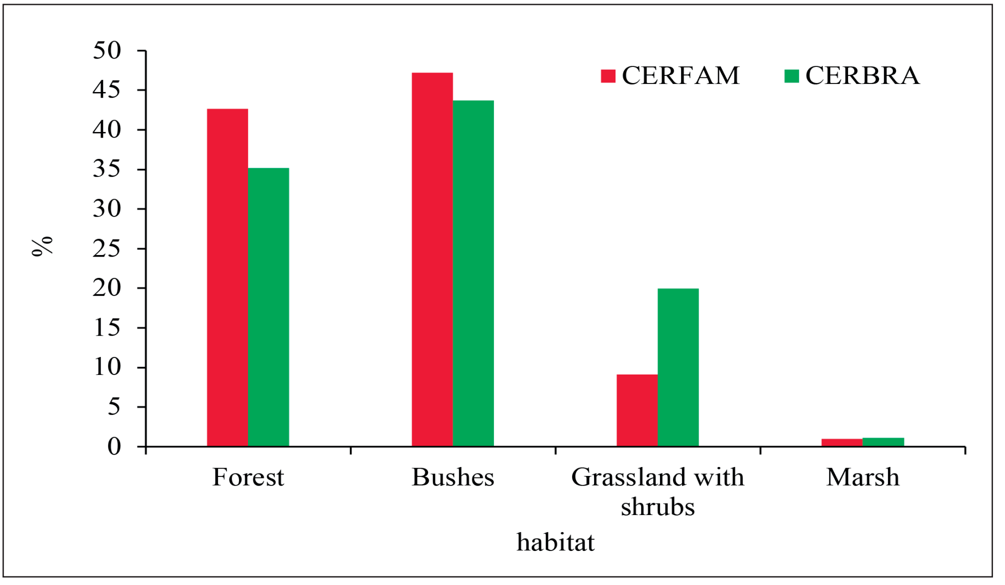

Figure 9. Capture rate in the four habitats at Tömörd, western Hungary. CERFAM: Eurasian Treecreeper, CERBRA: Short-toed Treecreeper

9. ábra A befogott madarak százalékos eloszlása a négy élőhely alapján Tömördön. CERFAM: hegyi fakusz. CERBRA: rövidkarmú fakusz

significant decreasing trend between the end of July and the early November *(Figure 5, 6)*. During 2001–2023, there was no significant shifts in the timing of first captures in either species (Eurasian Treecreeper GLM, slope = -0.01, SE = 0.51, G = 0.01, P = 0.98, Short-toed Treecreeper GLM, slope = -0.39, SE = 0.42, G = 0.88, P = 0.35).

The lengths of MSD of the two species were similar (r_{Sp} = 0.57, P = 0.01, *Figure 7, 8*). There was no long-term trend in the minimum length of MSD between 2001 and 2023 in either species (Eurasian Treecreeper GLM: slope = 0.32, SE = 0.43, G = 0.57, P = 0.45, Short-toed Treecreeper GLM: slope = 0.23, SE = 0.62, G = 0.14, P = 0.71). The Eurasian Treecreeper's average real length of time spent was 94.25 days (95% confidence interval: lcl 72.99, ucl 122.02), the Short-toed Treecreeper's was 84.31 days (95% confidence interval: lcl 65.84, ucl 108.03). The estimated daily survival probability between two capture days was 0.98, the capture probability of the birds was 0.03 for both species.

The distribution of the Short-toed Treecreeper by habitat (Shannon_H = 2.96) was significantly more diverse than that of the Eurasian Treecreeper (Shannon H = 2.84, t = -2.46, df = 1047, P = 0.01) *(Figure 9)*.

