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Winter site fidelity of the Great Tit (*Parus major*) revealed by recaptures of individuals roosting in nest-boxes

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Birds often return to the same locations where they have previously bred successfully or survived the winter, demonstrating site fidelity. This behaviour extends beyond breeding sites to include roosting and feeding areas, with individuals frequently recaptured at the same locations across years. In this study, we investigated the winter site fidelity of Great Tits and analysed how various factors (winter temperature, sex, age, site, date of first capture, and winter season) influence recaptures within and between winters. We monitored individuals roosting in nest boxes at two sites within Bratislava city, western Slovakia. Within-winter site fidelity was observed in 45.89% of birds (N = 146), meaning these individuals were recaptured at least once during the same winter at the same site. Among the tested variables, age and date of first capture in the season significantly influenced within-winter site fidelity. Older birds and those captured earlier in the season were more likely to be recaptured in the same winter. Between-winter site fidelity, defined as birds ringed and later recaptured in a different winter, was observed in 12.92% of 178 Great Tits. Age was a significant factor, with older individuals being more likely to be recaptured in subsequent winters. Furthermore, birds that were recaptured more often during their first winter had a higher likelihood of being recaptured in later winters, suggesting consistent long-term site use.

1. Introduction

Winter represents a critical period for the survival of non-migratory boreal birds (Newton 1998). During this time food resources are severely limited (Kendeigh 1961, Newton 1998), while energetic demands increase due to harsh weather and low temperatures (Kendeigh 1961, Cooper 1999). To cope with these challenges, many bird species rely on sites with reliable food availability (Saitou 1978, Orłowski 2006, Veľký & Krištín 2008) or roosting locations that provide favourable microclimatic conditions and protection from aerial predators (Stiefel 1976, Drent 1987, Thompson *et al.* 1990, Cooper 1999, Mainwaring 2011, Shipley *et al.* 2019). Such suitable feeding and roosting sites are often reused by individuals/flocks arriving from greater distances (Saitou 1978, Sydeman & Güntert 1983, Báldi & Csorgő 1997, Veľký & Krištín 2008). The strong association of wintering birds with these sites has been experimentally confirmed through observations of displaced individuals returning to their original roosting or feeding location (Winkel 1974, Krištín & Kaňuch 2017).

Birds find suitable roosting sites in various types of natural or artificial cavities. One of the most common cavity-roosting species is the Great Tit (*Parus major*), which typically roosts individually (Kluyver 1957, Stiefel 1976, Helle 1980, Krištín *et al.* 2001, Veľký 2006, Veľký & Krištín 2008, Zonov 2017). Enclosed cavities offer both improved thermal insulation and protection compared to open roosts (Kluyver 1957, Drent 1987, Winkel & Hudde 1988, Cooper 1999, Veľký & Krištín 2008, Shipley *et al.* 2019). However, these cavities are also more accessible to terrestrial predators, may contain parasites from previous nests, and might be limited in number, resulting in interspecific and intraspecific competition (Ligon *et al.* 1988, Christe *et al.* 1994, Merilä & Allander 1995, Dhondt *et al.* 2010, Typiak & Typiak 2018).

Several studies have documented repeated roosting by Great Tits at the same study site within a winter season (Creutz 1960, Czarnecki 1960, Mayer 1962, Busse & Olech 1968, Schmidt *et al.* 1985, Juškaitis 1986, Lempaszak 1988, Krištín *et al.* 2001, Veľký 2002) and across multiple winters (Czarnecki 1960, Mayer 1962, Busse & Olech 1968, Krištín *et al.* 2001). These individuals may benefit from improved winter survival at familiar sites with roosting holes (Von Haartman 1968, Drent 1987), potentially forming a long-term association with a given location, a behaviour commonly interpreted as site fidelity (*e.g.*, Busse & Olech 1968, Schmidt 1983, Krištín *et al.* 2001).

