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Crested Tits prefer pine forest but not mature forest: insights from an early spring passive acoustic survey

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The Crested Tit (*Lophophanes cristatus*) is a relatively common species in Finland but is declining likely due to increasing anthropogenic pressures and habitat degradation. Here, we study habitat preferences of Crested Tits in Southwest Finland. We conducted a passive acoustic survey of the species' presence and absence just prior to breeding in spring 2020 based on 1-week recordings made in 285 forested sites that were about 1 km from each other. We found that Crested Tits prefer a higher amount of pine foliage within a 100-meter radius but not at 400-meter radius. Contrary to our expectation, Crested Tit occurrences showed no preference for mature forests. Additionally, we found that Crested Tits avoid proximity to houses. No habitat preference was evident at the scale of 400-meter radius, probably because a significant proportion of habitat types are not used by the species at this scale. Lastly, despite the overall decline in the Crested Tit population in Finland, we found Crested Tits to be present in 68% of our sites, emphasizing the robustness of passive acoustic surveys as a valuable tool for studying avian habitat preferences and population monitoring. The findings contribute to our understanding of Crested Tit ecology in the face of habitat degradation and declining populations, offering insights for conservation measures in this region.

1. Introduction

Anthropogenic pressure is a leading factor behind the decline in bird species across Europe (Rigal *et al.* 2023). Forest specialist birds are particularly impacted due to their strong association with specific habitats, often mature forests (Gregory *et al.* 2007). This decline is particularly evident in northern Europe, including Finland, where populations of forest bird species have undergone rapid declines (Brotons *et al.* 2003, Gregory *et al.* 2007, Fraixedas *et al.* 2015, Conenna *et al.* 2017, Virkkala *et al.* 2018, Kumpula *et al.* 2023, Virkkala *et al.* 2023). In southern Finland, intense forest management has reduced habitat quality, contributing to observed avian declines (Fraixedas *et al.* 2015). The decline of forest birds is associated with both forest management and climate change (Fraixedas *et al.* 2015, Virkkala *et al.* 2023). A practical conservation plan and sustainable forest management actions require fundamental research on the relationship between habitat characteristics of forests and their inhabitants. Such research helps disentangle the effects of intensive management on the presence and population trends of forest species.

The Crested Tit (*Lophophanes cristatus*) is a common small passerine that inhabits coniferous forests (Lens & Dhondt 1994, Maícas & Haeger 2004, Berlusconi *et al.* 2022), where it primarily forages on trunks and thick branches (Atiénzar *et al.* 2009). Crested Tits nest in cavities and is considered a weak excavator, often relying on decaying wood. Thus, the availability of decaying wood may play a crucial role in maintaining suitable nesting conditions (Summers *et al.* 1999), despite challenges posed by forestry activities and habitat fragmentation. In addition to habitat composition, habitat fragmentation also plays a role, as Crested Tits tend to avoid fragmented areas (Lens & Dhondt 1994).

Although traditionally associated with mature forests, studies suggest that Crested Tits can also occupy pine plantations (Hartley 1987, Maícas & Haeger 2004). However, Crested Tit populations are declining, particularly in managed landscapes where key structural features such as deadwood and old-growth trees are reduced (Summers *et al.* 1999, BirdLife International 2024). As the species relies on decaying wood for nesting, retaining dead or dying trees has been recommended as a key management strategy to support suitable breeding habitat (BirdLife International 2024). Apart from habitat composition, biotic interactions such as predator presence may influence distribution. The Eurasian Pygmy Owl (*Glaucidium passerinum*), a predator of small passerines, may deter Crested Tits from using certain areas (Morosinotto *et al.* 2017).

Despite the growing interest in passive acoustic monitoring (PAM) for wildlife studies, there is limited research specifically focusing on the habitat associations of the Crested Tit using these modern tools. However, insights from PAM studies on other species (Linke *et al.* 2018, Arneill *et al.* 2020, Melo *et al.* 2021, Zhong *et al.* 2021, Astaras *et al.* 2022, Baroni *et al.* 2023, Wood *et al.* 2023) can provide valuable context and potential methodologies for future research on the Crested Tit. This knowledge gap is particularly relevant in Finland, where Crested Tit populations have shown regional variation and long-term decline. In the 1970s, southern populations exceeded three pairs/km², while northern densities dropped to 0.1 pair/km² (Järvinen & Väisänen 1978). Although the species reached peak abundance in the 1990s–2000s, recent estimates suggest that only half of that population remains today, with declines concentrated in the south but some growth in the north (Lehikoinen & Väisänen 2023). Despite its decline and suspected link to forestry practices (Berlusconi *et al.* 2022), relatively few studies have explored its habitat associations.

Climate change has advanced the breeding timing of many forest-dwelling birds (Crick & Sparks 1999, Ahola *et al.* 2007), likely due to both rising temperatures and changes in habitat selection during the pre-breeding period. The Crested Tit typically begins egg-laying in early April (Eeva *et al.* 2012). Our survey, conducted in March–April, thus targeted the early spring period when individuals are expected to have established territories and initiated pre-breeding behaviors.

Passive acoustic monitoring has become an increasingly valuable method for studying avian presence and absence, especially in remote or densely forested areas (Smith *et al.* 2020, Baroni *et al.* 2023). It allows for non-invasive, continuous data collection over extended periods, reducing observer bias and disturbance (Ross *et al.* 2023). Advances in computational tools, such as machine learning, enable efficient detection and classification of bird vocalizations from large datasets (Sueur *et al.* 2019). When combined with environmental and landscape data, this approach provides a comprehensive understanding of bird habitat use (Hagens *et al.* 2018, Yang *et al.* 2025), supporting informed conservation planning.

The decline of forest specialist birds, including the Crested Tit, highlights the need for detailed research into their habitat preferences and the factors influencing their distribution (Maícas & Haeger 2004). Our objective is to assess habitat associations of Crested Tits with forest structure, anthropogenic features, and the presence of predators. To this end, we conducted a passive acoustic survey during the pre-breeding period, recording at 285 sites across a forest gradient in Southwest Finland. We analyzed presence–absence data in relation to habitat characteristics derived from remote sensing. Specifically, we examined whether Crested Tit occurrences were associated with pine-dominated or mature forests, distance to buildings, and presence of Pygmy Owl. We used both 100 m and 400 m buffers to capture fine-scale and broader landscape patterns, corresponding to the species' vocal detection range and typical territory size, and following recommendations to account for habitat, distance, and frequency effects on detection probability in acoustic surveys (Orlando *et al.* 2021).

2. Materials and methods

2.1. Study area

The survey was carried out in March/April 2020 north of the city of Turku in south-western Finland (60°N, 22°E). The study area occupies approx. 370 km² within a mosaic of forests, agricultural areas, and a few peatland bogs. The dominant forest species in the study area are managed Norway Spruce (*Picea abies*), Scots Pine (*Pinus sylvestris*) forests, birch (*Betula pendula* and *Betula pubescens*) and European Aspen (*Populus tremula*).

2.2. Presence and absence data

We investigated habitat selection of the Crested Tit in southwest Finland. The passive acoustic survey data has been described in detail by Baroni *et al.* (2023) who used the data for studying the distribution of the Eurasian Pygmy Owl (hereafter Pygmy Owl) in the study area. To gather presence and absence data of Crested Tit, we analysed passive acoustic recordings collected from 285 sites within the study region. For the location of the recorders, we used the Finland Uniform Coordinate System (Finnish grid; YKJ, EPSG:2393), and selected the center of every 1-km grid cell. The grid cell has been skipped if we didn't find forest in a 100 m buffer around the center of the cell (totally 40 sites skipped, 30 were in the middle of large agricultural field and the other 10 were found in large treeless bog areas). Fig. 1B shows some examples of recorder locations in grid cells (in 100 m radius buffers).

Data were collected between 00:00 and 7:00 and between 16:00 and 20:00 UTC hours and from 16th of March and to 25th of April 2020. Each of the 285 sites was recorded for a full week between mid-March and late April 2020, resulting in a large dataset spanning over 2000 site-days, offering broad spatial coverage despite the short temporal frame. We used Autonomous Recording Units (ARUs)—specifically, AudioMoth devices—to passively monitor Crested Tit vocalizations. These ARUs are small, weatherproof sound recorders commonly used in ecological surveys to detect species presence via vocal activity. We estimate that ARUs detect Crested Tit vocalizations within 100–150 meters. In a previous study using the same setup (Baroni *et al*. 2023), recording made at several distances confirmed that the Pygmy Owl was not detected at the distance of neighboring ARUs. Given Crested Tit's quieter vocalization compared to Pygmy Owl, we are confident that spacing between ARUs was sufficient to avoid overlapping detections of Crested Tits. More details about the data can be found in Baroni *et al*. (2023). Our study design does not distinguish between residency and transient use; we treat presence detections as indicators of habitat use during early spring, aligning with the species' territorial and pre-breeding period. Presence was defined based on the manual identification of complete Crested Tit songs. We excluded alarm calls and incomplete vocalizations to avoid false detections. This conservative approach ensured that small or ambiguous vocalizations were not classified as presence. Our criteria differ from automated detection algorithms that may classify single chirps or fragments as presence. Consequently, our detection method emphasizes reliability and species-specific vocal behavior. As a result, our findings reflect site use rather than confirmed territory establishment or breeding.

2.3. Environmental variables

Habitat characteristics within two different radius buffers, 100 m (local scale) and 400 m (landscape scale), around each site were described with variables referring to the forest structure (Table 1). The 100 m buffer corresponds to the estimated reliable detection radius of the ARUs for Crested Tit calls. The 400 m buffer was chosen based on the species' estimated territory size and to assess broader landscape influences, while minimizing overlap between neighboring sampling sites.

To quantify habitat characteristics, we utilised the Multi-source National Forest Inventory data provided by the National Resources Institute Finland (Mäkisara *et al.* 2016), which allowed us to measure biomass of foliage for spruce and pine (10 kg/ha), as well as the areas of wetland and rocky substrates. For assessing anthropogenic impacts, specifically the distance from each study site to the nearest house, we employed Geographic Information System (GIS) tools using QGIS software (QGIS Development Team 2020).

The distance calculation was performed by overlaying the site locations with a map of residential structures. Using the QGIS platform, we calculated Euclidean distances from each site to the closest house. This method is well-documented in GIS literature for its accuracy in spatial analysis (QGIS Development Team 2020). By applying these tools, we were able to incorporate human influence into our habitat models, which is crucial for understanding the effects of anthropogenic pressures on habitat use.

For the age of the forest stands, we used

Table 1. List of explanatory variables used to explain Crested Tit occurrence, their definitions, source of data and descriptive statistics (range and mean).

Habitat variable	Explanation	Resource	Amount of variable within 100 m radius in applied sites
Pygmy Owl	Presence or absence of Pygmy Owl	Passive acoustic monitoring (Baroni *et al.* 2023)	Present in 63 sites (22%)
Sum pine foliage	Sum of pine foliage biomass	Multi-source National Forest Inventory	30–2.79 × 10^4 kg/ha (mean = 1.55 × 10^4)
Sum spruce foliage	Sum of spruce foliage biomass	Multi-source National Forest Inventory	361–1.33 × 10^5 kg/ha (mean = 4.06 × 10^4)
Sum deciduous foliage	Sum of deciduous foliage biomass	Multi-source National Forest Inventory	84–1.65 × 10^4 kg/ha (mean = 4.05 × 10^3)
Distance to house	Minimum distance from inhabited houses	Cartographical maps	43–3249 m (mean = 715.4)
Area for mature forest	Area of forest older than 80 years	Aerial photographs and satellite images	0–3.17 ha (mean = 0.27)
Area for clear cut	Area of clearcuts and young stands, *i.e.*, forest <15 years old	Aerial photographs and satellite images	0–3.05 ha (mean = 0.33)
Area for wetland	Area of wetland forest	Multi-source National Forest Inventory	0–2.25 ha (mean = 0.18)
Area for rocky	Area of rocky forest	Multi-source National Forest Inventory	0–0.95 ha (mean = 0.10)
Initial variables were excluded to avoid redundancy	Mean and standard deviation of Pine foliage biomass, Mean and standard deviation of spruce foliage biomass, Mean and standard deviation of deciduous foliage biomass, mean and standard deviation of canopy cover, minimum distance from main road, ems (Fragmentation index), Area of good forest, *i.e.*, forest >15 years old, Area of agricultural areas, Area of peatbogs, Total area of the raster layers included in the buffers		

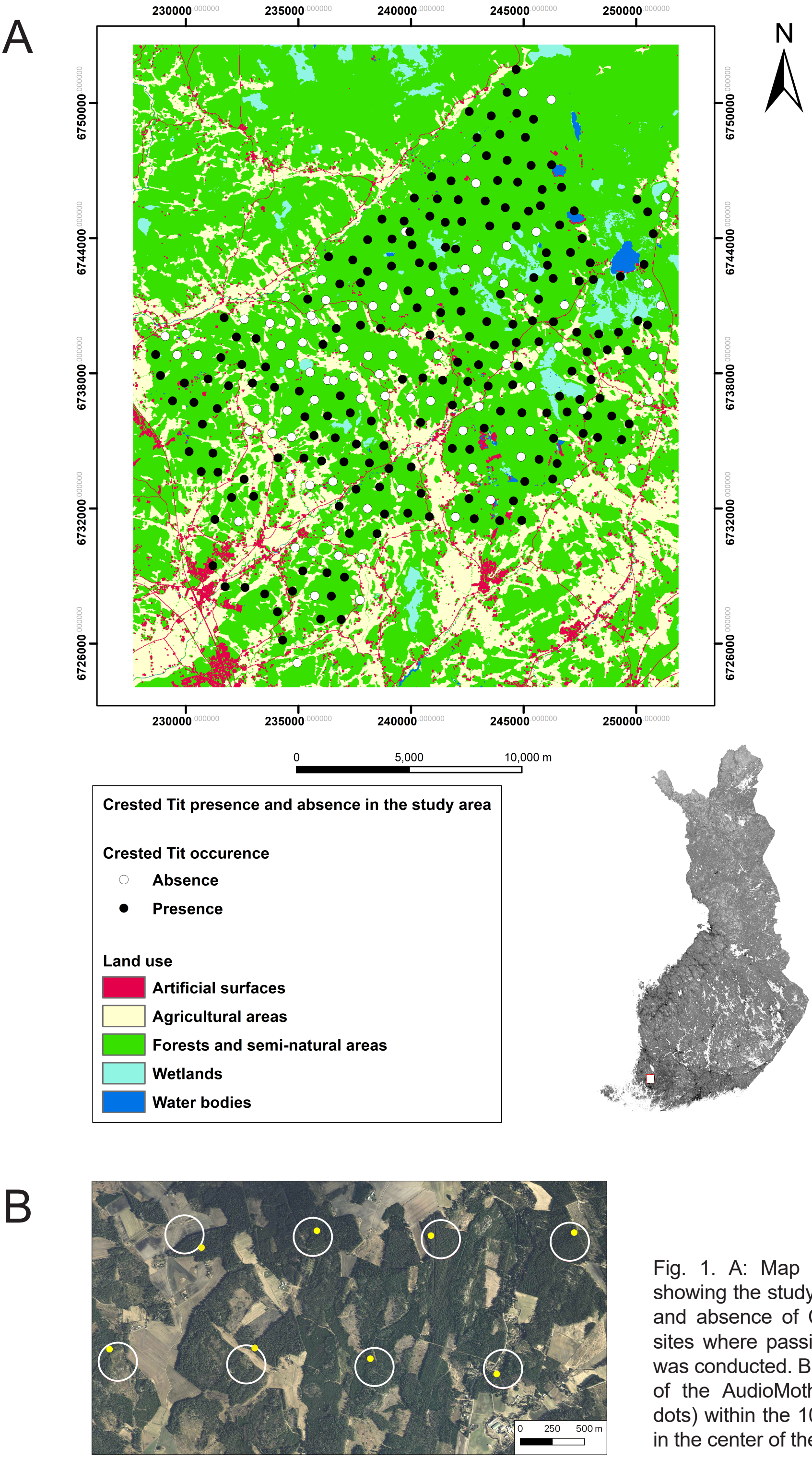

Fig. 1. A: Map of the study area showing the study grid and presence and absence of Crested Tits at the sites where passive acoustic survey was conducted. B: An example photo of the AudioMoth locations (yellow dots) within the 100 m radius buffers in the center of the grid cells (white).

available aerial photographs (from 1949 to 2020) and satellite images to classify all forest areas—*i.e.*, the area occupied by the 'canopy cover' layer from the National Forest Inventory—into the three variables: clear-cuts and young stands (forest age < 15 years), forest areas (forest age > 15 and < 80 years), and mature forest (forest age > 80 years old). Additionally, we included the presence or absence of Pygmy Owl at each detector (Baroni *et al*. 2023) to explore whether its occurrence influenced the presence of the Crested Tit.