Biometrics

Eurasian Treecreepers which were recaptured had significantly lower median fat score at first capture than those which were not; Short-toed Treecreepers which were recaptured had significantly higher median body mass and fat score at first capture *(Table 1)*. The median body mass at last capture of recaptured Eurasian Treecreepers was slightly higher (8.6 g) than their median body mass at first capture (Wilcoxon's test for matched pairs = 1802.50, n = 89, P = 0.01). The Short-toed Treecreeper's did not change significantly (W = 2177.50, P = 0.60). The median fat scores at last capture of recaptured Eurasian Treecreepers (W = 512.50, P = 0.06) and Short-toed Treecreepers (W = 454.50, P = 0.06) were not significantly different from their median fat scores at first capture (median body mass and fat score at first capture and n for recaptured birds in *Table 1*). The median wing lengths of non-recaptured and recaptured treecreepers during the three capture intervals were not significantly different *(Tables 2, 3)*. The median body mass and fat score of non-recaptured and recaptured individuals were generally significantly lower in July-August than in September or October-November *(Tables 2, 3)*. The length of MSD was not significantly associated with wing length and body mass in either species (P > 0.05). The length of MSD of Short-toed Treecreepers with higher proportion of body mass change (multiple linear model, slope =

Table 1. Comparison of biometrics (median, n) of non-recaptured (NR) and recaptured (R) Eurasian and Short-toed Treecreepers at first capture in the studied period at the Tömörd Bird Ringing Station. W = Wilcoxon's rank sum with continuity correction

1. táblázat A Tömördön gyűrűzött és nem visszafogott (NR), illetve visszafogott (R) hegyi és rövidkarmú fakuszok első befogáskor mért biometriai adatainak (median, n) összehasonlítása. W = Wilcoxon-féle rangsorösszeg-teszt folytonossági korrekcióval

		Wing length (mm)	Body mass (g)	Fat score
Eurasian Treecreeper	NR	63.00, 159	8.70, 169	1.00, 156
	R	63.00, 71	8.50, 86	0.00, 80
		W = 5182, P = 0.32	W = 7547, P = 0.61	W = 7763, P = 0.01
Short-toed Treecreeper	NR	61.00, 172	8.40, 184	0.00, 164
	R	61.00, 86	8.60, 101	1.00, 91
		W = 7295, P = 0.86	W = 7549, P = 0.01	W = 6193, P = 0.02

Table 2. Comparison of bimometrics (median, n) of captured and non-recaptured Eurasian and Short-toed Treecreepers in the three capture intervals of the studied period at the Tömörd Bird Ringing Station. Kruskal-Wallis test

2. táblázat A vizsgált időszak három fogási periódusában Tömördön gyűrűzött és nem visszafogott hegyi és rövidkarmú fakuszok biometriai adatainak (median, n) összehasonlítása. Kruskal-Wallis teszt

		Wing length (mm)	Body mass (g)	Fat score
Eurasian Treecreeper	Jul-Aug	63.50, 26	8.60, 28	0.00, 26
	Sep	62.00, 42	8.70, 47	1.00, 38
	Oct-Nov	63.00, 91	8.70, 94	2.00, 92
	Kruskal-Wallis	χ^2 = 5.26, P = 0.07	χ^2 = 0.35, P = 0.83	χ^2 = 30.32, P = 0.01
Short-toed Treecreeper	Jul-Aug	62.00, 47	8.10, 51	0.00, 46
	Sep	61.00, 71	8.50, 75	1.00, 71
	Oct-Nov	61.00, 54	8.30, 58	1.00, 47
	Kruskal-Wallis	χ^2 = 2.66, P = 0.26	χ^2 = 12.37, P = 0.01	χ^2 = 26.98, P = 0.01

Table 3. Comparison of biometrics (median, n) of captured and recaptured Eurasian and Short-toed Treecreepers in the three capture intervals of the studied period at the Tömörd Bird Ringing Station. Kruskal-Wallis test

3. táblázat A vizsgált időszak három fogási periódusában Tömördön gyűrűzött és visszafogott hegyi és rövidkarmú fakuszok biometriai adatainak (median, n) összehasonlítása. Kruskal-Wallis teszt