However, detailed information on factors influencing winter roosting site fidelity remain scarce and are primarily based on forest habitats outside urbanised landscape (Mayer 1962, Busse & Olech 1968, Schmidt 1983, Krištín *et al.* 2001). Data from urbanized environments are limited (Veľký 2002, 2006). Available evidence suggests lower recapture rates in urban areas, indicating that such habitat quality may influence site fidelity, although more comprehensive comparative studies are lacking. Previous research has found no clear influence of sex on roost site fidelity (Krištín *et al.* 2001), while the potential effects of winter season, winter temperature, date of first capture within the winter, and age have yet to be systematically examined. Nonetheless, data from homing experiments and mist-netting studies during winter suggest that older individuals tend to be recaptured more frequently, implying greater site fidelity (Winkel 1974, Croon *et al.* 1985).

The aim of our study was to investigate the factors influencing winter roost site fidelity in the Great Tit by analysing recaptures within and between winters and recapture rates, with respect to sex and age. We defined a winter site as a set of nest boxes used by individuals for roosting. Based on previous findings of higher mortality and lower habitat quality in urban environments (Loss *et al.* 2015), we hypothesized that recapture rates would be in study sites within city lower, compared to the other works from forests, where within-winter recaptures typically exceed 50% (Czarnecki 1960, Mayer 1962, Krištín *et al.* 2001). We further hypothesized that males and older individuals would exhibit higher fidelity due to their stronger territoriality and competitive behaviour (Kluyer 1957, Drent 1987, Sandell & Smith 1991, Newton 1998). Finally, we predicted that individuals recaptured multiple times within a single winter would be more likely to return in subsequent winters, possibly reflecting their higher social dominance or stronger site attachment formed during the breeding season (Kluyver 1957, Busse & Olech 1968, Winkel & Winkel 1980).

2. Materials and methods

2.1. Study site

The research was carried out at two locations within the city of Bratislava, Western Slovakia, which is characterized by a warm lowland climate with a mean annual temperature of +10.6 °C, annual precipitation of 561 mm (Holec *et al.* 2020). Winters in the region are typically mild (Konček 1979). The study areas included the Zoological Garden Bratislava (hereafter ZOO; coordinates: 48°9'49" N 17°4'14" E; altitude: 260 m a. s. l.; 11 ha) and the Botanical Garden of Comenius University (hereafter BG; coordinates: 48°08'46"N 17°04'24"E; altitude: 150 m a. s. l.; 6.5 ha). These two sites, which differ in terms of habitat and types of nesting boxes available, are 1.8 km apart by an aerial distance. However, we have never recorded individuals at both study sites.

At the ZOO, nest boxes were placed within an area predominantly consisting of a 70–85-year-old broad-leaved forest stand dominated by oaks (*Quercus robur* and *Q. petraea*), Black Locust (*Robinia pseudoacacia*), and Hornbeam (*Carpinus betulus*) with rich shrub and herb undergrowth. The site is bordered on two sides by an 80 ha forest of similar age and species composition, and on another side by an abandoned pear orchard (2.8 ha). A small portion of the study site borders a visitor area containing paved road and buildings. Since 2016, a total of 50 nest boxes of three types have been installed on tree trunks (heights 1.5–2.1 m, mean: 1.9 m), predominantly facing southeast or southwest: 29 boxes for Great Tits, 18 for Common Starlings (*Sturnus vulgaris*), and three for Blue Tits (*Cyanistes caeruleus*). Natural tree cavities are here relatively abundant, and some roosting individuals may have used these alternative sites, thus avoiding detection.

In contrast, the BG features a parkland with a variety of mostly non-native tree and shrub species, intensively planted lawns, and flowerbeds. Since the late 1990s, 30 nest boxes have been installed (heights 1.2–3.5 m, mean: 2.18 m), mostly facing southeast or northeast. Of these, 21 were designed for Common Starlings, eight for Great Tits, and one for Blue Tits. Nest boxes were installed on trees near paved pathways and buildings. A busy street and motorway bridge are in proximity, making this site more urbanized and with limited availability of natural cavities but with a greater presence of anthropogenic shelters.

2.2. Fieldwork

The research was conducted over six consecutive winters. At the ZOO site, data were collected from 2017/2018 to 2022/2023; at BG, from 2018/2019 to 2023/2024. To simplify analyses and interpretation sampling years were defined as 2017 for the winter 2017/2018, 2018 for the winter 2018/2019 and so on. Nest boxes were inspected weekly from October to February (Supplementary Table S1). Exceptions occurred in 2017 (inspections started in November), in 2020 (monitoring was limited from January due to COVID-19 restrictions), and in 2022 (early termination in January due to a bird flu epidemy at ZOO).