2.4. Data analysis

Presence/absence of Crested Tit in passive acoustic monitoring data were reported based on species call detection (0 = Crested Tit not detected, 1 = Crested Tit detected) and cluster analysis in Kaleidoscope version 5.4.2. Advanced classifiers were applied to reduce false positive identifications. In this method, we initially trained the software with some publicly available Crested Tit calls after which the classifier software used statistical pattern analysis to sort similar vocalizations. All Crested Tit identifications of the software were checked by at least two bird specialists (authors: P. Hamedani Raja and D. Baroni) to reduce any possible false positive identifications.

Collinearity among the explanatory habitat variables was first examined by computing a Pearson correlation matrix using the usdm package (Naimi *et al.* 2014). When a pair of variables showed a high bivariate correlation ($|r| > 0.70$), one variable from the pair was removed to reduce redundancy and avoid interpretational ambiguity, following recommendations by Zuur *et al.* (2010) and Dormann *et al.* (2013). The remaining variables were retained for further analysis. Table 1 lists the final set of habitat variables used in the models.

To assess any remaining multicollinearity, we calculated Variance Inflation Factor (VIF) values. All variables showed VIF values well below the commonly used threshold of 5 (Naimi *et al.* 2014), indicating acceptable levels of multicollinearity among the predictors.

The relationships between Crested Tit presence/absence and explanatory environmental variables were analysed by binomial generalized linear models (GLM). We included an exponentially decaying spatial autocorrelation to allow for the non-independence of detections that are close by in space. The model was implemented in glmmTMB (Brooks *et al.* 2017) in R 1.3.959 (R Core Team 2020).

3. Results

3.1. Crested Tit presence and absence data

Crested Tits were detected at 195 out of 285 sites (68%) during the one-week recording period (Fig. 1A).

3.2. Habitat preferences

Descriptive statistics for the habitat variables are presented in Table 1. At the 100-meter scale, Crested Tit occurrence showed a positive association with the amount of pine foliage (Estimate = 0.38, SE = 0.20, Chisq = 3.69, P = 0.055; Table 2A; Fig. 2A), although this did not reach conventional levels of statistical significance. Similarly, there was a weak positive association with distance to the nearest house (Estimate = 0.31, SE = 0.16, Chisq = 3.71, P = 0.054; Table 2A; Fig. 2B). These patterns may reflect ecologically meaningful preferences but should be interpreted with caution.

At the 400-meter scale, no strong associations were detected between Crested Tit presence and any of the measured habitat variables, but there was a similar tendency for a positive association with distance to the nearest house as at the 100 m scale (Table 2B). The association with pine foliage was weak and non-significant (Table 2B). Similarly, no significant relationship was found with the area of mature forest at either scale.

The presence of Pygmy Owl at a site was not associated with Crested Tit presence at either spatial scale (100 m: Estimate = -0.03, SE = 0.14, Chisq = 0.04, P = 0.834; 400 m: Estimate = -0.01, SE = 0.14, Chisq = 0.00, P = 0.960; Tables 2A and 2B).

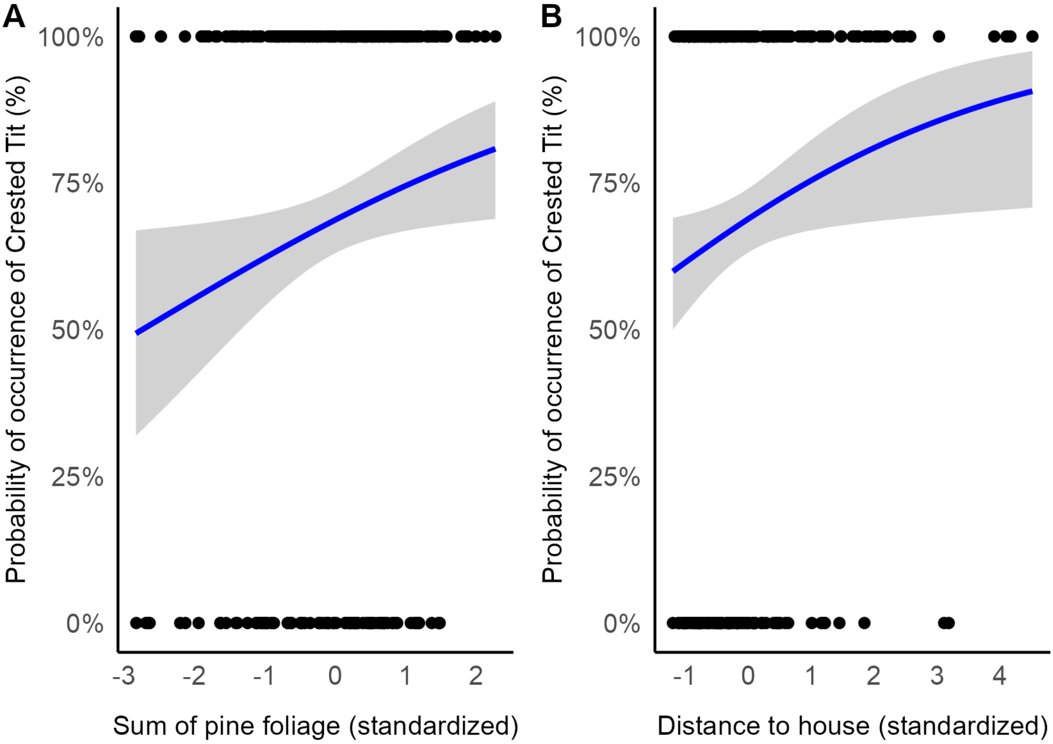

Fig. 2. Probability (expressed as a percentage) of Crested Tit presence in relation to A: Sum of pine foliage and B: Distance to the nearest house, within a 100 m radius buffer around the detector. In both graphs, the variables were standardized to a mean of zero and a unit standard deviation to allow comparison. The fitted relationships are represented by solid blue lines, with 95% confidence intervals around each line to indicate uncertainty. Data points are plotted as dots, showing Crested Tit presence (1) or absence (0) at each detector location.

4. Discussion

We studied habitat selection of Crested Tits using passive acoustic detection methods, based on a grid of 285 detector sites, with one site located in each forested km² across a region in southern Finland. The study was conducted in early spring, just prior to the onset of breeding. The results suggest that Crested Tits are more frequently associated with areas containing a higher amount of pine foliage within a 100 m radius, while this pattern is not apparent at the 400 m scale. The results also suggested that Crested Tits avoid human settlement, similarly both at 100 m and 400 m scale.

The preference of Crested Tits for habitats with higher amounts of pine foliage within a 100 m radius is consistent with some previous studies that highlight the importance of coniferous forests for this species (Lens & Dhondt 1993, Maícas & Haeger 2004, Atiénzar *et al.* 2009, Berlusconi *et al.* 2022). At the time we conducted the survey, Crested Tits were presumably already settled in their breeding territories, but they were not necessarily breeding yet. The habitat associations we here find may reflect the availability of food (insects) in pine forests (Summers *et al.* 1999, Atiénzar *et al.* 2009, Berlusconi *et al.* 2022). In addition, Crested Tits may prefer pine habitat to avoid interspecific competition with other tits (Alatalo *et al.* 1985, Summers *et al.* 1999). Importantly, we only found evidence for preference of pine forest at the spatial scale of 100 m radius and not at the larger scale (400 m radius) which likely reflects the limited feeding territory size of Crested Tits during this time of the year. This finding underscores the need for detailed habitat assessments at

Table 2. Mixed model estimates of effect sizes of various variables on Crested Tit occurrence, measured within 100 m A: and 400 m B: radii from the detector. Both models assumed binomial errors and accounted for spatial autocorrelation to address the non-independence of nearby detectors. For each variable, the estimate and its standard error (SE) are provided, with habitat variables standardized to a mean of zero and a unit variance to facilitate comparison of effect sizes. Statistical testing was conducted using a Wald chi-square test. We interpret near-significant values (*e.g.*, p = 0.054) with ecological caution and do not use asterisks to denote significance for p > 0.05. For definitions of variables, see Table 1.

Variable	Estimate	SE	Chisq	Df	P
A					
(Intercept)	0.83	0.13			
Pygmy Owl	-0.03	0.14	0.04	1	0.834
Sum pine foliage	0.38	0.20	3.69	1	0.055
Sum spruce foliage	0.03	0.18	0.03	1	0.853
Sum deciduous foliage	-0.21	0.15	1.91	1	0.167
Distance to house	0.31	0.16	3.71	1	0.054
Area for old forest	-0.20	0.15	1.86	1	0.172
Area for clear cut	-0.06	0.21	0.09	1	0.770
Area for wetland forest	0.17	0.17	0.93	1	0.334
Area for rocky forest	-0.10	0.16	0.45	1	0.503
B					
(Intercept)	0.81	0.13			
Pygmy Owl	-0.01	0.14	0.00	1	0.960
Sum pine foliage	0.08	0.22	0.13	1	0.717
Sum spruce foliage	0.10	0.22	0.21	1	0.648
Sum deciduous foliage	-0.14	0.18	0.66	1	0.416
Distance to house	0.31	0.17	3.15	1	0.076
Area for old forest	-0.24	0.15	2.60	1	0.107
Area for clear cut	-0.22	0.15	2.13	1	0.144

multiple spatial scales to accurately capture species-specific habitat requirements. The results highlight the importance of maintaining coniferous forest patches, particularly those with a high density of pine foliage, as a crucial element for the conservation of species like the Crested Tit, which rely on these habitats for foraging, especially during the breeding season.

We found no relationship between Crested Tit occurrence and proportion of mature forest, which contradicts the notion that old-growth forest is of key importance to this species (Berlusconi *et al.* 2022). In this study, mature forests are defined as patches of forest that have not been clearcut during the last 80 years as based on aerial photographs. While it can be argued how old a forest must be to be considered an "old-growth forest", we found no evidence that the amount of >80 years old forest affects Crested Tit occurrence. This finding is against our expectation since we expected opportunities for breeding for Crested Tits to be more abundant in older forests as this species relies on decaying trees to excavate their nest cavity. Importantly, Baroni *et al.* (2023) showed, using the same passive acoustic survey data used here, that another species associated with older forest, the Pygmy Owl, was associated with the amount of >80-year-old forest. One possible explanation for why we do not find this association for Crested Tit is that the availability of suitable nesting sites, such as decaying wood, may be more widespread across various forest types than previously thought. Additionally, our definition of mature forests (80 years) might not fully align with the specific habitat characteristics that Crested Tits require. Our results might indicate that the structural characteristics of mature forests in our study area are not critical for this species during the early spring period when our data were collected. It is possible that Crested Tits may rely more on mature forests later in the breeding season when resources such as old-growth trees and specific nesting sites become more relevant. Additionally, this lack of dependence on mature forests during our study period could suggest that younger or mixed-age forest stands, which provide a combination of foraging opportunities and shelter, may be sufficient for the species in the early part of the season.

Our findings indicate that Crested Tits tend to avoid houses. The result was basically similar at the 100 m and 400 m scale. We note that the results marginally do not meet conventional thresholds for statistical significance and should be interpreted cautiously. Given the strong correlation between distance to the house and distance to the road, we infer that, ecologically, the "distance to house" may also serve as an indicator of the proximity to human-made structures. The tendency of Crested Tits to avoid areas closer to human settlements aligns with previous findings that indicate a general avoidance of anthropogenic disturbances (Berlusconi *et al.* 2022). This avoidance may be linked to the lower quality of habitat near human-made structures or increased disturbance from human activities. One potential complication is that sites close to human settlement may have more noise and thereby drown the call of Crested Tit, but recordings were checked by human observers to avoid this bias. Interestingly, this finding contrasts markedly with findings that show that Great Tit and Blue Tit show more interest in urban areas, specifically for feeding and breeding (Cramp & Perrins 1993, Solonen & Hildén 2014). Human-created environments may therefore support competitors that are more adaptable than the Crested Tit to urban conditions. Hence, the avoidance of houses may also result from habitat segregation with other competitors. Whatever the mechanism, a preference of Crested Tits for forested environments over areas with human structures suggests that increasing construction of houses could negatively impact bird populations (Marzluff 2001, Chase & Walsh 2006, McKinney 2008). These findings reinforce the importance of minimizing urban encroachment into forest habitats and reducing the presence of artificial structures near key forested areas.

Interestingly, habitat preferences were more pronounced at the 100-meter scale compared to the broader 400-meter radius, suggesting that Crested Tit habitat selection occurs at a fine scale. This finding aligns with research on other small forest bird species, where immediate habitat features such as tree species composition and foliage density often play a more significant role in habitat selection than broader landscape characteristics (Reiley & Benson 2019). It is possible that the 100-meter radius captures the core foraging area for the Crested Tit, particularly during the breeding season, when individuals are likely to defend small territories and rely on specific localized resources.

Our study underscores the usefulness of the passive acoustic survey method, as it holds the potential to enhance our understanding of habitat selection for Crested Tits and other declining forest bird species. Importantly, the passive acoustic surveys, as employed in this study, offer a valuable and replicable means of data collection. This method not only aids in the study of habitat selection but also serves as a valuable tool for population monitoring. The cumulative detection probability achievable through passive acoustic surveys surpasses that of traditional point count surveys, making it an essential approach for both research and conservation efforts. Their non-invasive nature, continuous monitoring capabilities, and integration with advanced analytical methods make them a valuable addition to the field of ornithology, offering new avenues for research and conservation efforts. The scalability of this technique makes it a promising approach for ongoing monitoring efforts and biodiversity conservation projects.

Given the decline in Crested Tit populations, gaining deeper insights into their habitat selection becomes useful for effective conservation planning. Considering the limited sample size and the one-week survey period, our conclusions should be interpreted cautiously. The absence of a significant preference for certain habitat features or the lack of evidence for predator influence could be influenced by the temporal and spatial limitations of our study. While data were collected over a limited time period, the spatial extent and number of sites allow robust conclusions about early spring habitat use. Future research with larger sample sizes, extended survey periods, and additional habitat variables could provide a more comprehensive understanding of Crested Tit habitat preferences and their response to environmental factors. In conclusion, our study highlights the importance of fine-scale habitat features, such as pine foliage, in shaping the occurrence of the Crested Tit, while also highlighting the species' sensitivity to anthropogenic disturbance. The lack of reliance on mature forests during the early spring period suggests that forest management strategies should consider the seasonal variability of habitat use. Conservation efforts should prioritize maintaining coniferous patches and protect forest edges from encroaching urbanization to support the long-term viability of Crested Tit populations.

Töyhtötiaisten esiintymistodennäköisyys kasvoi alkukeväisen kartoituksen perusteella männyn neulasmassan mutta ei varttuneen metsän pinta-alan kanssa

Töyhtötiainen (*Lophophanes cristatus*) on Suomessa melko yleinen laji, mutta sen kanta on taantumassa, todennäköisesti lisääntyvän ihmistoiminnan aiheuttaman paineen ja elinympäristöjen heikentymisen vuoksi.

Tutkimme töyhtötiaisen elinympäristövaatimuksia Lounais-Suomessa. Teimme passiivisen akustisen kartoituksen lajin esiintymisestä juuri ennen pesimäkautta keväällä 2020. Kartoitus perustui viikon mittaisiin äänityksiin 285 metsäisessä kohteessa, jotka sijaitsivat noin kilometrin välein toisistaan.

Tulosten mukaan töyhtötiainen suosii paikkoja, joissa on kaukokartoitusaineiston mukaan runsaasti männyn neulasmassaa sadan metrin säteellä. Odotuksistamme poiketen emme havainneet töyhtötiaisen esiintymistodennäköisyyden kasvavan varttuneen metsän osuuden kanssa. Lisäksi havaitsimme, että töyhtötiainen karttaa rakennettuja alueita ja rakenteita, mikä saattaa liittyä kilpailun välttelyyn muiden lintulajien kanssa ihmisasutuksen läheisyydessä. Elinympäristöpreferenssejä ei havaittu 400 metrin säteellä kartoituspisteestä, mikä voi johtua siitä, että kyseisellä säteellä merkittävä osa elinympäristöistä ei ole lajin käytössä.

Vaikka töyhtötiaiskanta on Suomessa yleisesti taantumassa, havaitsimme lajin esiintyvän 68 %:ssa kartoituspisteistämme, mikä vahvistaa passiivisen akustisen seurannan luotettavuutta hyödyllisenä menetelmänä lintujen elinympäristövaatimusten ja populaatioiden seurannassa. Tulokset parantavat ymmärrystämme töyhtötiaisen ekologiasta elinympäristöjen heikentyessä ja populaatioiden pienentyessä sekä tarjoavat tietoa suojelutoimien tueksi.