		Wing length (mm)	Body mass (g)	Fat score
Eurasian Treecreeper	Jul-Aug	65.00, 32	8.45, 44	0.00, 39
	Sep	63.00, 21	8.80, 23	1.00, 23
	Oct-Nov	63.00, 18	8.40, 19	1.00, 18
	Kruskal-Wallis	$\chi^2 = 2.89$, P = 0.23	$\chi^2 = 8.87$, P = 0.01	$\chi^2 = 19.17$, P = 0.01
Short-toed Treecreeper	Jul-Aug	61.00, 54	8.50, 65	1.00, 57
	Sep	61.00, 24	8.75, 28	2.00, 26
	Oct-Nov	62.00, 8	8.40, 8	1.00, 8
	Kruskal-Wallis	$\chi^2 = 0.11$, P = 0.94	$\chi^2 = 10.55$, P = 0.01	$\chi^2 = 19.16$, P = 0.01

Table 4. Results of the multiple linear model test with proportion of body mass change (PBM) as dependent variable and body mass, wing length at first capture as independent variables of recaptured Eurasian and Short-toed Treecreepers

4. táblázat A visszafogott hegyi és rövidkarmú fakuszok testtömeg-változás aránya (PBM) és a madarak első befogáskor mért szárnyhossza és testtömege között feltételezett kapcsolat sokváltozós lineáris modellel ellenőrzött eredményei

Group	Factors	slope	SE	t	P value
Eurasian Treecreeper	Body mass	-0.06	0.01	-5.53	0.01
	Wing length	0.01	0.00	3.42	0.01
Short-toed Treecreeper	Body mass	-0.08	0.01	-7.32	0.01
	Wing length	0.02	0.00	5.01	0.01

-12.44, SE = 4.98, t = -2.49, P = 0.01) decreased. There was no such correlation in Eurasian Treecreepers (P > 0.05). Individuals with lower body masses and longer wing lengths upon arrival gained a significantly higher proportion of body mass (PBM) than heavier birds and birds with shorter wings in both species *(Table 4)*.

Discussion

Comparison of capture dynamics and habitat selection

Both species are relatively common breeders in the forests of western Hungary (Gyurácz & Kóta 2020). Although the annual capture dynamics of the species were different, the annual captures of both species indicated stable populations between 2001 and 2023, which are partly in line with national and European results (Gyurácz 2022a, 2022b, PECBMS 2023). Both species colonize new areas quickly, even small patches of habitats. The Eurasian Treecreeper's population declined moderately between 1980 and 2021 in Europe, but the population change was unknown in Hungary. The Finnish, Italian and Swiss population increased, while its populations declined in Greece, Ukraine, Scandinavia, the numbers of French and British birds were stable in recent decades (Knaus 2020b). The Short-toed Treecreeper's population increased moderately in Europe between 1982 and 2021, and the Hungarian breeding population was stable (annual average population change 1.3 ± 3.5%) between 1999 and 2018 (Gyurácz 2022a, 2022b, PECBMS 2023). The population trend was positive in Scandinavia, Netherlands, Poland, Spain, Italy and France in recent decades. The population was also stable in Germany, but short-term declines were reported from Poland, Austria, the Czech Republic, Ukraine, Albania and Turkey (Knaus 2020a).