Inspections followed a standardized protocol (Busse & Olech 1968, Krištín *et al.* 2001, Veľký 2006, Zvářal 2010) commencing 15 minutes after sunset. All nest boxes were opened, roosting birds were carefully removed under white head lamp light, ringed, aged (birds in their first winter were categorized as "young", and those in their second or later winters as "old", except for winter 2017) and sexed using the criteria of Svensson (1992). Birds were returned to the same box immediately after handling. Care was taken to avoid escape; no birds escaped from nest box after procedures.

2.3. Data analysis

We defined recaptures within a winter as instances where birds were captured at least twice within the same winter. The fidelity rate was calculated as the number of positive controls (instances when the bird was found roosting) divided by the number of inspections in that winter. This rate ranged from >0 to 1, (1 = the bird was recaptured during all inspections in the winter). In the within winter recaptures, we analysed fidelity rate only for birds recaptured within a winter. For this we stated term fidelity rate of recaptured birds.

Recaptures between winters refer to individuals captured in more than single winter (0

= captured in one winter, 1 = captured during more than one winter).

We define the date of first capture as the Julian date of the night check, when the bird was recorded for the first time in a given season, with October 1 = 1.

Mean winter temperatures (October 1 – March 1) were computed from monthly means provided by the nearby Bratislava-Mlynská dolina meteorological station (within 1.5 km of both study sites).

2.3.1. Nest box use analysis

First, we assessed the overall occupancy of the nest boxes and the preference for a certain type of nest box during the monitored years at two locations. In a binomial generalized linear model (GLM) used, we set the presence of roosting Great Tit in the nest box as a dependent variable (1 = occupied at least once by a roosting Great Tit during the season, 0 = Great Tit did not roost, N = 320). We chose site (BG, ZOO), winter (2018, 2019, 2021, 2022), and nest box type (type Common Starling, Great Tit, Blue Tit) as explanatory variables.

2.3.2. Within-winter analysis

We analysed data for 146 aged and sexed birds, excluding the winter 2017 during which we did not record the age of the captured birds, 2020 since we stopped the field work early (see section 2.2) and 2023 during which we conducted research only in BG. A GLM with binomial distribution was used to analyse recaptures within winter (1 = bird recaptured, 0 = not recaptured *i.e.* recorded once in winter) with the following predictors: mean winter temperature, sex (M or F), age (young or old), site (ZOO or BG), date of first capture (1 = October 1), winter (2018, 2019, 2021 and 2022) and interaction of sex and age (Table 1).

To compare the proportion of birds recaptured in winter (*i.e.*, what percentage of all birds recorded in a given month were recaptured within

Table 1. Within-winter recaptures, according to winter temperature, sex, age, site, date of first capture, winter and interaction between sex and age with predictor test criterium (χ^2) and p-values (P) for the corresponding model. Significant values are marked in bold. N shows the number of recorded birds.

Predictor		% of recaptured	N	χ^2	P
Winter temperature			146	0.68	0.41
Sex	Male	45.95	111	0.02	0.88
	Female	45.71	35		
Age	Young	38.23	102	**7.91**	**<0.01**
	Old	61.36	44		
Site	BG	38.46	39	2.11	0.15
	ZOO	48.60	107		
Date of first capture			146	**5.42**	**0.02**
Winter	2018	43.64	55	1.72	0.42
	2019	45.71	35		
	2021	39.39	33		
	2022	60.87	23		
Interaction sex and age			146	0.17	0.68

Table 2. Mean fidelity rate of recaptured birds for different winter temperature, sex, age, site, date of first capture, winter and interaction between sex and age with predictors test criterium (F) and p-values (P) from the corresponding model. Significant values are marked in bold. N shows the number of recorded birds.

Predictor		Mean ± SE	N	F	P
Winter temperature			67	0.02	0.97
Sex	Male	0.35 ± 0.04	51	2.79	0.10
	Female	0.22 ± 0.05	16		
Age	Young	0.23 ± 0.03	39	**4.26**	**0.01**
	Old	0.44 ± 0.07	28		
Site	BG	0.36 ± 0.07	15	0.71	0.40
	ZOO	0.31 ± 0.04	52		
Date of first capture			67	**8.13**	**<0.01**
Winter	2018	0.39 ± 0.07	24	0.96	0.39
	2019	0.37 ± 0.08	16		
	2021	0.26 ± 0.08	13		
	2022	0.21 ± 0.04	14		
Interaction sex and age			67	0.51	0.47

winter) between different months, we used Pearson's chi-square test (2×5 contingency table).