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References

Ahola, M., Laaksonen, T., Eeva, T. & Lehikoinen, E. 2007: Climate change can alter competitive relationship between resident and migratory birds. — Journal of Animal Ecology 76: 1045–1052. https://doi.org/10.1111/j.1365-2656.2007.01294.x

Alatalo, R.V., Gustafsson, L., Lindén, M. & Lundberg, A. 1985: Interspecific competition and niche shifts in tits and the goldcrest: an experiment. — Journal of Animal Ecology 54: 977–984. https://doi.org/10.2307/4391

Arneill, G.E., Critchley, E.J., Wischnewski, S., Jessopp, M.J. & Quinn, J.L. 2020: Acoustic activity across a seabird colony reflects patterns of within-colony flight rather than nest density. — Ibis 162: 416–428. https://doi.org/10.1111/ibi.12740

Astaras, C., Valeta, C. & Vasileiadis, I. 2022: Acoustic ecology of tawny owl (*Strix aluco*) in the Greek Rhodope Mountains using passive acoustic monitoring methods. — Folia Oecologica 49: 110–116. https://doi.org/10.2478/foecol-2022-0012

Atiénzar, F., Barba, E., Holleman, L.J.M. & Belda, E.J. 2009: Nesting habitat requirements and nestling diet in the Mediterranean populations of Crested Tits *Lophophanes cristatus*. — Acta Ornithologica 44: 101–108. https://doi.org/10.3161/000164509X482678

Baroni, D., Hanzelka, J., Raimondi, T., Gamba, M., Brommer, J.E. & Laaksonen, T. 2023: Passive acoustic survey reveals the abundance of a low-density predator and its dependency on mature forests. — Landscape Ecology 38: 1939–1954. https://doi.org/10.1007/s10980-023-01667-1

Berlusconi, A., Martinoli, A., Wauters, L., Tesoro, G., Martini, S., Clerici, E., Guenzani, G., Pozzi, G., Rubolini, D., Morganti, M. & Martinoli, A. 2022: Year-round multi-scale habitat selection by Crested Tit (*Lophophanes cristatus*) in lowland mixed forests (northern Italy). — Avian Research 13: Article 100058. https://doi.org/10.1016/j.avrs.2022.100058

BirdLife International. 2024: Species factsheet: Crested Tit *Lophophanes cristatus*. — Downloaded from https://datazone.birdlife.org/species/factsheet/crested-tit-lophophanes-cristatus on 17/10/2024.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M. & Bolker, B.M. 2017: Modeling zero-inflated count data with glmmTMB. — bioRxiv 132753. https://doi.org/10.1101/132753

Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A. & Rajasärkkä, A. 2003: Effects of landscape structure and forest reserve location on old-growth forest bird species in northern Finland. — Landscape Ecology 18: 377–393. https://doi.org/10.1023/A:1026148825138

Conenna, I., Valkama, J. & Chamberlain, D. 2017: Interactive effects of climate and forest canopy cover on Goshawk productivity. — Journal of Ornithology 158: 799–809. https://doi.org/10.1007/s10336-017-1432-0

Cramp, S. & Perrins, C.M. (ed.) 1993: Handbook of the birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. VII. — Oxford University Press, Oxford.

Crick, H.Q.P. & Sparks, T.H. 1999: Climate change related to egg-laying trends. — Nature 399: 423–424. https://doi.org/10.1038/20839

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. 2013: Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. — Ecography 36: 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Eeva, T., Andelmin, P., Hokkanen, T., Riivari, P., Ahola, M.P., Laaksonen, T. & Lehikoinen, E. 2012: Breeding time trends of the Crested Tit (*Lophophanes cristatus*) in southern Finland: comparison of data sources. — Journal of Ornithology 153: 653–661. https://doi.org/10.1007/s10336-011-0783-1

Fraixedas, S., Lehikoinen, A. & Linden, A. 2015: Impacts of climate and land-use change on wintering bird populations in Finland. — Journal of Avian Biology 46: 63–72. https://doi.org/10.1111/jav.00441

Gregory, R.D., Vorisek, P., van Strien, A., Gmelig Meyling, A.W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. & Burfield, I.J. 2007: Population trends of widespread woodland birds in Europe. — Ibis 149: 78–97. https://doi.org/10.1111/j.1474-919X.2007.00698.x

Hagens, S.V., Rendall, A.R. & Whisson, D.A. 2018: Passive acoustic surveys for predicting species' distributions: optimising detection probability. — PLoS ONE 13(7): e0199396. https://doi.org/10.1371/journal.pone.0199396

Hartley, P.H.T. 1987: Ecological aspects of the foraging behaviour of Crested Tits *Parus cristatus*. — Bird Study 34(2): 107–111. https://doi.org/10.1080/00063658709476945

Järvinen, O. & Väisänen, R.A. 1978: Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. — Journal of Ornithology 119: 441–449. https://doi.org/10.1007/BF01643135

Kumpula, S., Vatka, E., Orell, M. & Rytkönen, S. 2023: Effects of forest management on the spatial distribution of the Willow Tit (*Poecile montanus*). — Forest Ecology and Management 529: 120694. https://doi.org/10.1016/j.foreco.2022.120694

Lehikoinen, A. & Väisänen, R.A. 2023: Pesivien maalintujen kannanmuutokset Suomessa 1975–2022. — Linnutvuosikirja 2022: 14–29. (In Finnish; English title: Monitoring population changes of land bird species breeding in Finland in 1975–2022.)

Lens, L. & Dhondt, A.A. 1993: Individual variation in mate care by alpha males in Crested Tit winter flocks. — Behavioral Ecology and Sociobiology 33: 79–85. https://doi.org/10.1007/BF00171659

Lens, L. & Dhondt, A.A. 1994: Effects of habitat fragmentation on the timing of Crested Tit *Parus cristatus* natal dispersal. — Ibis 136(2): 147–152. https://doi.org/10.1111/j.1474-919X.1994.tb01078.x

Linke, S., Gifford, T., Desjonquères, C., Tonolla, D., Aubin, T., Barclay, L., Karaconstantis, C., Kennard, M.J., Rybak, F. & Sueur, J. 2018: Freshwater ecoacoustics as a tool for continuous ecosystem monitoring. — Frontiers in Ecology and the Environment 16: 231–238. https://doi.org/10.1002/fee.1779

Maícas, R. & Haeger, J.F. 2004: Pine plantations as a breeding habitat for a hole-nesting bird species, Crested Tit (*Parus cristatus*), in southern Spain. — Forest Ecology and Management 195(1–2): 267–278. https://doi.org/10.1016/j.foreco.2004.03.021

Mäkisara, K., Katila, M., Peräsaari, J. & Tomppo, E. 2016: The multi-source national forest inventory of Finland — methods and results 2013. — Natural Resources and Bioeconomy Studies 10, Natural Resources Institute Finland (Luke). http://urn.fi/URN:ISBN:978-952-326-186-0

Marzluff, J.M. 2001: Worldwide urbanization and its effects on birds. — In Avian Ecology and Conservation in an Urbanizing World (ed. Marzluff, J.M., Bowman, R. & Donnelly, R.): 19–47. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-1531-9_2

McKinney, M.L. 2008: Effects of urbanization on species richness: a review of plants and animals. — Urban Ecosystems 11: 161–176. https://doi.org/10.1007/s11252-007-0045-4

Melo, I., Llusia, D., Bastos, R.P. & Signorelli, L. 2021: Active or passive acoustic monitoring? Assessing methods to track anuran communities in tropical savanna wetlands. — Ecological Indicators 132: 108305. https://doi.org/10.1016/j.ecolind.2021.108305

Morosinotto, C., Villers, A., Varjonen, R. & Korpimäki, E. 2017: Food supplementation and predation risk in harsh climate: interactive effects on abundance and body condition of tit species. — Oikos 126: 863–873. https://doi.org/10.1111/oik.03476

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. 2014: Where is positional uncertainty a problem for species distribution modelling? — Ecography 37(2): 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Orlando, G., Varesio, A. & Chamberlain, D. 2021: Field evaluation for playback surveys: species-specific detection probabilities and distance estimation errors in a nocturnal bird community. — Bird Study 68(1): 90–99. https://doi.org/10.1080/00063657.2021.1968790

QGIS Development Team. 2020: QGIS Geographic Information System. — Open-Source Geospatial Foundation Project.

R Core Team. 2020: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria.

Reiley, B.M. & Benson, T.J. 2019: Avian fitness consequences match habitat selection at the nest-site and landscape scale in agriculturally fragmented landscapes. — Ecology and Evolution 9(12): 7173–7183. https://doi.org/10.1002/ece3.5288

Rigal, S., Dakos, V., Alonso, H. & Devictor, V. 2023: Farmland practices are driving bird population decline across Europe. — Proceedings of the National Academy of Sciences 120(21): e2216573120. https://doi.org/10.1073/pnas.2216573120

Ross, S.R.P.J., O'Connell, D.P., Deichmann, J.L., Desjonquères, C., Gasc, A., Phillips, J.N., Sethi, S.S., Wood, C.M. & Burivalova, Z. 2023: Passive acoustic monitoring provides a fresh perspective on fundamental ecological questions. — Functional Ecology 37(4): 959–975. https://doi.org/10.1111/1365-2435.14275

Smith, D.G., Truskinger, A., Roe, P. & Watson, D.M. 2020: Do acoustically detectable species reflect overall diversity? A case study from Australia’s arid zone. — Remote Sensing in Ecology and Conservation 6(3): 286–300. https://doi.org/10.1002/rse2.173

Solonen, T. & Hildén, M. 2014: Breeding phenology in Great and Blue Tits (Parus spp.): are urban populations more resistant to climate change than rural ones? — Ornis Fennica 91(4): 209–219. https://doi.org/10.51812/of.133858

Sueur, J., Krause, B. & Farina, A. 2019: Climate change is breaking Earth's beat. — Trends in Ecology and Evolution 34(11): 971–973. https://doi.org/10.1016/j.tree.2019.07.014

Summers, R.W., Mavor, R.A., Buckland, S.T. & MacLennan, A.M. 1999: Winter population size and habitat selection of Crested Tits *Parus cristatus* in Scotland. — Bird Study 46(2): 230–242. https://doi.org/10.1080/00063659909461135

Virkkala, R., Rajasärkkä, A., Heikkinen, R.K., Kuusela, S., Leikola, N. & Pöyry, J. 2018: Birds in boreal protected areas shift northwards in the warming climate but show different rates of population decline. — Biological Conservation 226: 271–279. https://doi.org/10.1016/j.biocon.2018.08.015

Virkkala, R., Määttänen, A.-M. & Heikkinen, R.K. 2023: Clear-cuts and warming summers caused forest bird populations to decline in a southern boreal area. — Forest Ecology and Management 548: Article 121397. https://doi.org/10.1016/j.foreco.2023.121397

Wood, C.M., Champion, J., Brown, C., Brommelsiek, W., Laredo, I., Rogers, R. & Chaopricha, P. 2023: Challenges and opportunities for bioacoustics in the study of rare species in remote environments. — Conservation Science and Practice 5: e12941. https://doi.org/10.1111/csp2.12941

Yang, Y., Ye, Z., Zhang, Z. & Xiong, Y. 2025: Investigating the drivers of temporal and spatial dynamics in urban forest bird acoustic patterns. — Journal of Environmental Management 376: Article 124554. https://doi.org/10.1016/j.jenvman.2025.124554

Zhong, E., Guan, Z., Zhou, X., Zhao, Y., Li, H., Tan, S. & Hu, K. 2021: Application of passive acoustic monitoring technology in the monitoring of western black crested gibbons. — Biodiversity Science 29: 109–117. https://doi.org/10.17520/BIODS.2020215

Zuur, A.F., Ieno, E.N. & Elphick, C.S. 2010: A protocol for data exploration to avoid common statistical problems. — Methods in Ecology and Evolution 1(1): 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Ornis Fennica 102: 14–27. 2025

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.

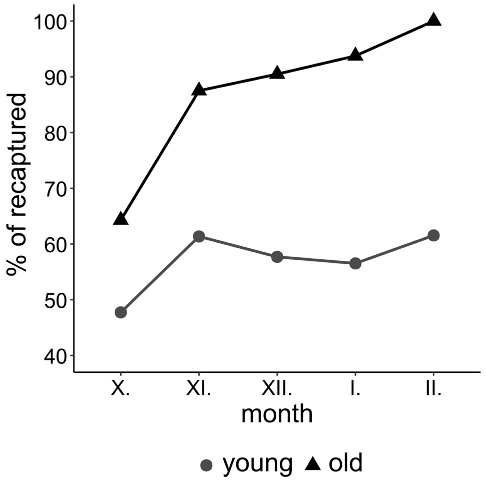

Fig. 1. Percentage of Great Tits recaptured within winter in different months according to their age.

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%).

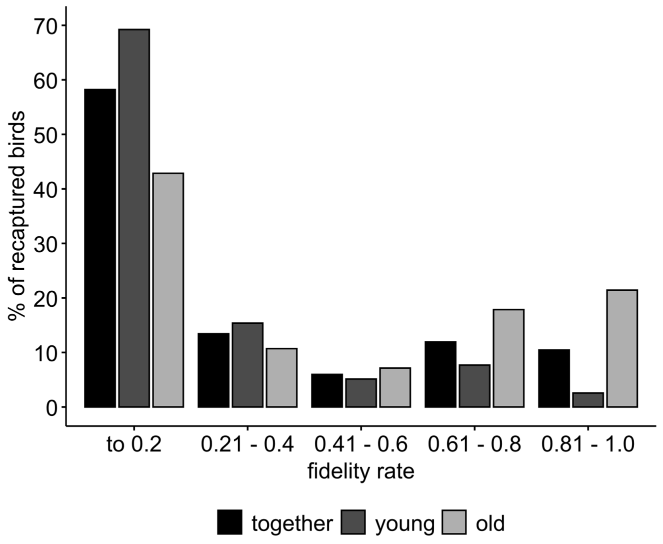

Fig. 2. Distribution of fidelity rates in recaptured birds (N = 67) according to their age (young: N = 39; old: N = 28).

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

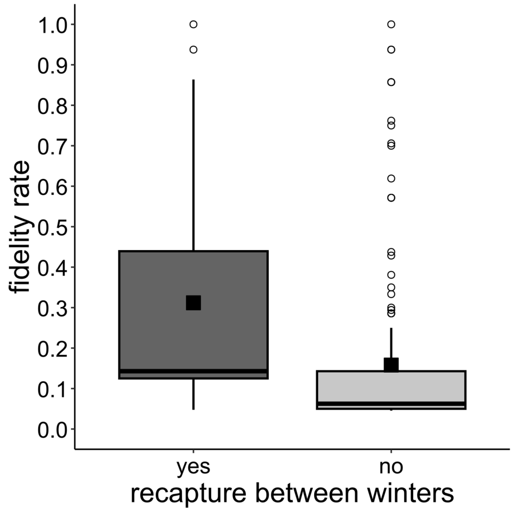

Fig. 3. Differences in fidelity rates during the first winter between individuals that were not recaptured (N = 155) and those that were recaptured (N = 23) between winters. Mean values are marked with squares.

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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References

Báldi, A. & Csorgő, T. 1991: Effect of environmental factors on tits wintering in a Hungarian marshland. — Ornis Hungarica 1: 29–36.

Báldi, A. & Csorgő, T. 1997: Spatial arrangement of roosting Great Tits (*Parus major*) in a Hungarian forest. — Acta Zoologica Acedemiae Scientarium Hungariae 34: 295–301.

Beklová, M. 1972: Age structure and mortality of the Czechoslovakian populations of the *Turdus merula* L. 1758, *Sturnus vulgaris* L. 1758 and *Parus major* L. 1758. — Zoologické listy 21: 337–346.

Busse, P. & Olech, B. 1968: On some problems of birds spending night in nest boxes. — Acta Ornithologica 11: 1–26. (In Polish with English summary)

Christe, P., Opplinger, A. & Richner, H. 1994: Ectoparasite affects choice and use of roost sites in the Great Tit, *Parus major*. — Animal Behaviour 47: 895–898. https://doi.org/10.1006/anbe.1994.1121

Cooper, S. J. 1999: The thermal and energetic significance of cavity roosting in Mountain Chickadees and Juniper Titmice. — Condor 101: 863–866. https://doi.org/10.2307/1370077

Creutz, G. 1960: Die Nächtigungsweise von Höhlenbrütern in künstlichen Nistgeräten. — Der Falke 7: 121–125. (In German)

Croon, B., Schmidt K.-H., Mayer A. & Mayer F.-G. 1985: Site-fidelity and migratory behaviour in Tits (*Parus major*, *P. caeruleus*, *P. ater*, *P. palustris*) in the nonbreeding period. — Die Vogelwarte 33: 8–16. (In German with English summary)

Czarnecki, Z. 1960: Observations of the nocturnal habits of the Great Tit (*Parus major* L.) in the winter. — Ekologia Polska Seria B 6: 191–197. (In Polish with English summary)

De Laet, J. 1984: Site-related dominance in the great Tit *Parus major major*. — Ornis Scandinavica 15: 73–78. https://doi.org/10.2307/3675940

Dhondt, A. A., Blondel, J. & Perret, P. 2010: Why do Corsican Blue Tits *Cyanistes caeruleus ogliastrae* not use nest boxes for roosting. — Journal of Ornithology 151: 95–101. https://doi.org/10.1007/s10336-009-0430-2

Drent, P. J. 1987: The importance of nestboxes for territory settlement, survival and density of the Great Tit. — Ardea 75: 59–71.