The winter weather has affected the survival of the species in western Hungary, just as it has in other parts of Europe (Svensson 1981, Peach *et al*. 1995, Csörgő & Karcza 2000). In the northern and eastern parts of the Eurasian Treecreeper's range, there are irregular fluctuations in populations which may be linked to variations in the primary winter diet of the species, because they eat mainly seeds of pine and spruce as well as insects and spiders in winter (Cramp 1998, Harrap 2008). Usually, the small resident passerines show the largest population declines after hard winters because their potential prey animals become less available during cold and snow (Graber & Graber 1979, Gibbons *et al*. 1993). Our studies have demonstrated the positive effect of milder February on annual captures. In the Eurasian Treecreeper a significant relationship has been found between autumn numbers and mean April temperatures at two eastern Baltic sites (Sokolov *et al*. 2002). In case of high breeding success and high winter survival, and especially in years with early and warm spring, irruptive movements can occur. Irruptions of Eurasian Treecreepers usually occur in northern Europe when there is an early and warm spring. Significant correlation has been found between autumn captures of Coal Tits *(Periparus ater)*, also an irruptive migrant, and Eurasian Treecreepers in the eastern Baltics (Sokolov *et al*. 2002). In western Hungary, Coal Tits, like Eurasian Treecreepers, migrate in highly variable numbers in different years, with invasions in 2010 for both species (Takács *et al*. 2021). A highly significant relationship was found between autumn captures of juvenile Coal Tits and annual captures during the subsequent spring. This suggests that after an irruption, some juveniles survive the migration and winter and move back to the breeding area (Sokolov *et al*. 2002). This probably also occurs after an irruption of Eurasian Treecreepers.

During the migration season, both treecreeper species can occur in almost any habitat type (BirdLife Hungary 2023a, 2023b), but our studies showed that the Eurasian Treecreeper was more strongly associated with the scrubland and forest edge at the study site than the Short-toed Treecreeper. The Eurasian Treecreeper also showed a stronger preference for mature stands and large trees in the breeding season (Thibault 2023). Both species occurred in small numbers due to the lack of thick trunk trees in the marsh. Where the two species co-occur, contradictory results have been obtained when examining the species dominance relationship (Thielcke 1962, Clausel & Toft 1972).

Both species occurred at the study area during the post-breeding dispersal period, but the Short-toed Treecreeper was more common than the Eurasian Treecreeper. Both species breed in the forests around the study area (Gyurácz 2022a, 2022b), and individuals captured before the end of August are thought to be dispersing. There were two autumn capture peaks in September and October for the Eurasian Treecreepers and just one in September for the Short-toed Treecreepers. Similar to the treecreepers, the autumn migration dynamics of short-distance migratory tits in Hungary was also different. The annual capture peak of the Coal Tit was also in September, which was different from the October migration peak of Blue Tit *(Cyanistes caeruleus)* and Great Tit *(Parus major)*, but similar to that of Marsh Tit *(Poecile palustris)* (Lukács 2022).

One Eurasian Treecreeper ringed in Slovakia was recovered in Hungary and no Short-toed Treecreepers captured abroad have been found in Hungary since 1908. The furthest Eurasian Treecreeper recovery was 25 kilometres, the furthest Short-toed Treecreeper recovery was 17 kilometres (BirdLife Hungary 2023b), so we assume that the altitudinal migrant treecreepers captured in the September and October waves may have come from higher breeding areas, mainly from the Kőszeg Mountains, about 20 km from the study site: the regular migrants could fly a similar distance from here. In autumn, as the weather becomes less favourable in higher regions, more bird species are unable to access food and move to lower regions of Hungary, not only from the Hungarian mountains but also from the surrounding mountain regions (Csörgő *et al*. 2009). The Eurasian Treecreepers breeding in northern Europe migrate longer distances, but may also overwinter in western and southern Europe (Cramp 1998). The wing lengths of migratory birds captured in central Hungary also suggested that the birds originated from further north (Csörgő & Karcza 2000). It is more common to find resident Short-toed Treecreepers (Schepers 1997, Cramp 1998) but, as in Germany and central Hungary (Bauer & Kaiser 1991, Csörgő & Karcza 2000), our results also show that there were regular migrants of this species, although in lower numbers. The wing lengths of birds captured in the three capture intervals did not differ significantly, so it is assumed that the reason for the separation of the three capture intervals is not due to different post-breeding movement strategies of sex and age groups or populations (Cramp 1998). The higher body mass and fat stores of birds in September and October indicate both a higher proportion of migrants and the preparation of the winter population (Berthold 1993, Brodin 2000).