To examine factors influencing fidelity rates of recaptured birds, we applied a gaussian family GLM with log-transformed fidelity rate as the dependent variable (residuals normality: Shapiro-Wilk test: P = 0.22). Predictors included mean winter temperature, sex, age, site, date of first capture, winter, and interaction of sex and age (Table 2).

Note that one "bird" does not equal one "individual" in analyses of within-winter recapture. When we recaptured the same individual in two different winters, it was considered two separate birds, due to the change in age group between winters.

2.3.3. Between-winter analysis

Recapture data from all 178 ringed individuals across the winters 2017 to 2023 were analysed, including the incomplete winter 2020 to preserve the integrity of long-term recapture records. Although inclusion of the most recent winters lowers the likelihood of between-winter recapture (due to lack of opportunity for future recapture), these were retained for comparability with other studies (*e.g.*, Krištín *et al.* 2001). We used 2×2 contingency tables with Fisher's exact tests to assess effects of site, age, and sex on between-winter recaptures.

2.3.4. Analysis of correlation in recaptures between and within winter

To analyse the factors influencing recapture between winters (dependent variable: recapture in more than one winter = 1 *vs*. recapture in only one winter = 0), we used GLM with binomial distribution, using site, recapture within winter (yes = 1 or no = 0), and fidelity rate in the first winter when the bird was recorded (analysed for winters 2017 to 2023) as predictors.

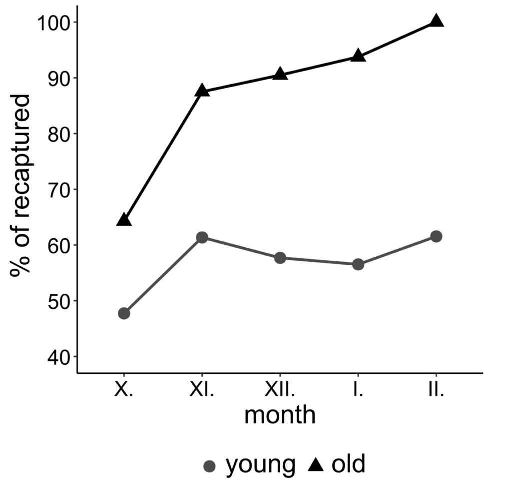

Fig. 1. Percentage of Great Tits recaptured within winter in different months according to their age.

2.3.5. Used software

Statistical analyses were conducted in PAST version 4.04 (Hammer *et al.* 2001) for Fisher's, chi square tests and summary statistics, and in R (version 4.4.3) using the default package stats for GLM and ANOVA (R Core Team 2025). Results were considered statistically significant at $P < 0.05$. Arithmetic means are presented with standard error (mean ± SE). Sample sizes are given either in the text or in parentheses.

Data visualization was carried out in R (version 4.4.3) using the packages ggplot2 (Wickham 2016) and ggpubr (Kassambara 2023) and later edited in Inkscape (version 1.3) (Inkscape project 2023).

3. Results

The Great Tit was the most abundant bird species (85.13% from 908 roosting attempts in winters 2017 to 2023) using nest boxes for roosting at both sites. Of 320 nest boxes (80 nest boxes, 4 winters), 46.88% were occupied at least once per winter by roosting Great Tits (ZOO: 48.5% of 200 nest boxes; BG: 44.17% of 120 nest boxes). Great Tit type of nest boxes was the most frequently used (72.48%, N = 149), compared to type Common Starling (26%, N = 150) and Blue Tit (14.29%, N = 21). Nest box type significantly influenced nest box use of roosting Great Tits. Other factors (site, winter) were not significant (Supplementary Table S2).

3.1. Recaptures within a winter

Of the 146 birds recorded, 45.89% were recaptured during the same winter. The age of the birds and the date of first capture had a significant effect on within-winter recapture (Table 1). Old individuals were recaptured more often than young ones. In addition, recaptured birds were caught earlier in the season than birds recorded only once during the winter (Supplementary Fig. S1). Other factors examined, such as winter temperature, sex, site, or winter, were not significant (Table 1).