Ekner, A. & Tryjanwski, P. 2008: Do small hole nesting Passerines detect cues left by a predator? A test on winter roosting sites. — Acta Ornithologica 43(1): 107–111. https://doi.org/10.3161/000164508X345392

Grüebler, M. U., Vidmer S., Korner-Nievergelt, F. & Naef-Daenzer, B. 2014: Temperature characteristics of winter roost-sites for birds and mammals: tree cavities and anthropogenic alternatives. — International Journal of Biometeorology 58: 629–638. https://doi.org/10.1007/s00484-013-0643-1

Hammer, Ø., Harper, D. A. T., Ryan, P. D. 2001: PAST: Paleontological Statistics Software Package for Education and Data Analysis — Palaeontologia Electronica, 4: 1– 9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Helle, P. 1980: A Great Tit *Parus major* roosting in snow. — Ornis Fennica 57: 175–176.

Hildén, O. 1978: Adult:juvenile and sex ratios in a winter population of the Great Tit in southern Finland. — Ornis Fennica 55: 120–125. (In Finnish with English abstract)

Holec, J., Feranec, J., Šťastný, P., Szatmári, D., Kopecká, M. & Garaj, M. 2020: Evolution and assessment of urban heat island between the years 1998 and 2016: case study of the cities Bratislava and Trnava in western Slovakia. — Theoretical and Applied Climatology 141: 979–997. https://doi.org/10.1007/s00704-020-03197-1

Inkscape project 2023: Inkscape. https://inkscape.org.

Juškaitis, R. 1986: Nocturnal occupation of nesting boxes in post-breeding period. — In Ecology of birds of Lithuanian SSR, 3. Anthropogenous Effect on Avifauna and Protection of it: 150–196. Academy of Sciences of the Lithuanian SSR, Institute of Zoology and Parazitology, Vilnius. (In Russian with English summary)

Kassambara, A. 2023: ggpubr: ´gggplot2´based publication redy plots — R package version 0.6.0. https://CRAN.R-project.org/package=ggpubr.

Kendeigh, Ch. 1961: Energy of birds conserved by roosting in cavities. — The Wilson Bulletin 73: 140–147.

Kluyver, H. N. 1957: Roosting habits, Sexual Dominance and Survival in the Great Tit. — Cold Spring Harbour Symposium on Quantitative Biology 22: 281–285. https://doi.org/10.1101/SQB.1957.022.01.027

Konček, M. (ed.) 1979: Klíma a bioklíma Bratislavy — Vydavateľstvo Slovenskej akadémie vied, Bratislava. (In Slovak)

Krištín, A. & Kaňuch, P. 2017: Stay or go? Strong winter feeding site fidelity in small woodland passerines revealed by a homing experiment. — Journal of Ornithology 158: 53–61. https://doi.org/10.1007/s10336-016-1362-2

Krištín, A., Mihál, I. & Urban, P. 2001: Roosting of the great tit, *Parus major* and the nuthatch, *Sitta europaea* in nest boxes in an oak-hornbeam forest. — Folia zoologica 50: 43–53.

Lempaszak, U. 1988: Roosting of hole birds in the orchard. — Przegląd zoologiczny 32: 247–260. (In Polish with English summary)

Ligon, J. D., Carey, C. & Ligon, S. H. 1988: Cavity roosting, philopatry, and cooperative breeding in the Green Woodhoopoe may reflect a physiological trait. — The Auk 105: 123–127.

Loss, S. R., Will, T. & Marra, P. P. 2015: Direct Mortality of Birds from Anthropogenic Causes. — Annual Review of Ecology, Evolution, and Systematic 46: 99–120. https://doi.org/10.1146/annurev-ecolsys-112414-054133

Mainwaring, M. C. 2011: The use of nestboxes by roosting birds during the non-breeding season: a review of the costs and benefits. — Ardea 99: 167–176. https://doi.org/10.5253/078.099.0206

Mayer, G. 1962: Untersuchungen an einer Kohlmeisenpopulation im Winter. — Naturkundliches Jahrbuch der Stadt Linz 8: 295–328. (In German)

Merilä, J. & Allander, K. 1995: Do Great Tits (*Parus major*) Prefer Ectoparasite-free Roost Sites? An Experiment. — Ethology 99: 53–60. https://doi.org/10.1111/j.1439-0310.1995.tb01088.x

Möckel, R. 1992: Effect of Waldsterben (forest damage due to airborne pollution) on the population dynamics of Coal Tit (*Parus ater*) and Crested Tit (*Parus cristatus*) in the western Erzgebirge. — Ökologie der Vögel 14: 1–100. (In German with English Summary)

Newton, I. 1998: Population limitation in birds. — Academic Press, London.

Orłowski, G. 2006: Habitat selection and winter food resources of the Water Pipit *Anthus spinoletta* in south-western Poland. — Acta Ornithologica 41(1): 41–48. https://doi.org/10.3161/068.041.0110

Payevsky, V. A. 2006: Mortality Rate and Population Density Regulation in the Great Tit, *Parus major* L.: A Review. — Russian Journal of Ecology 37: 180–187. https://doi.org/10.1134/S1067413606030064

Perrins, C. M. & McCleery, R. H. 1985: The effect of age and pair bond on the breeding success of Great Tits *Parus major*. — Ibis 127: 306–315. https://doi.org/10.1111/j.1474-919x.1985.tb05072.x

R Core Team 2025: R: A language and Environment for statistical computing. — R Foundation for statistical computing, Vienna. https://www.R-project.org/.

Rodríguez, S., Van Noordwijk, A. J., Alvarez, E. & Barba, E. 2016: A recipe for postfledging survival in Great Tits *Parus major*: be large and be early (but not too much). — Ecology and Evolution 6: 4458–4467. https://doi.org/10.1002/ece3.2192

Saitou, T. 1978: Ecological study of social organization in the Great Tit, *Parus major* L.: I. Basic structure of the winter flocks. — Japan Journal of Ecology 28: 199–214.

Saitou, T. 1979a: Ecological study of social organization in the Great Tit, *Parus major* L.: IV. Pair formation and establishment of territory in the members of basic flock. — Journal of the Yamashina Institute for Ornithology 11: 171–188.

Saitou, T. 1979b: Ecological study of social organization in the Great Tit*, Parus major* L.: III. Home range of the basic flocks and the dominance of the members in a basic flock. — Journal of the Yamashina Institute for Ornithology 11: 171–188.

Saitou, T. 2002: Factors affecting divorce in the Great Tit *Parus major*. — Ibis 144: 311–316. https://doi.org/10.1046/j.1474-919X.2002.00016.x

Sandell, M. & Smith, H., G. 1991: Dominance, prior occupancy, and winter residency in the Great Tit (*Parus major*). — Behavioral Ecology and Sociobiology 29: 147–152. https://doi.org/10.1007/BF00166490

Schmidt, K.-H. 1983: Investigation of population dynamics of Great Tits (*Parus major*) throughout the year. — Ökologie der Vögel 5: 135–202. (In German with English summary)

Schmidt, K.-H., Berressem, H., Beressem, K. G. & Demuth, M. 1985: Studies on Great Tits (*Parus major*) during winter – possibilities and limits of nocturnal checks. — Journal für Ornithologie 126: 63–71. (In German with English summary)

Shipley, A. A., Sheriff, M. J., Pauli, J. N. & Zuckenberg, B. 2019: Snow roosting reduces temperature-associated stress in a wintering bird. — Oecologia 109: 309–321. https://doi.org/10.1007/s00442-019-04389-x

Stiefel, A. 1976: Ruhe und Schlaf bei Vögeln. — A. Ziemsen Verlag, Wittenberg-Lutherstadt. (In German)

Svensson, L. 1992: Identification guide to European passerines. — published by author, Stockoholm.

Sydeman, W. J. & Güntert, M. 1983: Winter communal roosting in the Pygmy Nuthatch. — Snag habitat management, proceedings of the symposium, June 7 – 9 1983, Flagstaff, Arizona: 121–124. Flagstaff, Arizona. Rocky Mountain Forest and range experimental station, Fort Collins (Colorado).

Thompson, W. L., Yahner, R. H. & Storm, G. L. 1990: Winter use and habitat characteristics of Vulture communal roosts. — The Journal of Wildlife management 54: 77–83.

Tyller, Z., Paclík, M. & Remeš, V. 2012: Winter night inspections of nest boxes affect their occupancy and reuse for roosting by cavity nesting birds. — Acta Ornithologica 47: 79–85. https://doi.org/10.3161/000164512X653944

Typiak, J. & Typiak, M. 2018: Two cases of tits fights to the death in competition for winter roost sites. — Fragmenta faunistica 61: 65–70. https://doi.org/10.3161/00159301FF2018.61.1.065

Typiak, J. A., Typiak, M. J. & Mazgajski, T. D. 2019: Nest box use for winter roosting within a flock of tits. — Polish Journal of Ecology 67: 148–158. https://doi.org/10.3161/15052249PJE2019.67.2.005

Veľký, M. & Krištín A. 2008: Ako vtáky prežívajú nepriaznivé zimné obdobie? — Institute of Forest Ecology SAS, Zvolen. (In Slovak)

Veľký, M. 2002: Wintering and roosting of birds in nest boxes in urban environment. Tichodroma 15: 60–70. (In Slovak with English summary)

Veľký, M. 2006: Patterns in winter-roosting and breeding of birds in nest-boxes. — Tichodroma 18:89–96. (In Slovak with English abstract)

Von Haartman, L. 1968: The evolution of resident versus migratory habit in birds. Some considerations. — Ornis Fennica 45: 1–7.

Wickham, H. 2016. ggplot2: Elegant graphic for data analysis — Springer-Verlag, New York.

Winkel, W. & Hudde, H. 1988: Nest-box roosting of birds in winter. — Die Vogelwarte 34: 174–188. (In German with English summary)

Winkel, W. & Winkel, D. 1980: On mate fidelity in Great, Blue and Coal Tits (*Parus major*, *P. caeruelus* and *P. ater*). — Die Vogelwarte 30: 325–333. (In German with English summary)

Winkel, W. 1974: On the transportation of Great Tits and Blue Tits (*Parus major* and *P. caeruleus*) outside the breeding season, in the coastal area of North-west Germany. — Die Voglewarte 27: 264–278. (In German with English summary)

Zang, H. & Kunze, P. 2009: Nestbox-Roosting of Great Tits *Parus major*, Blue Tits *P. caeruleus* and Nuthatches *Sitta europaea* in winter from 1982/83 to 2006/07 in nestbox-study areas in the Harz Mountains. — Ornithologisches Jahhrbericht Museum Heineanum 27: 43–60. (In German with English summary)

Zonov, G. B. 2017: Winter roostings of tits in Predbajkale. — The Russian Journal of Ornithology 26: 2748–2753. (In Russian)

Zvářal, K. 2010: Roosting birds the nest-boxes in forest habitats. — Tichodroma 22: 39–43. (In Czech with English abstract)

Online supplementary material

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

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Local variation in sex ratios in three species of wintering ducks: the need for large-scale sampling

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This study investigates the hypothesis that site characteristics and flock size influence the sex ratios of wintering ducks by examining three species: the Mallard (*Anas platyrhynchos*), the Goldeneye (*Bucephala clangula*), and the Long-tailed Duck (*Clangula hyemalis*) in the Gulf of Gdańsk, southern Baltic. Birds were counted in mid-January along approximately 160 km of shoreline in the western part of the Gulf of Gdańsk and the estuarine sections of the Vistula River on the southern Baltic coast. Only flocks in which the sex of all individuals was identified were included in the analysis. The sex ratios of the three study species varied across the five habitat types within the study area but did not vary with species-specific flock size. In Mallards the lowest proportion of males was recorded along the open seacoast and municipal beach, suggesting that these areas are primarily occupied by paired birds. The higher proportion of males at other sites is likely due to the shift of unpaired individuals to these locations, where the overall number of this species is the highest. In the Goldeneye the highest percentage of females was observed in the most sheltered areas, while the lowest percentage, alongside low individual numbers, occurred along the open seacoast. These patterns suggest that Goldeneye density and sex ratio are influenced by female tolerance to adverse weather conditions, as this species shows the greatest size difference between males and females among the species studied. Long-tailed Ducks exhibited a more uniform sex ratio across the study area, likely due to their frequent movements to access areas with abundant food resources. This study highlights spatial variations in duck sex ratios within a single water body and underscores the need for large scale sampling to obtain representative sex ratio estimates.

1. Introduction

The sex ratio often varies temporally and spatially in bird populations (*e.g.* Nichols & Haramis 1980, Meissner & Krupa 2017, Brides *et al.* 2017, Fox *et al.* 2018) and is a crucial component of population structure, as they are closely related to demography, behaviour, and population dynamics (Donald 2007, Lee *et al.* 2011, Székely *et al.* 2014, Larsson 2022). Hence, adult sex ratios can provide useful information on population structure and potential differences in survival rates of males and females (Donald 2007). For many bird populations, sex ratios differ from equilibrium and are mostly biased towards males (*e.g.* Even *et al.* 2001, Kosztolányi *et al.* 2011, Brides *et al.* 2017, Serrano-Davies *et al.* 2022, but see: Jaatinen *et al.* 2010, Grieves *et al.* 2024). Skewed sex ratios in a species may arise from various factors, including unequal sex ratios at fertilization or differences in sex-specific mortality rates among juveniles and adults. However, sex-specific adult mortality is the most significant predictor of the adult sex ratio (Székely *et al.* 2014).

The duck species studied in this context exhibit balanced sex ratios both as embryos and at the hatching stage (Blums & Mednis 1996). However, the sex ratio among adult ducks in the temperate zone is biased towards males in all the studied species (*e.g.* Campbell 1977, Nichols & Haramis 1980, Larsson 2022, Wood *et al.* 2021, Meissner & Witkowska 2023). Sex difference in post-fledging survival rates is the main factor responsible for skewed adult sex ratio, because in ducks only females participate in incubation and chick-rearing and are therefore more vulnerable to predator pressure during breeding (Bellebaum & Mädlow 2015, Lehikoinen *et al.* 2018, Wood *et al.* 2021).

An unbalanced sex ratio may have consequences on pairing behaviour. A low number of females forces very early pairing. By early pairing females gain increased foraging efficiency and survival due to male defence and vigilance, while males benefit from increased mate acquisition and improved female condition (Rodway 2007). That is why, in Northern Hemisphere ducks, a pair bond is established in autumn or early winter, and the male must remain close to his partner and actively defend her from other males until insemination occurs and the female begins incubation (Cramp & Simmons 1977). Remaining, unpaired, males cause the male-biased sex ratio, which in winter period may vary between habitats and sites on a local (Pounder 1976, Campbell 1977, Meissner & Witkowska 2023), regional (Nilsson 1976, Rodway *et al.* 2015, Larsson 2022) and continental scale (Carbone & Owen 1995, Brides *et al.* 2017). In local breeding populations, male-skewed sex ratios are likely to affect critical demographic rates such as breeding success, particularly in species experiencing a long-term decline in the proportion of females (Pöysä *et al.* 2019, Homolková *et al.* 2024). Moreover, trends in sex ratios at individual sites may not reflect patterns observed at larger spatial scales, as demonstrated in the Common Pochard (*Aythya ferina*) (Brides *et al.* 2017, Frew *et al.* 2018). Therefore, extensive monitoring is necessary to record the proportion of males and females for an accurate assessment of the population's structure.

Among other factors, a significant difference in body mass between male and female ducks may influence the sex ratio observed in wintering populations at a given site. Birds maintain some of the highest body temperatures among animals, relying on internal metabolic heat production to offset heat loss in cold environments (Ruben 1996). Moreover, mass-specific energy expenditure is significantly and negatively associated with body mass (Furness & Speakman 2008). Consequently, energy requirements for basic maintenance increase as body size decreases (Kendeigh 1970). Therefore, females, which are smaller than males, have a lower physiological tolerance to low temperatures and are especially susceptible to periods of harsh weather and food shortage (Nichols & Haramis 1980, Jorde *et al.* 1984, Meissner & Markowska, 2009). Therefore, female ducks tend to prefer moderate winter climates in temperate zones, as they require relatively more energy for daily survival (Sayler & Afton 1981). As a result, higher proportion of females was observed in places well protected against wind and with lower susceptibility to waves (Nilsson 1970a, Nichols & Haramis 1980, Woolington 1993). These size differences between males and females also have an impact on differential migration of sexes, where females winter further south in milder climate condition than males (Carbone & Owen 1995, Evans & Day 2001). Moreover, males prefer to winter near the breeding grounds, but their larger size and social dominance over females force the latter to winter further south (Nichols & Haramis 1980, Hepp & Hair 1984, Carbone & Owen 1995). There is also a hypothesis that, in some duck species, the sexes have different flocking tendencies, with males or females being more common in larger flocks or in areas with higher conspecific abundance (Nilsson 1970a, Owen & Dix 1986, Kestenholtz 1990). However, it was not fully confirmed in other studies (Woolington 1993, Söderholm 2003, Rodway 2006, Meissner & Witkowska 2023).