Comparison of movement ecology

Our results have shown both similarities and differences in the movement strategies of the species. The number of birds captured only once was about double that of birds recaptured in both species each year, which means that most of the birds continue to migrate after a short rest. The length of time spent and daily "survival" probabilities of the two species were similar, indicating that the habitats in the study area provide favorable feeding conditions for resident and stopover individuals of both species (Chernetsov 2012). Most of the birds of both species captured in August are present until November and probably overwinter in the study area. The equal, very low capture probabilities of the two species also suggest similar seasonal and diurnal activity. The length of time spent were not correlated to body size or condition of individuals at first capture in either of the treecreeper species.

Here, comparing the body mass and fat stores of recaptured and non-recaptured individuals of the two species, opposite results were found. One possible explanation for the difference is the different migration strategies of the two species. In Eurasian Treecreepers, which have a higher migratory activity, the non-recaptured individuals, with the higher fat score, were able to continue to migrate; in the mainly resident Short-toed Treecreeper, the recaptured individuals with higher body mass, and which consequently had a better competitive ability, remained in the study area. In other studies, as in the Eurasian Treecreeper in this study, individuals of pre-Saharan migrants caught only once showed a higher body mass than repeatedly recaptured birds during autumn and spring migrations (Petterson & Hasselquist 1985, Biebach *et al*. 1986, Kuenzi *et al*. 1991). However, the strategies of migrant individuals of the two species showed other differences and similarities. Individuals of both species did not gain fat stores significantly between their first and last recaptures, suggesting that they either stay on the site for longer periods, or migrate only short distances. The recaptured Short-toed Treecreepers that increased their body mass more stayed in the study area for shorter periods of time; this was not the case for the Eurasian Treecreepers, but this may be due to fewer recaptured Eurasian Treecreepers. Wing length was a significant determinant of proportion of body mass change (PBM) at Tömörd in both species. If the larger birds with longer wings are competitively dominant at stopover or overwintering sites, they probably forage more efficiently and accumulate more fat (Jarska *et al.* 2015).

Conclusions

A long-term capture-recapture study provided an opportunity to explore the autumn movements of the two sibling treecreeper species and the associated behavioral strategies. Both species occurred at the study area during the post-breeding dispersal period, but the Short-toed Treecreeper was more common than the Eurasian Treecreeper. Both species have both migrants and residents in their stable populations, but the dynamics of migrants are different. There were two autumn capture waves in September and October for the Eurasian Treecreepers and just one in September for the Short-toed Treecreepers. Wing length was a significant determinant of proportion of body mass change in both species. During the migration season, the Eurasian Treecreeper was more strongly associated with the scrubland and forest edge than the Short-toed Treecreeper.

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Appendix

Appendix 1. Annual captures, recaptures of the studied species at the Tömörd Bird Ringing Station, 2001–2023

1. függelék A vizsgált fajok éves fogása és visszafogása Tömördön, 2001–2023

	Eurasian Treecreeper			Short-toed Treecreeper		
	Capture	Capture once	Recapture	Capture	Capture once	Recapture
2001	12	7	5	17	9	8
2002	7	4	3	21	14	7
2003	7	5	2	11	8	3
2004	5	3	2	18	14	4
2005	9	6	3	12	12	0
2006	15	8	7	9	6	3
2007	16	12	4	20	15	5
2008	12	7	5	11	8	3
2009	12	8	4	8	6	2
2010	36	27	9	5	4	1
2011	4	0	4	7	4	3
2012	10	9	1	8	7	1
2013	11	5	6	3	1	2
2014	14	9	5	11	3	8
2015	18	14	4	17	13	4
2016	6	3	3	11	7	4
2017	9	6	3	17	10	7
2018	6	4	2	3	0	3
2019	14	10	4	16	9	7
2020	13	7	6	17	9	8
2021	6	4	2	18	11	7
2022	16	11	5	30	19	11
2023	9	4	5	22	13	9
Total	267	173	94	312	202	110

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