Recaptures within a winter varied significantly between months (χ^2 test: $P = 0.026$) with the lowest proportion of recaptured birds within the winter occurring in October and noticeable increase from October to November (Supplementary Table S3). This pattern was observed across sexes and age groups but was statistically significant only in old birds (Fig. 1, Supplementary Table S3).

More than half (58.21%) of the within-winter recaptured birds (N = 67) were recorded during two to four inspections (*i.e.*, had a fidelity rate ≤ 0.2) (Fig. 2). Only one bird was recorded during all night checks throughout the season. The average fidelity rate of recaptured birds was 0.32 ± 0.04 (mean ± SE). Fidelity rates of recaptured birds were significantly affected by age and date of first capture with recaptured old birds showing higher fidelity rates than young birds and fidelity decreasing with later date of first capture (Supplementary Fig. S2).

3.2. Recaptures between winters

Of the 178 recorded individuals, 23 individuals (12.92%) were recaptured between winters. No significant difference was observed between sites (Fisher's exact test: $P = 0.62$) with 16 individuals out of 131 at ZOO (12.21%) and 7 out of 47 at BG (14.89%).

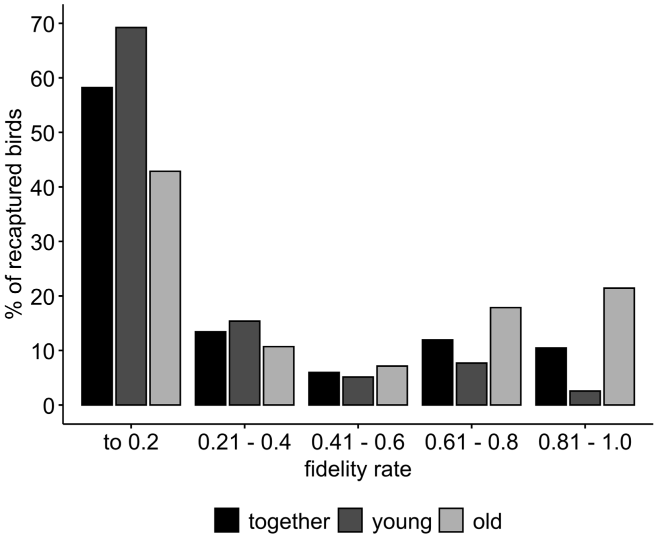

Fig. 2. Distribution of fidelity rates in recaptured birds (N = 67) according to their age (young: N = 39; old: N = 28).

Among the 23 individuals recaptured between winters, 17 individuals (73.91%) were captured during two, five individuals (21.74%) during three, and one individual during four winters. Two individuals (recorded during two and three seasons) did not appear in the winter immediately following ringing but were recaptured later.

The proportion of males recaptured between winters was 14.63% (18 out of 123), compared to 9.26% in females (5 out of 54), though the difference was not significant (Fisher's exact test: P = 0.47). Age groups differed significantly in recaptures between winters (Fisher's exact test: P = 0.028). Of the 24 individuals categorized as old (aged during their first roosting record ever) were 25% (N = 6) recaptured between winters, while from 121 individuals categorized as young it was only 8.26% (N = 10). Seven individuals recaptured between winters were not aged during their first roosting record ever (winter 2017).

3.3. Correlation in recaptures between and within winter

Nearly half of the individuals recaptured between winters (11 out of 23 individuals, *i.e.* 47.83%) were also recaptured within each of these winters. However, 6 individuals (*i.e.* 26.1%) were recorded only once per winter during both the initial and subsequent winters.

Among birds recaptured between winters (N = 23), 60.87% were also recaptured within their first winter. Among individuals recorded in only one winter (N = 155), recapture during their first winter was 43.23%.

The fidelity rate (during the first winter) significantly differed between individuals recaptured between winters and those recorded only once (Supplementary Table 4). Individuals with higher within-winter fidelity rates were more likely to be recaptured in a following winter (Fig. 3). Other factors, such as study site (P = 0.63) and within-winter recapture (P = 0.11) did not influence the probability of recapture in a following winter (Supplementary Table S4).