This study aimed to test the hypothesis that the sex ratio in wintering ducks is influenced by site characteristics and flock size. We examined three species differing in size and habitat requirements. The Mallard (*Anas platyrhynchos*) is an omnivorous dabbling duck adapted to an extremely wide range of habitats. In winter, it forages mostly on various plants and, to a lesser extent, aquatic invertebrates (Delnicki & Reinecke 1986, Combs & Fredrickson 1990, Dabbert & Martin 2000). It is the largest species among those compared in this study and winters in large numbers across Europe, including in urbanized areas (Cramp & Simmons 1977, Figley & VanDruff 1982, Meissner *et al.* 2015, Wetlands International 2025). The mean body mass of male Mallards is about 1150 g, while that of females is approximately 1000 g (Cramp & Simmons 1977). Thus, males are about 14% heavier than females. The Goldeneye (*Bucephala clangula*) is smaller than the Mallard, with male body mass around 1050 g and female body mass about 730 g (Cramp & Simmons 1977). This represents the largest sex-based difference in body mass among the species studied, with males being approximately 42% heavier than females. The Goldeneye belongs to the diving ducks, obtaining food from the bottom of waterbodies. Its main prey in winter includes molluscs, crustaceans, and polychaetes in various proportions (Cramp & Simmons 1977, Custer & Custer 1996, Bourget *et al.* 2007). The Goldeneye winters in large numbers in Europe, primarily in freshwater or brackish habitats, but also in coastal areas (Cramp & Simmons 1977, Wetlands International 2025). The Long-tailed Duck (*Clangula hyemalis*), another diving duck, is smaller than the Goldeneye, with male body mass around 780 g and female body mass about 700 g (Cramp & Simmons 1977). Thus, males are approximately 12% heavier than females, a difference similar to that observed in the Mallard. It spends winter mainly in offshore marine habitats, feeding mainly on bivalves as well as crustaceans, fish, and fish eggs (Skov & Kube 1996, Jamieson *et al.* 2001, Forni *et al.* 2022). The Baltic Sea is its main wintering site in Europe (Skov *et al.* 2011, Wetlands International 2025).

2. Materials and methods

2.1. Bird counts

The study was conducted in mid-January from 1988 to 1995 in the western part of the Gulf of Gdańsk and the estuarine sections of the Vistula River (southern Baltic coast) (Fig. 1). Birds were counted in January during the weekend closest to the middle of the month, along approximately 160 km of shoreline, with each individual or group of birds recorded separately. Only flocks in which the sex of all birds was identified were

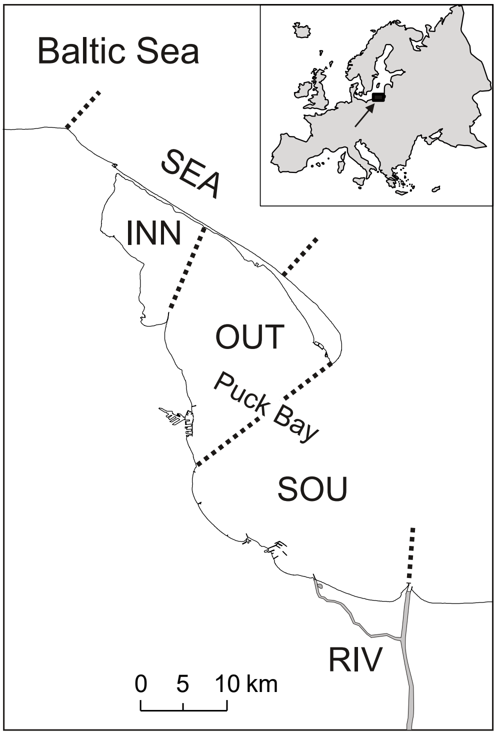

Fig. 1. Study area. The boundaries between the distinguished parts of the study area (see Table 1) are shown with dotted lines.

included in the study, representing about 50% of all flocks recorded. Each person counting birds was assigned a coastal section of 10 to 16 kilometres to walk. The boundaries between sections were placed at natural divisions along the coastline, and it was assumed that the likelihood of counting the same bird flocks twice was low and did not significantly affect the quality of the data collected. Single birds were omitted from the analyses. There were 520 singleton Mallards (males exclusively), 160 Goldeneyes (98 males and 62 females), and 1110 Long-tailed Ducks (893 males and 217 females). These accounted for 2.1%, 0.8%, and 1.3% of all birds of these species, respectively. The total number of flocks included in analyses was 894 in Mallard, 1766 in Goldeneye and 1322 in Long-tailed Duck.

Not all first winter Goldeneye males obtain adult plumage in January and some of them may be still indistinguishable from females, especially when observing in large flocks from a large distance. In Long-tailed Duck first-year males in January resemble adults, while in Mallards the difference in plumages between first-year and adult males are very subtle and in these two species young males are easy distinguishable from females (Cramp & Simmons 1977).

2.2. Study area

The western part of the Gulf of Gdańsk is a water body with diverse environmental conditions. It includes the open sea, exposed to winds, and Puck Bay, which is shallower and sheltered from winds, particularly those blowing from the westerly sector, which account for 40–50% of all winds in the region, and even more during the winter (Majewski 1990, Cieślikiewicz & Cupiał 2024). The wind waves are much higher in the areas exposed to the wind, *i.e.* on the coast of the open sea and along the southern coast of the Puck Bay. Whereas, in the inner and outer parts of the Bay of Puck, the size of the waves is much smaller (Cieślikiewicz *et al.* 2017). The inner part of the Puck Bay is the shallowest part of the study area and freezes over most quickly and to the greatest extent, while the outer part is only partially covered by ice during harsh winters (Korzeniewski 1993). In the seasons under study, winter weather in January was mild and only in 1993 partial icing occurred on the inner and, to a lesser extent, outer parts of the Bay of Puck and parts of the estuarine section of the Vistula. In January 1993 waterbirds stayed numerously in all parts of the study area, hence it is assumed that differences in ice cover had no influence on sex ratio in bird flocks.

Five parts of the study area were identified based on wind cover, susceptibility to icing, depth, slope steepness, bottom characteristics, and phyto- and zoobenthos abundance (Herra & Wiktor 1985, Korzeniewski 1993, Kruk-Dowgiałło 1998, Gic-Grusza *et al.* 2009, Dyrcz 2017, Badur & Cieślikiewicz 2018, Janas *et al.* 2019, Sokołowski *et al.* 2021, Miernik *et al.* 2023) (Table 1, Fig. 1). This division corresponds to the ecosystem units of the Gulf of Gdansk based on the morphology and dynamics of water masses that determine the living conditions of bottom vegetation and fauna as well as the environmental quality of coastal water masses (Andrulewicz *et al.* 2004, Błeńska & Osowiecki 2015). The boundary between inner and outer part of the Puck Bay is widely used in other studies, while its southern part is characterised by greater depths, the absence of reed beds and the presence of urban beaches where people feed the birds intensively (Korzeniewski 1993, Meissner & Ciopcińska 2007). Due to the low number of Long-tailed Ducks in the inner part of the Puck Bay, the inner and outer parts were combined in the analyses for this species.

2.3. Data analysis

The mean bird number per 1 km of coastline was used to determine the part of the study area of greatest importance for each of the three species. It was assumed that gregarious behaviour of ducks (Owen & Black 1990) combined with a heterogeneous availability of resources leads to a concentration of individuals on sites with the best quality (Loring *et al.* 2013, Pap *et al.* 2013, Cervencl *et al.* 2015). To compare densities of studied species between parts of the study area, the Kruskal-Wallis test was used with post-hoc Dunn test (Zar 2010). Using a Generalized Linear

Table 1. Characteristics of the study area parts distinguished in this study.

Name and abbreviation	Midpoint coordinates	Total length of the coast	Characteristics
Open sea (SEA)	54.760 N 18.522 E	31.6 km	Fully exposed to winds. Highest water waves in windy conditions. Sandy bottom. Lack of coastal plants and reedbeds. About 11 km with rows of piles overgrown with periphyton. Depth increasing rapidly with distance from shore. Benthic fauna (molluscs, crustaceans and polychaetes) in moderate densities. Very low number macrophytes.
Inner part of the Puck Bay (INN)	54.723 N 18.488 E	34.3 km	The shallowest part of the study area. Good wind protection. Waving very low. Usually at least partially iced over in moderate winter. Sandy bottom. Very high densities of zoo- and phytobentos. Coast overgrown by plants and often by reedbeds.
Outer part of the Puck Bay (OUT)	54.627 N 18.646 E	28.0 km	Moderately protected from western and northern winds. Waving in winter usually low. Moderate waving only for eastern wind. Bottom mainly sandy with some areas of mud and coarse sediment. High spatial variability of zoo- and phytobenthos densities. Sandy coasts with low number of reedbeds.
Southern part of the Puck Bay (SOU)	54.420 N 18.717 E	36.1 km	Fully exposed only to north-eastern and eastern winds. Sandy bottom. Lack of coastal plants and reedbeds. Depth increasing slowly with distance from shore. About 15 km of municipal beaches, where people regularly feed birds. High densities of benthic fauna. Low and moderate densities of macrophytes.
Riverine habitats (RIV)	54.310 N 18.932 E	27.0 km	Shallow (mainly 3-4 m deep) estuarine sections of the Vistula River and a small coastal lake. Banks are vegetated and partially with reedbeds. Muddy and sandy bottom. Good wind protection. Waving very low. No recent data on zoo- and phytobentos. Very high number of wintering bentophages suggests a high density of zoobenthos.

Model (GLM) (McCullagh & Nelder 1989), the proportion of males (response variable) was modelled as a function of part of the study area (categorical explanatory variable) and flock size (continuous variable) in each of the three species separately. Preliminary analyses with the use of ‘performance’ R package (Lüdecke *et al.* 2021) revealed a significant deviation from normality of residuals in all three models. As proportion of males shows only positive values and their distribution was right-skewed, we employed a GLM with a gamma error distribution and a logarithmic link function (Dunn & Smyth 2018), which brought the distribution of the residuals close to a normal distribution. Performance of obtained models were assessed using the ‘performance’ R package (Lüdecke *et al.* 2021). In the models concerning Goldeneye and Long-tailed Duck, the variance inflation factor (VIF) was below 2.0, indicating low multicollinearity. In contrast, for the Mallard, the VIF exceeded 100, revealing extremely high collinearity, with variance over 100 times greater than in the case of orthogonal predictors (Hair *et al.* 1995). After excluding the smallest flocks of two and three birds, the VIF value dropped to 7, which is considered acceptable, as values below 10 are generally not regarded as problematic for multicollinearity (Dormann *et al.* 2012). As a result of this exclusion, the number of Mallard flocks included in the analysis decreased to 630. In all models there were no influential observations and no deviations from linearity. Only in the case of the Goldeneye and Long-tailed Duck was slight heterogeneity of variances observed, which is typically not problematic for GLMs, especially when sample sizes are sufficient (Hair *et al.* 1995). Therefore, it was assumed that there are no major deviations from the assumptions of the linear model that could affect obtained results.

The open sea coastal area is fully exposed to winds from the prevailing directions in winter and characterized by the highest waves (Table 1) In some duck species the proportion of males wintering in such conditions is expected to be high (Nilsson 1970a, 1976, Campbell 1977). Hence, when determining the effect of part of the study area on proportion of males, the open sea was set as the baseline for comparisons. We performed post-hoc comparisons using linear contrasts with the package 'emmeans' (Length 2021). The statistical significance of observed differences was evaluated considering P < 0.05. All analyses were performed in R 4.4.2. Differences in body mass between males and females were calculated using a weighted average of the data provided by Cramp and Simmons (1977), taking into account differences in bird numbers between different samples.

3. Results

The highest number of Mallards was recorded in outer and inner parts of the Puck Bay and in the riverine habitats. Their densities in southern part of the Puck Bay and in the seacoast were significantly lower (Fig. 2). The Goldeneye also revealed lower densities in these two parts of the study area, but the highest number in the inner part of the Puck Bay and in riverine habitats (Fig. 2). In contrast to these two species, Long-tailed Duck densities were highest along the open seacoast and in the riverine habitats with significantly lower numbers in Puck Bay (Fig. 2).

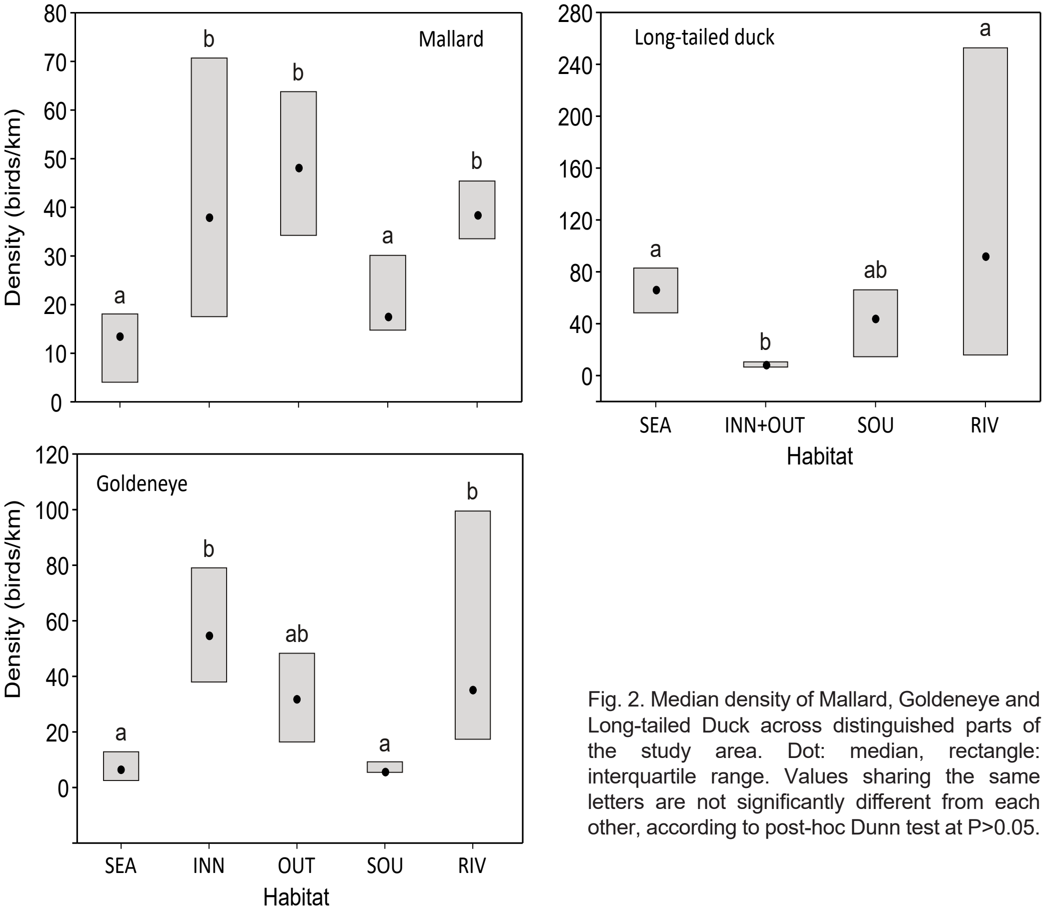

Fig. 2. Median density of Mallard, Goldeneye and Long-tailed Duck across distinguished parts of the study area. Dot: median, rectangle: interquartile range. Values sharing the same letters are not significantly different from each other, according to post-hoc Dunn test at P>0.05.

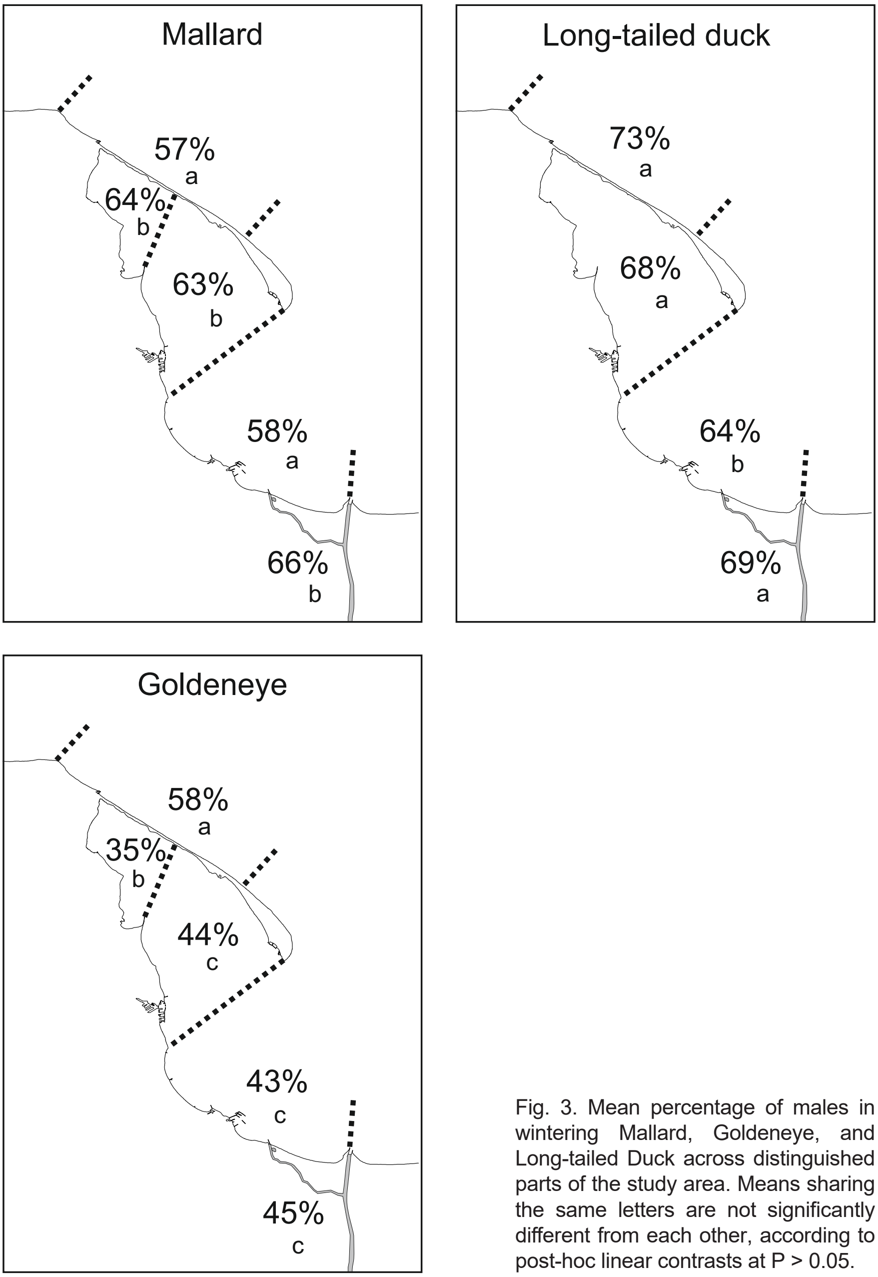

Fig. 3. Mean percentage of males in wintering Mallard, Goldeneye, and Long-tailed Duck across distinguished parts of the study area. Means sharing the same letters are not significantly different from each other, according to post-hoc linear contrasts at $P > 0.05$.

Conspicuous variability of mean densities of Goldeneye and Long-tailed Duck in riverine habitats is due to the appearance of very high numbers of these species only in the last four years of the survey.

The proportion of males in all three species differed significantly between distinguished parts of the study area (Tables S1, S2, S3). In Mallards, the percentage of males was highest in the estuarine section of the Vistula River and in the inner and outer parts of the Puck Bay. In the open seacoast and the southern part of Puck Bay, the percentage was significantly lower (Fig. 3). Contrary to the Mallard, the proportion of males in Goldeneyes reached its maximum in the open sea coastal section fully exposed to winds, while it was lowest in the inner part of Puck Bay. In other parts, the proportion of males in this species had intermediate values (Fig. 3). In Long-tailed Ducks, the proportion of males in flocks was more evenly distributed across the study area, with a significantly lower value only in the southern part of Puck Bay (Fig. 3). For all three species, there was no significant relationship between the proportion of males in a flock and flock size (Tables S1, S2, S3).

4. Discussion

The most of ducks from temperate zone show seasonal monogamy and male-biased sex ratio (Nilsson 1970a, Rohwer & Anderson 1988). Thus, a large number of males have little opportunity for reproduction. The pairing process occurs very early and in Mallard almost all females are paired in January (Johnson & Rohwer 1998, Jonsson & Gardarsson 2001). Once a pair bond is established, paired males remain close to their mates, engaging in mate guarding (Goodburn 1984, Meissner & Markowska 2009). Male attendance offers paired females benefits of increased social status, better access to food and less harassment from conspecifics, whereas males' benefit is mate acquisition (Ashcroft 1976, Hepp & Hair 1984, Rohwer & Anderson 1988). The lowest proportion of male Mallards along the section of the open seacoast and the southern part of Puck Bay suggests that this area is mainly occupied by paired birds. Paired males achieve a higher hierarchical position in the flock than unpaired ones (Bossema & Roemers 1985) and show a tendency to remain at the wintering site during deteriorating weather conditions, while unpaired males left these sites, resulting in a less skewed sex ratio (Meissner & Witkowska 2023). Strong aggression by paired males towards unpaired ones (Hepp and Hair 1984, Johnson & Rohwer, 1998, Schummer *et al.* 2020) results in the latter being forced out of areas where females with their mates are present (Meissner & Witkowska 2023). Hence, a shift in the occurrence of unpaired males toward sites offering better overwintering conditions seems a likely explanation for their higher proportion among Mallards observed in the inner and outer Puck Bay and the estuarine section of the Vistula River, where the number of wintering birds of this species was significantly higher than in two other areas. Females remaining with their partners in open sea suboptimal habitat experience less pressure from conspecifics in accessing food in the form of periphyton overgrowing rows of wooden piles (Table 1). In the southern part of the Puck Bay the proportion of males was also low, as it was in open sea coast. Mallards concentrated here mainly along municipal beach, where 89% of all birds of this species observed in this part of the study area were noted. Along the municipal beach, people intensively feed waterbirds in winter and Mallard shows strong tendency to stay in large number in such places due to additional food resources available (Avilova & Eremkin 2001, Meissner *et al.* 2015, Witkowska *et al.* 2024). Exploiting abundant anthropogenic food resources may be profitable especially for females, which are smaller than males by about 14% of their body mass and thus are more sensitive to low temperatures in winter (Pattenden & Boag 1989, Jónsson 2010). Therefore, females remained here together with males they paired with, resulting in a lower proportion of males at such sites. This is in line with the study conducted in an urbanized area documenting the sex-dependent response of Mallards to temperature changes during the winter period. In severe weather conditions, females remained with their paired mates, whereas unpaired males possibly left the town (Meissner & Witkowska 2023).

The inclusion of groups of two and three birds in the GLM analysis resulted in very high collinearity in the model. Groups of two Mallards consisted of 87% paired birds, with the remaining 13% being two males. In groups of three individuals, the majority (81%) comprised two males and one female, while all other cases consisted of three males. This is due to the typical pairing behaviour of this species (Cramp & Simmons 1977). The GLM analysis, including groups of two and three birds and accounting for high collinearity, produced the same results, with the same significant differences between designated parts of the study area in the post-hoc test.

Among the three species studied, the difference in body mass between males and females was largest in the Goldeneye. Similar to another study on the sex ratio of this species (Campbell 1977), the lowest percentage of Goldeneye males was found in the inner Puck Bay, the area most sheltered from the predominant western and north-western winds. Wind speed is important in increasing physiological cold stress (Krishnan *et al.* 2023), so topographical features of the area surrounding a water body and prevailing wind patterns may contribute to differences in sex ratios at a site (Bennett & Bolen 1978, Krishnan *et al.* 2023). The proportion of males was intermediate in the rest of the Puck Bay and the estuary of the Vistula River, which are somewhat less sheltered from the winds. Along the open seacoast the percent of males was the highest together with low number of birds stayed there. Hence, the density and the sex ratio of Goldeneye reflect differences in tolerance towards adverse weather conditions of females. Especially since, in this species males are larger than females by 42% by body mass (Cramp & Simmons 1977). Therefore, the smaller and lighter Goldeneye females are predicted to select habitats with more moderate winter weather conditions (Campbell 1977, Sayler & Afton 1981), as they require relatively greater amounts of energy for existence and have lower resistance to food shortages during periods of low temperatures and long winter nights. However, in the Goldeneye, some first-year males may still be difficult to distinguish from females in January (Cramp & Simmons 1977). These young males, with no clearly visible signs of breeding plumage, remain unpaired, but their presence lowers the proportion of males in flocks. Nevertheless, the number of juvenile males wintering in northern latitudes seems to be rather low (Nilsson 1970a, Sayler & Afton 1981). Therefore, their presence may have only a minor influence on the obtained results.

In non-breeding period the Long-tailed Duck reveals strong preference to open seas habitats (Cramp & Simmons 1977). Therefore, its number was the lowest in inner and outer parts of the Puck Bay and the highest along the open seas coast, as the open sea areas gather the vast majority of wintering Long-tailed Ducks in the Baltic (Skov *et al.* 2011). The high numbers of birds of this species in the Vistula estuary is due to large flocks entering this part of the river at dawn and remaining there until dusk (authors' unpublished data). This behaviour of Long-tailed Ducks was observed only in last four years of the study and its cause is unknown, but these birds were observed diving frequently there, which suggests foraging. The sex ratio in the Long-tailed Duck is the most balanced among the species studied. Only in the Long-tailed Duck the percent share of males in the inner and outer parts of the Puck Bay was similar to open seacoast. Movements of Long-tailed Ducks over Hel Peninsula, between these parts of the study area, are observed quite frequently (authors' unpublished data). Whereas, in Vistula estuary Long-tailed Ducks stay only during daytime with large number of birds arriving in the morning and departing before night. It is likely that the small concentrations of this species outside the open sea are short-lived and involve males and females in similar proportions that are present in the open sea resulting in not significant differences in male proportions between these areas. Only along southern coast of the Puck Bay the proportion of males was significantly lower. The sexually-selected behaviour and the formation of large groupings in areas of abundant food may explain the differences in winter distribution of both sexes in wintering sea ducks, which was found in Harlequin Duck (*Histrionicus histrionicus*), a sea duck similar in size to Long-tailed Duck. In this species, unpaired birds were more likely to move to exploit sites with abundant food resources, where they obtained nutritional benefits and facilitated courtship and mate sampling (Rodway 2006). If such behaviour also applies to the Long-tailed Duck, it may explain the observed movements of birds between regions of the study area and only slight differences in the proportion of males in this species.

In each of the three species studied, flock size had no effect on the observed sex ratio. However, the flock sizes used in the analyses exceeded 100 birds in only 8.5%, 3.5% and 2.3% of the Mallard, Goldeneye and Long-tailed Duck respectively, and the number of flocks above 300 individuals ranged in these species from three to seven. There is only one publication that demonstrated such a trend and included flocks of more than 1,000 individuals (Owen & Dix 1986), whereas another study, which also analysed flocks of this size, found no such relationship (Evans *et al.* 2001). Moreover, the sex ratio of ducks in large flocks is very difficult to determine, and the error in estimating the number of birds in flocks of approximately 1,000 individuals can be as high as 10% (Nilsson 1970a). Therefore, in our study, we avoided determining sex ratios in such large flocks. Thus, on the one hand, the variability in flock size in our study may not be sufficient to demonstrate a possible effect of flock size on sex ratio. On the other hand, however, sex ratios in duck flocks may be strongly influenced by the habitat conditions in which the birds stay than by flock size. In general, more smaller duck females than males has been observed in shallower and more calm water bodies (Nilsson 1970a, Campbell 1977, Sayler & Afton 1981, this study), which was related to larger food requirements of the females making it necessary for them to feed longer or more frequently than the males (Nilsson 1970b, Kaminski & Prince 1981, Munday & Rose 2022). Therefore, the marked differences in sex ratios between different parts of the study area may also reflect local differences in food resources.

Intersexual competition for food has been identified as an important factor influencing sex ratios in duck groupings during winter (*e.g.* Hepp & Hair 1984, Alexander 1987, Choudhury & Black 1991). However, by January, all Mallard females and the majority of female Goldeneyes and Long-tailed Ducks are paired and protected by their mates from aggression by other individuals (*op. cit.*). Therefore, the sex ratio of ducks at a given site seems to be a result of the interaction of various ecological and behavioural traits that compromise against different selection pressures, such as sexual segregation within habitats and intersexual competition for food (Nilsson 1970a, Campbell 1977, Sayler & Afton 1981, Duncan & Marquiss 1993).

The sex ratio at breeding and wintering sites is a fundamental demographic parameter that provides valuable information on the differential survival rates of the sexes. This offers important insights into population dynamics and can indicate demographic factors contributing to population decline (Donald 2007, Brides *et al.* 2017). However, differences in sex ratios between closely located areas of the study site also have implications for planning further research on the sex structure of wintering ducks and highlight the need for large-scale sampling to obtain representative estimates of the sex ratio for a given species as it was shown for Common Pochard (Brides *et al.* 2017, Frew *et al.* 2018). Furthermore, in such surveys, bird counts should be conducted across a variety of habitats, including areas sheltered from the wind as well as those exposed to stronger wave action, since this factor appears to significantly influence local differences in sex ratio. In species such as the Mallard, which often rely on food provided by humans, the sex ratio may differ between sites where birds are fed and sites where they are not. This factor should therefore also be taken into account.

Paikallinen vaihtelu talvehtivien sorsalintujen sukupuolijakaumassa kolmella lajilla: Laajamittaisen havainnoinnin tarve

Tässä tutkimuksessa tarkastellaan hypoteesia, jonka mukaan alueen ominaisuudet ja parven koko vaikuttavat talvehtivien sorsalintujen sukupuolijakaumaan. Tutkittavana oli kolme lajia: sinisorsa (*Anas platyrhynchos*), telkkä (*Bucephala clangula*) ja alli (*Clangula hyemalis*) Gdańskinlahdella, eteläisellä Itämerellä. Linnut laskettiin tammikuun puolivälissä noin 160 km:n pituisella rantaviivalla Gdańskinlahden länsiosassa ja Veikseljoen suistoalueilla eteläisellä Itämeren rannikolla. Analyysiin sisällytettiin vain ne parvet, joissa kaikkien yksilöiden sukupuoli voitiin määrittää. Kolmen tutkitun lajin sukupuolijakaumat vaihtelivat tutkimusalueen viiden eri elinympäristötyypin välillä, mutta eivät lajikohtaisen parven koon mukaan. Sinisorsalla pienin koiraiden osuus havaittiin avoimella merenrannalla ja kaupunkirannalla, mikä viittaa siihen, että nämä ovat pääasiassa pariutuneiden lintujen alueita. Muiden alueiden suurempi koiraiden osuus johtuu todennäköisesti pariutumattomien yksilöiden siirtymisestä näille alueille, joissa lajin kokonaismäärä on suurin. Telkällä suurin naaraiden osuus havaittiin suojaisimmilla alueilla, kun taas pienin osuus, yhdessä yksilömäärän kanssa, esiintyi avoimella merenrannalla. Nämä mallit viittaavat siihen, että telkän tiheys ja sukupuolijakauma liittyvät naaraiden sietokykyyn epäsuotuisia sääolosuhteita kohtaan, sillä tutkituista lajeista telkällä on suurin kokoero koiraiden ja naaraiden välillä. Allilla sukupuolijakauma oli tasaisempi koko tutkimusalueella, mikä johtuu todennäköisesti lajin aktiivisesta liikkumisesta alueille, joilla oli runsaasti ravintoa. Tutkimus korostaa sorsalintujen sukupuolijakauman alueellista vaihtelua yhden vesialueen sisällä ja osoittaa, että edustavien sukupuolijakauma-arvioiden saamiseksi tarvitaan laajamittaista havainnointia.

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References

Alexander, W.C. 1987: Aggressive behavior of wintering diving ducks (Aythyini). — Wilson Bulletin 99: 38–49

Andrulewicz, E., Kruk-Dowgiałło, L. & Osowiecki, A. 2004: An expert judgement approach to designating ecosystem typology and assessing the health of Gulf of Gdansk. — In Managing the Baltic Sea. Coastline Reports 2: 53–61 (ed. Schernewski, G. & Löser, N.). EUCC, Rostock.

Ashcroft, R.E. 1976: A function of the pairbond in the Common Eider. — Wildfowl 27: 101–105.

Avilova, K.V., Eremkin, G.S. 2001: Waterfowl wintering in Moscow (1985-1999): dependence on air temperatures and the prosperity of the human population. — Acta Ornithologica 36: 65–71.

Badur, J. & Cieślikiewicz, W. 2018: Spatial variability of long-term trends in significant wave height over the Gulf of Gdansk using System Identification techniques. — Oceanological and Hydrobiological Studies 47: 190 –201. https://doi.org/10.1515/ohs-2018-0018.

Bellebaum, J., & Mädlow, W. 2015: Survival explains sex ratio in an introduced Mandarin Duck *Aix galericulata* population. — Ardea 103: 183–187. https://doi.org/10.5253/arde.v103i2.a7.