4. Discussion

Overall, 46.88% of nest boxes were occupied at least once during the winter by roosting Great Tits, with Great Tit type nest box being used significantly more often. Recaptures within winter in one of the nest boxes at the study site reached 45.89%, indicating that this species can be considered intra-seasonally faithful (Busse & Olech 1968, Krištín *et al.* 2001). Recaptures within the season were significantly higher in old

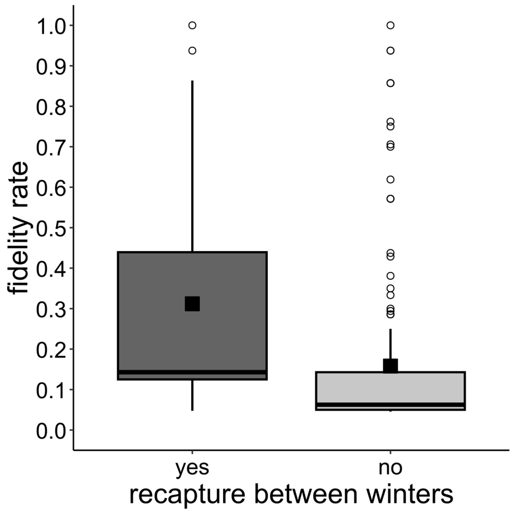

Fig. 3. Differences in fidelity rates during the first winter between individuals that were not recaptured (N = 155) and those that were recaptured (N = 23) between winters. Mean values are marked with squares.

birds and birds with earlier date of first capture. Also, fidelity rates of 67 recaptured birds have been significantly higher in old birds and birds with earlier date of first capture. Of the 178 ringed Great Tit individuals, 12.92% were recaptured between winters, suggesting they can be considered inter-seasonally faithful (Busse & Olech 1968, Krištín *et al.* 2001). Recaptures between winters were higher in old individuals. Furthermore, individuals with higher fidelity rates (*i.e.*, recaptured more often within the same winter) were more likely to be recaptured between winters.

The observed recaptures within a winter (45.89%) are similar to those found in other urban environments (Table 3). Higher values of within winter recaptures in forest habitats compared to urbanized landscapes could indicate habitat differences, though no significant differences were found between the two distinct localities (park BG and oak forest ZOO). This could suggest that the impact of urban environments may affect a broader scale than just specific habitats, potentially due to higher predation risk in cities or their lower attractiveness for wintering birds (Loss *et al.* 2015). Alternatively, birds may prefer warmer and safer shelters in human buildings or natural tree cavities (Veľký & Krištín 2008, Grüebler *et al.* 2014). This shift for the alternative shelters, which leads to a lower number of recaptures, could be more pronounced in BG where most Common Starling nesting boxes are located which are significantly less preferred by the roosting Great Tits compared to the smaller nest boxes type Great Tit.

Neither the number of recaptures within winter nor the fidelity rate of recaptured birds differed significantly between winters. However, other studies (Mayer 1962, Schmidt 1983) have observed strong variability in recaptures within winter (68.42%–83.25%). These variations (at least in Mayer 1962) are likely due to the different age structure of roosting birds that markedly changes between winters (Schmidt 1983, Zang & Kunze 2009, Typiak *et al.* 2019). We also hypothesized that in colder winters with increasing nest box occupancy (Busse & Olech 1968, but not Báldi & Csorgő 1991), nest boxes

Table 3. Results obtained by winter capturing of Great Tits roosting in nest boxes at various locations from previous studies.

Locality	Habitat	Winters	Author	% of recaptured	Fidelity rate
Central Poland	Oak-pinewood	1954–1956	Czarnecki (1960)	62.10	
SE Austria	Floodplain forest	1957–1960	Mayer (1962)	76.36	0.48
Central Germany	Mixed forest with oak	1971–1975	Schmidt (1983)	68.00	0.68
Central Slovakia	City gardens	1999	Veľký (2002)	35.71	0.53
Central Slovakia	City gardens	2003–2004	Veľký (2006)	43.33	

should be reused by more birds (higher number of recaptures per season) or more often by the same individuals (higher fidelity rate of recaptured birds), but the influence of winter temperatures in our results was not significant.