Bennett, J.W. & Bolen, E.G. 1978: Stress response in wintering Green-winged Teal. — Journal of Wildlife Management 42: 87–86. https://doi.org/10.2307/3800692

Blums, P. & Mednis, A. 1996: Secondary sex ratio in Anatinae. — Auk 113, 505–511. https://doi.org/10.2307/4088920

Błeńska, M. & Osowiecki, A. 2015: Biotic typology of Polish marine areas based on bottom macrofauna communities. — Bulletin of the Maritime Institute in Gdańsk 30: 167–173. https://doi.org/10.5604/12307424.1186449

Bossema, I. & Roemers, E. 1985: Mating strategy, including mate choice in Mallards. — Ardea 73: 147–157.

Bourget, D., Savard, J.-P.L. & Guillemette, M. 2007: Distribution, diet and dive behavior of Barrow's and Common Goldeneyes during spring and autumn in the St. Lawrence Estuary. — Waterbirds 30: 230–240. https://doi.org/10.1675/1524-4695(2007)30[230:ddadbo]2.0.co;2

Brides, K., Wood, K.A., Hearn, R.D. & Fijen, T.P.M. 2017: Changes in the sex ratio of the common pochard *Aythya ferina* in Europe and North Africa. — Wildfowl 67: 100–112.

Campbell, L.H. 1977: Local variations in the proportion of adult males in flocks of Goldeneye wintering in the Firth of Forth. — Wildfowl 28: 77–80.

Carbone, C., Owen, M. 1995: Differential migration of the sexes of Pochard *Aythya ferina*: results from a European survey. — Wildfowl 46: 99–108.

Cervencl, A., Troost, K., Dijkman, E., de Jong, M., Smit, C.J., Leopold, M.F. & Ens, B.J. 2015: Distribution of wintering Common Eider *Somateria mollissima* in the Dutch Wadden Sea in relation to available food stocks. — Marine Biology 162: 153–168. https://doi.org/10.1007/s00227-014-2594-4

Choudhury, S., Black, J.M. 1991: Testing the behavioural dominance and dispersal hypothesis in Pochard. — Ornis Scandinavica 22: 155–159. https://doi.org/10.2307/3676546

Cieślikiewicz, W. & Cupiał, A. 2024: Long-term statistics of atmospheric conditions over the Baltic Sea and meteorological features related to wind wave extremes in the Gulf of Gdańsk. — Oceanologia 66: 180–195. https://doi.org/10.1016/j.oceano.2023.10.002

Cieślikiewicz, W., Dudkowska, A., Gic-Grusza, G. & Jędrasik, J. 2017: Extreme bottom velocities induced by wind wave and currents in the Gulf of Gdańsk. — Ocean Dynamics 67: 1461–1480. https://doi.org/10.1016/10.1007/s10236-017-1098-4

Combs, D.L. & Fredrickson, L.H. 1990: Foods used by male mallards wintering in southeastern Missouri. — Journal of Wildlife Management 60: 603–610. https://doi.org/10.2307/3802078

Cramp, S., Simmons, K.E.L. (ed.) 1977: Handbook of the birds of Europe the Middle East and North Africa. Vol. 1. — Oxford University Press, Oxford.

Custer, C.M. & Custer, T.W. 1996: Food habits of diving ducks in the Great Lakes after the Zebra Mussel invasions. — Journal of Field Ornithology 67: 86–99. https://www.jstor.org/stable/4514086

Dabbert, C.B. & Martin, T.E. 2000: Diet of mallards wintering in Greentree Reservoirs in southeastern Arkansas. — Journal of Field Ornithology 71: 423–428. https://doi.org/10.1648/0273-8570-71.3.423

Delnicki, D. & Reinecke, K.J. 1986: Mid-winter food use and body weights of Mallards and Wood Ducks in Mississippi. — Journal of Wildlife Management 50: 43–51. https://doi.org/10.2307/3801486

Donald, P.F. 2007: Adult sex ratios in wild bird populations. — Ibis 149: 671–692. https://doi.org/10.1111/j.1474-919x.2007.00724.x

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. 2013: Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. — Ecography 36: 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Duncan, K. & Marquiss, M. 1993: The sex/age ratio, diving behaviour and habitat use of Goldeneye *Bucephala clangula* wintering in northeast Scotland. — Wildfowl 44: 111–120.

Dunn, P.K. & Smyth, G.K. 2018: Generalized Linear Models with examples in R. — Springer New York. https://doi.org/10.1007/978-1-4419-0118-7

Dyrcz, C. 2017: Analysis of ice conditions in the Baltic Sea and in the Puck Bay. — Scientific Journal of Polish Naval Academy 58: 13–41. https://doi.org/10.5604/01.3001.0010.6581

Gic-Grusza, G., Kryla-Staszewska, L., Urbański, J., Warzocha, J. & Węsławski, J.M. (ed.) 2009: Atlas of Polish marine area bottom habitats: Environmental valorization of marine habitats. — Broker-Innowacji, Gdynia.

Grieves, L.A., Hing, S., Tabh, J. & Quinn, J.S. 2024: Offspring sex ratio in a communal breeding bird is male-biased when pre-breeding rainfall is low. — Journal of Avian Biology e03262. https://doi.org/10.1111/jav.03262

Evans, D.M. & Day, K.R. 2001: Migration patterns and sex ratios of diving ducks wintering in Northern Ireland with specific reference to Lough Neagh. — Ringing & Migration 20: 358–363. https://doi.org/10.1080/03078698.2001.9674263

Even, JG., Clarke, R.H., Moysey, E., Boulton, R.L., Crozier, R.H. & Clarke, M.F. 2001: Primary sex ratio bias in an endangered cooperatively breeding bird, the black-eared miner, and its implications for conservation. — Biological Conservation 101: 137–145. https://doi.org/10.1016/S0006-3207(01)00022-2

Figley, W. K. & VanDruff, L.W. 1982: The ecology of urban Mallards. — Wildlife Monographs 81: 3–39.

Forni, P., Morkūnas, J. & Daunys, D. 2022: Response of Long-tailed Duck (*Clangula hyemalis*) to the change in the main prey availability in its Baltic wintering ground. — Animals 12: 355. https://doi.org/10.3390/ani12030355

Fox, A.D. & Cristensen, T. K. 2018: Could falling female sex ratios among first-winter northwest European duck populations contribute to skewed adult sex ratios and overall population declines? — Ibis 160: 929–935. https://doi.org/10.1111/ibi.12649

Frew, R.T., Brides, K., Clare, T., MacLean, L., Rigby, D., Tomlinson, C.G. & Wood, K.A. 2018: Temporal changes in the sex ratio of the Common Pochard *Aythya ferina* compared to four other duck species at Martin Mere, Lancashire, UK. — Wildfowl 68: 140–154.

Furness, L.J. & Speakman, J.R. 2008: Energetics and longevity in birds. Age 30: 75–87. https://doi.org/

10.1007/s11357-008-9054-3

Goodburn, S.F. 1984: Mate guarding in the Mallard *Anas platyrhynchos*. — Ornis Scandinavica 15: 261–265. https://doi.org/10.2307/3675935

Hair, J.F., Anderson, R.E., Tatham, R.L. & Black, W.C. 1995: Multivariate data analysis. — Prentice-Hall, Englewood Cliffs, NJ.

Hepp, G.R. & Hair, J.D. 1984: Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. — Condor 86: 251–257. https://doi.org/10.2307/1366992

Herra, T. & Wiktor, K. 1985: Composition and distribution of bottom fauna in coastal zone of the Gulf of Gdańsk proper. — Studia i Materialy Oceanologiczne 46: 114–142.

Homolková, M., Musil, P., Pavón-Jordán, D., Gajdošová, D., Musilová, Z., Neužilová, Š., Zouhar, J. 2024. Changes in the adult sex ratio of six duck species breeding populations over two decades. — Avian Research 15: 100187. https://doi.org/10.1016/j.avrs.2024.100187

Jaatinen, K., Lehikoinen, A. & Lank, DB. 2010: Female-biased sex ratios and the proportion of cryptic male morphs of migrant juvenile Ruffs (*Philomachus pugnax*) in Finland. — Ornis Fennica 87: 125–134. https://doi.org/10.51812/of.133751

Jamieson, S.E., Robertson, G.J. & Grant Gilchrist, H. 2001: Autumn and winter diet of Long-tailed Duck in the Belcher Islands, Nunavut, Canada. — Waterbirds 24: 129–132. https://doi.org/10.2307/1522253

Janas, U., Burska, D., Kendzierska, H., Pryputniewicz-Flis, D. & Łukawska-Matuszewska, K. 2019: Importance of benthic macrofauna and coastal biotopes for ecosystem functioning – Oxygen and nutrient fluxes in the coastal zone. — Estuarine, Coastal and Shelf Science 225: 106238. https://doi.org/10.1016/j.ecss.2019.05.020

Johnson, W.P. & Rohwer, F.C. 1998: Pairing chronology and agonistic behaviors of wintering Green-winged Teal and Mallards. — Wilson Bulletin 110: 311–315. http://www.jstor.org/stable/4163954

Jonsson, J.E. & Gardarsson, A. 2001: Pair formation in relation to climate: mallard, Eurasian wigeon and Eurasian teal wintering in Iceland. — Wildfowl 52: 55–68.

Jorde, D.G., Krapu, G.L., Crawford, R.D. & Hay, M.A. 1984: Effects of weather on habitat selection and behavior of Mallards wintering in Nebraska. — Condor 86: 258–265. https://doi.org/10.2307/1366993

Jónsson, J.E. 2010: Sex ratios of Eurasian wigeon, mallard and common eider in Iceland. — Náttúrufræðingurinn 79: 118–124. (in Icelandic with English summary)

Kaminski, R.M. & Prince, H.H. 1981: Dabbling duck activity and foraging responses to aquatic macroinvertebrates. — Auk 98: 115–126. https://doi.org/10.2307/3807868

Kendeigh S.C. 1970: Energy requirements for existence in relation to size of bird. — Condor 72: 60–65. https://doi.org/10.2307/1366475

Kestenholtz, M. 1990: Verteilungsmuster von Stock-, Reiher- und Tafelente, Gänsesäger und Blässhuhn im Winterhalbjahr am Sempachersee. — Ornithologische Beobachter 87: 131–145.

Kosztolányi, A., Barta, Z., Kupper, C. & Székely, T. 2011: Persistence of an extreme male-biased adult sex ratio in a natural population of polyandrous bird. — Journal of Evolutionary Biology 24: 1842–1846. https://doi.org/10.1111/j.1420-9101.2011.02305.x

Korzeniewski, K. 1993: The Puck Bay. — Foundation for the Development of the University of Gdańsk, Gdańsk. (in Polish)

Krishnan, G., Devaraj, C., Silpa, M.V. & Sejian, V. 2023: Thermoregulation in Birds. In Textbook of veterinary physiology (ed. Das, P.K., Sejian, V., Mukherjee, J. & Banerjee, D.). Springer, Singapore. https://doi.org/10.1007/978-981-19-9410-4_29

Kruk-Dowgiałło, L. 1998: Phytobenthos as an indicator of the state of environment of the Gulf of Gdańsk. — Oceanological Studies 4: 105–121.

Larsson, K. 2022: Age and sex ratios in the declining West Siberian/North European population of Long-tailed Duck wintering in the Baltic Sea: Implications for conservation. — Ornis Fennica 99: 117–131. https://doi.org/10.51812/of.113681

Lee, A.M., Sæther, B.E. & Engen, S. 2011: Demographic stochasticity, allee effects, and extinction: the influence of mating system and sex ratio. — American Naturalist 177: 301–313. https://doi.org/10.1086/658344

Lehikoinen, A., Christensen, T.K., Öst, M., Kilpi, M., Saurola, P. & Vattulainen, A. 2008: Large-scale change in the sex ratio of a declining eider *Somateria mollissima* population. — Wildlife Biology 14: 288–301. https://doi.org/10.29.81/0909-6396(2008)14[288:lcitsr]2.0.co;2

Lenth, R.V. 2021: emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.1. — https://cran.r-project.org/web/packages/emmeans/

index.html

Loring, P.H., Paton, P.W.C., McWilliams, S.R., McKinney, R.A. & Oviatt, C.A. 2013: Densities of wintering scoters in relation to benthic prey assemblages in a North Atlantic estuary. — Waterbirds 36, 144–155. https://doi.org/10.1675/063.036.0204

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P. & Makowski, D. 2021: performance: An R Package for Assessment, Comparison and Testing of Statistical Models. — Journal of Open Source Software 6: 3139. https://doi.org/10.21105/joss.03139

Majewski, A. (ed.) 1990: Gulf of Gdańsk. — Wydawnictwa Geologiczne, Warszawa. (in Polish)

McCullagh, P. & Nelder, J.A. 1989: Generalized Linear Models. — Chapman and Hall, London. https://doi.org/10.1007/978-1-4899-3242-6

Meissner, W., Ciopcińska, K. 2007: Behaviour of Mute Swans *Cygnus olor* wintering at a municipal beach in Gdynia, Poland. — Ornis Svecica 17: 148–153. https://doi.org/10.34080/os.v17.22685

Meissner, W. & Krupa, R. 2017: Sex-related differences in autumn migration timing of adult common sandpipers *Actitis hypoleucos* (Linnaeus, 1758) (Charadriiformes: Scolopacidae). — European Zoological Journal 84: 136–140. https://doi.org/10.1080/11250003.2016.1278474

Meissner, W. & Markowska, K. 2009: Influence of low temperatures on behaviour of mallards (*Anas platyrhynchos* L.). — Polish Journal of Ecology 57: 799–803.

Meissner, W., Rowiński, P., Polakowski, M., Wilniewczyc, P. & Marchowski, D. 2015: Impact of temperature on the number of mallards, *Anas platyrhynchos*, wintering in cities. — North-Western Journal of Zoology 11: 213–218.

Meissner, W. & Witkowska, M. 2023: The effect of the temperature on local differences in the sex ratio of Mallards *Anas platyrhynchos* wintering in an urban habitat. — Acta Oecologica 119: 103900. https://doi.org/10.1016/j.actao.2023.103900

Miernik, N.A., Janas, U. & Kendzierska, H. 2023: Role of macrofaunal communities in the Vistula River plume, the Baltic Sea—Bioturbation and bioirrigation potential. — Biology 12: 147. https://doi.org/10.3390/biology12020147

Munday, C. & Rose, P. 2022: Environmental and social influences on the behaviour of free-living Mandarin Ducks in Richmond Park. — Animals 12: 2554. https:// doi.org/10.3390/ani12192554.

Nichols, J.D., Haramis G.M., 1980: Sex-specific differences in winter distribution patterns of Canvasback, — Condor 82: 406–416. https://doi.org/10.2307/1367565

Nilsson, L. 1970a: Local and seasonal variation in sex-ratios of diving ducks in South Sweden during the nonbreeding season. — Ornis Scandinavica 1: 115–128. https://doi.org/10.2307/3676029

Nilsson, L. 1970b: Food seeking activity of south Swedish diving ducks in the non-breeding season. — Oikos 21: 145–154. https://doi.org/10.2307/3543670

Nilsson. L. 1976: Sex-ratios of Swedish Mallard during the non-breeding season. — Wildfowl 27: 91–94.

Owen, M. & Black, J.M. 1990: Waterfowl Ecology. — Blackie and Son, Ltd., Glasgow.

Owen, M. & Dix, M. 1986: Sex ratios in some common British wintering ducks. — Wildfowl 37: 104–112.

Pap, K., Nagy, L., Balogh, C., G.-Tóth, L. & Liker, A. 2013: Environmental factors shaping the distribution of common wintering waterbirds in a lake ecosystem with developed shoreline. — Hydrobiologia 716: 163–176. https://doi.org/10.1007/s10750-013-1560-3

Pattenden, R.K. & Boag, D.A. 1989: Skewed sex ratio in a northern wintering population of mallards. — Canadian Journal of Zoology 67: 1084–1087. https://doi.org/10.1139/z89-152

Pounder, B. 1976: Wintering flocks of Goldeneyes at sewage outfalls in the Tay Estuary. — Bird Study 23: 121–131. https://doi.org/10.1080/00063657609476490

Pöysä, H., Linkola, P., Paasivaara, A. 2019. Breeding sex ratios in two declining diving duck species: between-year variation and changes over six decades. — Journal of Ornithology 160:1015–1023. https://doi.org/10.1007/s10336-019-01682-7

Rodway, M.S. 2006: Have winter spacing patterns of harlequin ducks been partially shaped by sexual selection? — Waterbirds 29: 415–426. https://doi.org/10.1675/1524-4695(2006)29[415:hwspoh]2.0.co;2

Rodway, M.S. 2007. Timing of pairing in waterfowl II: Testing the hypotheses with Harlequin Ducks. — Waterbirds 30: 506–520. https://doi.org/10.1675/1524-4695(2007)030[0506:topiwi]2.0.co;2

Rodway, M.S., Regehr, H.M., Boyd, W.S. & Iverson, S.A. 2015: Age and sex ratios of sea ducks wintering in the Strait of Georgia, British Columbia: Implications for monitoring. — Marine Ornithology 43: 141–150.