While male dominance (Kluyver 1957) could suggest that more aggressive males drive out submissive females, leading to a higher proportion of males among recaptured individuals, our data (as well as Krištín *et al.* 2001) did not support the hypothesis of sex influencing recaptures within the winter, probably also due to small sample size. On the other side, our results clearly show that age plays a significant role in recaptures within winter, as well as the fidelity rate of recaptured birds, with old birds achieving significantly higher values. One possible explanation for this could be the higher mortality of young birds during their first year (Beklová 1972, Hildén 1978, Rodríguez *et al.* 2016). However, it is important to note that a significant mortality occurs in months of post fledging dispersal during summer and autumn (Möckel 1992, Payevsky 2006), before they claim winter sites in September and October (Drent 1987).

The age-dependent patterns in recapture within winter, and fidelity rate of recaptured birds, could be related to the higher social dominance of old individuals, particularly in males defending winter territories (Kluyver 1957, De Laet 1984, Drent 1987, Bládi & Corgő 1991, Sandell & Smith 1991). However, it is important to note that winter territoriality differs significantly from spring territoriality. During winter days, resident birds may leave their territories to forage over longer distances (often in flocks), sometimes more than 5 km to urban areas, before returning to their roosts in their winter territories (Báldi & Csorgő 1997, Veľký & Krištín 2008). Submissive young birds, which fail to settle in vacant territories (De Laet 1984, Drent 1987), may risk fatal conflicts with resident birds when occupying their roost sites (Schmidt *et al.* 1985, Drent 1987, Typiak & Typiak 2018), or they may use less suitable shelters in tree crowns (Kluyver 1957) that are prone to higher energy losses (Kenedigh 1961, Cooper 1999) and increased predation risk by owls (Drent 1987). The fact that older birds are strongly attached to their roosts has been confirmed by homing experiments (Winkel 1974). For females who do not defend their winter territories, proximity to a mate from the previous breeding season may be an advantage, reducing the likelihood of divorce, as divorce rates tend to decrease with shorter distances between pair members (Saitou 2002). Pairs that remain together for multiple breeding seasons show higher breeding success (Perrins & McCleery 1985). These pairs also tend to use nest boxes for winter roosting in higher numbers compared to pairs that have experienced divorce, with the pair members roosting close to each other (Winkel & Winkel 1980). Close relationships between pair members from the previous breeding season are also seen in winter flocks. In these flocks, most adults nest within 100 m of the centre of flock activity (Saitou 1978, 1979a). After all, different age groups may also be differently sensitive to disturbance caused by the check method used (Tyller *et al.* 2012, Typiak & Typiak 2019), with young birds likely being more sensitive to human disturbance. However, more detailed information on this is lacking.

In addition, the time when birds began to use nesting boxes for roosting (measured as the date of first capture in winter) played a significant role in recaptures within the winter, same as in the fidelity rate of recaptured birds. Birds caught earlier in winter may have had the advantage of prior residency at the roosting site (Sandell & Smith 1991), probably in the territory from the previous breeding season or winter (Saitou 1979a, De Laet 1984, Drent 1987).

On the other hand, lower proportion of birds recaptured within a winter in October compared to other months illustrate the autumn Great Tit migration in Central Europe, which occurs predominantly in October and November (Mayer 1962, Busse & Olech 1968, Juškaitis 1986, Matejka unpublished). Similar patterns have been noted in both roosting birds (Lemapszak 1988) and birds at feeders (Croon *et al.* 1985). The more pronounced difference in old individuals could illustrate a partial turnover between breeding and wintering populations (Mayer 1962, Schmidt 1983). Unfortunately, breeding birds were not systematically ringed in our study sites.

The proportion of individuals recaptured between winters (12.92%) falls within the range reported for other habitats, despite variations in the frequency of night checks (Czarnecki 1960, Mayer 1962, Busse & Olech 1968, Krištín *et al.* 2001). An exception to this pattern is central Germany, where one-third of individuals were recaptured between winters (Schmidt 1983). Recaptures between winters were significantly more frequent among older birds. This may be attributed to factors such as prior residency, winter territoriality, or the presence of a former breeding partner nearby (Saitou 1978, Winkel & Winkel 1980, Drent 1987, Bládi & Corgő 1991, Sandell & Smith 1991). These factors likely also explain our finding that individuals recaptured between winters showed higher roost site fidelity during their first winter, when they were initially recorded as roosting. Nonetheless, further research is needed to better understand the dynamics between recaptures within and between winters, as well as the roles of roosting dominance and survival—areas that remain insufficiently explored.

However, our results indicate a certain degree of winter roosting site fidelity of Great Tits; it is important to note that the method used in this study may have influenced the results. Weekly handling of birds sleeping in nest boxes (a commonly used method, see *e.g.* Czarnecki 1960, Busse & Olech 1968, Krištín *et al.* 2001, Veľký 2006) could lead to birds avoiding areas where they were disturbed or switching to alternative shelters (see *e.g.* Saitou 1979b, Schmidt *et al.* 1985, Tyller *et al.* 2012, Typiak *et al.* 2019, but not in Ekner & Tryjanowski 2008). Alternative roosting sites, possibly more suitable and preferred for roosting (Saitou 1979b, Grüebler *et al.* 2014) such as natural tree cavities and shelters in buildings, were also present at our study sites. These factors (the method used and the availability of alternative shelters) likely led to an underestimation of site fidelity, particularly with respect to recapture rates. Therefore, our results on fidelity and recapture rates within and between seasons should be interpreted as minimum estimates of site fidelity.

Despite these potential limitations, we believe the general patterns and trends observed in our study are valid, as similar results have been confirmed in other studies of roosting, recaptures at feeders, or homing experiments (*e.g.* Winkel 1974, Drent 1987, Croon *et al.* 1985). Additionally, the handling method used for nighttime checks is the oldest and most widespread approach (Mainwaring 2011), which provides a basis for comparing our results with those from other studies (see Table 3). On the other hand, there is a lack of studies evaluating recaptures of roosting birds using less invasive methods (*e.g.*, passive integrated transponder (PIT) marking). The actual impact of the study method on the recapture rate of individuals has not yet been investigated, as Tyller *et al.* (2012) did not examine individually marked birds but rather nest box occupancy. Therefore, further research on the impact of study methods on recapture of roosting birds is greatly needed.

Talvinen paikkauskollisuus talitiaisella (*Parus major*) selvisi yksilöiden uudelleenpyynnillä pesäpöntöissä yöpymisen yhteydessä

Linnut palaavat usein samoille alueille, joilla ne ovat aiemmin onnistuneesti pesineet tai selviytyneet talvesta, osoittaen paikkauskollisuutta. Tämä käyttäytyminen ulottuu pesimäalueiden lisäksi myös yöpymis- ja ruokailupaikkoihin, ja yksilöitä pyydetään usein uudelleen samoilta alueilta vuosien mittaan. Tässä tutkimuksessa tarkastelimme talitiaisten talvista paikkauskollisuutta ja analysoimme, kuinka eri tekijät – kuten talvilämpötila, sukupuoli, ikä, alue, ensimmäisen pyynnin päivämäärä ja talvikausi – vaikuttavat yksilöiden uudelleenpyyntiin saman tai eri talven aikana. Seurasimme pesäpöntöissä yöpyviä yksilöitä kahdella alueella Bratislavan kaupungissa, Länsi-Slovakiassa. Saman talven aikainen paikkauskollisuus havaittiin 45,89 %:lla linnuista (N = 146), eli nämä yksilöt pyydettiin uudelleen ainakin kerran saman talven aikana samalta alueelta. Testatuista muuttujista ikä ja ensimmäisen pyynnin ajankohta vaikuttivat merkittävästi talven sisäiseen paikkauskollisuuteen. Vanhemmat linnut ja ne, jotka pyydettiin aikaisemmin kauden aikana, pyydettiin todennäköisemmin uudelleen saman talven aikana. Talvien välinen paikkauskollisuus, joka määritellään lintujen rengastamisena ja myöhempänä uudelleenpyyntinä eri talvena, havaittiin 12,92 %:lla 178 talitiaisesta. Myös tässä ikä oli merkittävä tekijä: vanhemmat yksilöt pyydettiin todennäköisemmin uudelleen seuraavina talvina. Lisäksi linnut, jotka pyydettiin useammin ensimmäisen talvensa aikana, pyydettiin todennäköisemmin uudelleen myöhempinä talvina, mikä viittaa jatkuvaan pitkäaikaiseen alueen käyttöön.

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Online supplementary material

Supplementary material available in the online version of the article includes Tables S1–S4 and Figures S1–S2.