Rohwer, F.C. & Anderson, M.C. 1988: Female biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. — Current Ornithology 5: 187–221. https://doi.org/10.1007/978-1-4615-6787-5_4

Ruben, J. 1996: Evolution of endothermy in mammals, birds and their ancestors. — In Animals and temperature: phenotypic and evolutionary adaptation (ed. Johnston, I.A. & Bennett, A.F.): 347–376. Cambridge University Press, Cambridge.

Sayler, R.D. & Afton, A.D. 1981: Ecological aspects of Common Goldeneyes *Bucephala clangula* wintering on the upper Mississippi River. — Ornis Scandinavica 12: 99–108. https://doi.org/10.2307/3676033

Schummer, M.L., Anthony, A.B., Kleespies, S.M., Ankenman, G., Ligouri, M., Bleau, A., Droke, J., Cohen, J., Kowalski, K., Morlock, F. & Eckler, J. 2020: Aggression and behavioural dominance in wintering mallard *Anas platyrhynchos* and American black Duck *A. rubripes*. — Wildfowl 70: 167–178.

Serrano-Davies, E., Traba, J., Arroyo, B., Mougeot, F., Cuscó, F., Mañosa, S., Bota, G., Faria, N., Villers, A., Casas, F., Attie, C., Devoucoux, P., Bretagnolle, V. & Morales, M.B. 2022: Biased adult sex ratios in Western Europe populations of Little Bustard *Tetrax tetrax* as a potential warning signal of unbalanced mortalities. — Bird Conservation International 33: e40. https://doi.org/10.1017/S0959270922000430

Skov, H., Heinänen, S., Žydelis, R., Bellebaum, J., Bzoma, S., Dagys, M., Durinck, J., Garthe, S., Grishanov, G., Hario, M., Kieckbusch, J.J., Kube, J., Kuresoo, A., Larsson, K., Luigujoe, L., Meissner, W., Nehls, H.W., Nilsson, L., Petersen, I.K., Roos, M.M., Pihl, S., Sonntag, N., Stock, A., Stipniece, A., Wahl, J. 2011: Waterbird populations and pressures in the Baltic Sea. — Nordic Council of Ministers. Copenhagen.

Skov, H. & Kube, J. 1996: Habitat selection, feeding characteristics, and food consumption of long-tailed ducks, *Clangula hyemalis*, in the southern Baltic Sea. — In: The ecology of macrozoobenthos and sea ducks in the Pomeranian Bay (ed. Kube, J.). Meereswissenschaftliche Berichte 18: 83–100.

Sokołowski, A., Jankowska, E., Balazy, P. & Jędruch, A. 2021: Distribution and extent of benthic habitats in Puck Bay (Gulf of Gdańsk, southern Baltic Sea). — Oceanologia 63: 301–320. https://doi.org/10.1016/j.oceano.2021.03.001

Söderholm, S. 2003: Könsfördelning hos övervintrande brunand *Aythya ferina* i Erstaviken, Sörmland. — Ornis Svecica 13: 17–23. https://doi.org/10.34080/os.v13.22816

Székely, T., Liker, A., Freckleton, R.P., Fichtel, C. & Kappeler, P.M. 2014: Sex-biased survival predicts adult sex ratio variation in wild birds. — Proceedings of the Royal Society B: Biological Sciences 281: 20140342. https://doi.org/10.1098/rspb.2014.0342

Wetlands International 2015: Waterbird Population Estimates. — http://wpe.wetlands.org/

Wood, K.A., Brides, K., Durham, M.E., Hearn, R.D. 2021: Adults have more male-biased sex ratios than first-winter juveniles in wintering duck populations. — Avian Research 12: 51. https://doi.org/10.1186/s40657-021-00286-1

Woolington, D.W. 1993: Sex ratios of canvasbacks wintering in Louisiana. — Journal of Wildlife Management 57: 751–758. https://doi.org/10.2307/3809075

Zar, J.H. 2010: Biostatistical analysis. — Prentice Hall, Upper Saddle River, New Jersey.

Online supplementary material

Supplementary material available in the online version of the article includes Tables S1-S3.

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Migratory protogyny and condition-dependent arrival in Icelandic Red-necked Phalaropes

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In many migratory birds, arrival at breeding grounds is sexually asynchronous. This pattern is often explained by the idea that early arrival benefits the sex under stronger sexual selection by improving access to mates through territoriality. However, in species where females arrive first and are non-territorial, this explanation falls short. One alternative is that early-arriving females are simply in better condition. Here we report, for the first time, evidence of migratory protogyny in the Icelandic population of Red-necked Phalaropes (*Phalaropus lobatus*), a shorebird with reversed sexual dimorphism. We also present the first direct test of the condition-dependent hypothesis in a protogynous species, using arrival data, morphometric measurements, and leukocyte profiles. Although females arrived significantly earlier than males, we found no evidence that early arrival was linked to superior body condition. Leukocyte profiles did not suggest marked sex differences either, although we had insufficient statistical power to test this. Our results point instead to the role of sex-specific migratory strategies and intrasexual competition in shaping arrival timing. With its unique life history, *P. lobatus* offers a powerful model for studying the evolution of sex-biased migration. We encourage further research integrating fine-scale tracking, reproductive monitoring, and physiological data to better understand the ecological and evolutionary drivers of migratory protogyny.

1. Introduction

Ever since Gätke's observations in 1895, which showed that males of numerous passerines and waders consistently preceded females in Heligoland, migratory protandry (male-first arrival) has been regarded as the prevailing pattern in migratory birds (Coppack & Pulido 2009). This pattern has traditionally been explained by the mate-opportunity hypothesis, which posits that early arrival benefits males by allowing them to establish territories and increase their chances of obtaining mates, particularly in polygynous species (Morbey *et al.* 2012). Territorial acquisition has therefore been regarded as a key driver of sex-biased arrival schedules.

However, this explanation does not apply to species in which the competing sex does not defend territories to gain access to mates. In such systems, early arrival cannot be interpreted through the lens of territorial advantage, and other selective pressures must be considered. A striking example occurs in species that show migratory protogyny, where females arrive earlier than males, a pattern that is exceptionally rare among birds. The Red-necked Phalarope (*Phalaropus lobatus*) is one of the few known examples. This shorebird exhibits reversed sex roles and sexual dimorphism, with females being more ornamented, engaging in aggressive courtship, and leaving all parental care to males. Earlier arrival by females has been documented in the North American breeding populations (Jehl 1986, Reynolds *et al.* 1986), suggesting that migratory protogyny is a consistent element of its phenology.

Although the Red-necked Phalarope is non-territorial, migratory protogyny in this species has still been interpreted through the mate-opportunity hypothesis. In this context, earlier arrival may enhance female access to mates through direct competition, rather than through territorial defense. This interpretation is supported by several characteristics of the species' reproductive system: females compete vigorously for mates, and the majority of pair bonds remain intact throughout nesting (Reynolds *et al.* 1986). Further, extra-pair paternity appears to be rare in its sister species, Grey Phalarope (*P. fulicarius*) (Krietsch *et al.* 2022), suggesting that low levels of extra-pair paternity may be a shared trait across phalaropes. Together, these traits suggest that the mate-limitation model may explain why early arrival could be advantageous for females.

An alternative, and not mutually exclusive, explanation is the condition-dependent hypothesis. Also known as the body size hypothesis, this model proposes that the larger sex may be better able to cope with harsh environmental conditions and may complete migration more efficiently. As a result, the more resilient sex would tend to arrive earlier (Kissner *et al.* 2003). In the case of phalaropes, females are larger and may be physiologically better equipped to tolerate early-season challenges or even to skip stopovers during migration (Morbey *et al.* 2012).

Whereas previous studies have considered sexual size dimorphism in relation to migratory timing (Kissner *et al.* 2003), no research to date has evaluated whether individual-level variation in energy stores (*i.e.* body condition) influences the order of arrival in phalaropes. Moreover, hematological parameters, such as leukocyte profiles and heterophil-to-lymphocyte ratios, are increasingly used as non-invasive indicators of physiological state (Davis *et al.* 2008, Hatch *et al.* 2010), yet these measures have not been applied to the topic of migratory protogyny. While these indices do not provide a direct measure of immune competence, they can offer insight into the variation in stress physiology at arrival. Measuring both energetic and stress-related hematological indices may help to clarify whether early-arriving individuals are in superior health, and whether this could help explain the emergence of migratory protogyny in sex-role reversed systems.

In this study, we offer a preliminary test of the condition-dependent hypothesis in a population of Red-necked Phalaropes breeding in northern Iceland. We first describe the sex-specific arrival patterns of adults at the breeding grounds. We then compare body condition estimates between early and late arriving individuals. Finally, we present a descriptive analysis of hematological parameters, to explore potential sex differences in physiological stress upon arrival.

2. Materials and methods

We studied the arrival phenology of Red-necked Phalaropes at the Rif Field Station in Raufarhöfn (66°27′15″N, 15°57′00″W; Fig. S1), a village approximately 12.5 km south of the Arctic Circle on the eastern side of the Melrakkaslétta peninsula, Iceland. Although the peninsula had not been previously confirmed as a breeding site for this species, we documented breeding activity on 26 June 2023 by capturing a male with a chick (66°29'20"N, 16°14'49.6"W). This late-June confirmation prompted us to focus our census on the period from late May to early June, which we expected would capture the pre-breeding settlement phase of Red-necked Phalaropes in the area.

We conducted an 18-day field census from 23 May to 10 June 2022. On Monday, Wednesday, and Friday mornings, we counted all visible males and females at six fixed observation points along a 24-km road covering the eastern and northern sections of the peninsula (Fig. S1). Each observation at each site lasted 4 to 6 minutes, adjusted to the number of birds present, to standardize the survey effort across days. Sexing was based on pronounced sexual dichromatism: females have a dark gray cap and a bright rusty-red neck, while males exhibit a browner cap and a duller rust-colored neck (Rubega *et al.* 2020).

To assess whether the proportion of males among sexed individuals changed over time, we fitted a binomial generalized linear model (GLM) using daily counts of males and females as the response variable and day of the year as the predictor. To account for potential temporal non-independence (*e.g.*, repeated observations of the same individuals), we examined residuals for autocorrelation. No significant autocorrelation was detected (Fig. S2), supporting the assumption of independence.

From 2021 to 2023, we captured 18 adults (9 males and 9 females) at feeding ponds using 12×1 m mist nets to obtain standard morphometric measurements. Sex differences in morphometric traits were evaluated using one-tailed t-tests. Body condition was estimated using the scaled mass index (SMI) with wing length as a body size proxy (Peig & Green 2009). Finally, we tested the relationship between arrival timing and body condition using a linear model, with ln-transformed SMI as the response variable and days since first arrival as the predictor.

During May and June 2022, blood smears were collected from 6 males and 5 females by puncturing the brachial vein, following standard procedures (Bennett 1970). Time from capture to blood collection did not exceed 7 minutes. Leukocyte profiles were obtained by examining randomly selected microscope fields until 50 leukocytes per smear were counted. We calculated the heterophil-to-lymphocyte (H/L) ratio, a common proxy of stress in avian studies (Davis *et al.* 2008). Due to the limited sample size, we did not perform statistical analyses on hematological variables.

3. Results and discussion

We recorded pronounced migratory protogyny in the Icelandic population of Red-necked Phalaropes, with the proportion of males increasing significantly over the 18-day census period (GLM: $\beta = 0.180 \pm 0.037$, $z = 4.8$, $p < 0.001$, $n = 197$; Fig. 1A). This pattern supports the view that migratory protogyny is a consistent feature of this species' migratory strategy.

Morphometric analyses showed that females were significantly larger and heavier than males (Table 1). But interestingly, despite this marked difference in body mass, the sexes had comparable body condition, as measured by the scaled mass index ($p = 0.815$). Individual body condition showed no relationship between arrival timing (linear model: $\beta = –0.00027$, $p = 0.944$, $n = 18$). Leukocyte profiles from a subset of individuals (6 males, 5 females) also revealed

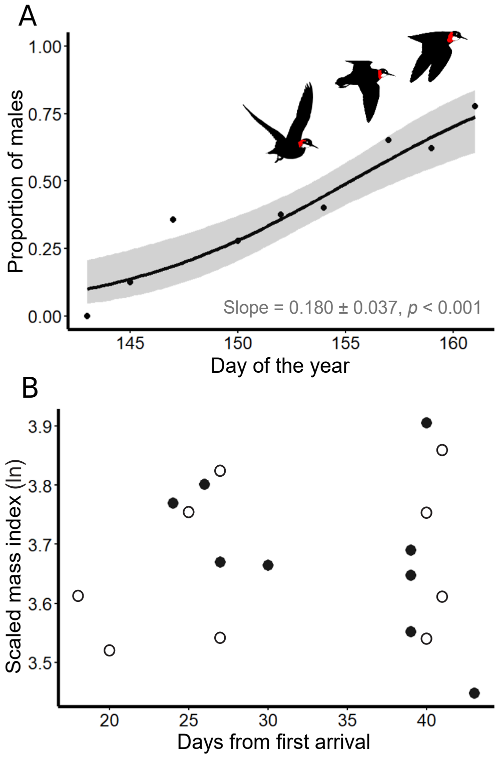

Fig. 1. A) Variation in the proportion of male Red-necked Phalaropes (*Phalaropus lobatus*) during the 2022 breeding season in the Melrakkaslétta peninsula, Iceland (n = 197). Values close to 0 indicate a female bias, close to 1 indicate a male bias, and 0.5 represents an equal proportion of males to females. The solid black line shows the regression line from a binomial generalized linear model, and the gray ribbon represents the 95% confidence interval around the fitted trend, indicating an increasing number of males relative to the day. B) Variation in body condition in female (white) and male (black) phalaropes captured between 18 and 43 days after spotting the arrival of the first individual in the breeding area in the Melrakkaslétta peninsula (linear model: $\beta = -0.00027 \pm 0.00386$, $p = 0.944$, $n = 18$).

similar heterophil-to-lymphocyte (H/L) ratios, with no consistent sex-specific patterns. Overall, these findings provide no support for the condition-dependent hypothesis, which predicts that early-arriving individuals should be in a superior condition.

Although we found no evidence that early-arriving females were in better condition, they did have longer wings and greater body mass than males (Table 1). These traits may enhance migratory efficiency by enabling faster and more stable flight (Sullivan *et al.* 2019, Harvey *et al.* 2022) or by reducing the need for extended stopovers. Direct evidence for this idea is scarce; however, one case study by van Bemmelen *et al.* (2019) tracked a single female Red-necked Phalarope breeding in Iceland that completed spring migration faster than most conspecific males. Although she stopped at all four known staging sites, her stay at each was shorter than two days, suggesting a more rapid migratory pace than that of males. Because this observation is limited to one individual and could reflect chance or stochastic environmental conditions (Lindström 2020), it cannot be taken as representative. In the same study, van Bemmelen *et al.* (2019) also analyzed a Swedish population (5 females, 7 males) and found no significant sex differences in departure from non-breeding grounds or in overall migration speed (all $p > 0.1$). Although this lack of differences may not be generalizable across populations, together these findings suggest that migratory protogyny in phalaropes is unlikely to stem from superior body condition at departure, but may instead involve subtle, sex-specific differences in migration pace or time-allocation strategies.

Theoretical models by Morbey and Hedenström (2020) suggest that faster migration, achieved either through increased flight efficiency or reduced stopover time, can facilitate earlier arrival when earlier breeding confers fitness benefits. Moreover, although based on passerines with conventional sex roles, Deakin *et al.* (2023) found that earlier arrival was associated with larger body and wing size in males and energetically efficient wing morphology, pointing to a broader association between flight morphology and migratory timing. In our study, females had wings 7% longer than males, which matches the species with the greatest wing sexual dimorphism in Deakin *et al.* (2023). Wing shape and size are critical for flight efficiency (Sullivan *et al.* 2019); therefore, wings 7% larger in females might make considerable performance differences over migrations of ~10 000 km. However, further research is needed to determine the relevance of wing size in shaping phalaropes' migratory protogyny.

Hypothetically, if female Red-necked

Phalaropes are able to complete spring migration faster than males, potentially by spending less time at stopover sites, this could have physiological consequences. Stopovers are important for the recovery of immune function in migratory birds (Eikenaar *et al.* 2023), and longer or more intense migratory bouts are expected to suppress certain immune parameters (Nebel *et al.* 2012). In our study, males and females seem to have comparable leukocyte profiles, but this cannot be confirmed due to the low sample size. Assuming both sexes begin spring migration with a similar immune baseline, one possibility is that females possess a greater ability to restore immune balance shortly after arrival. This is supported by evidence that some immune traits can recover rapidly once physical exertion ceases (Eikenaar *et al.* 2020, 2023). Nevertheless, more fine-scale temporal sampling, especially immediately upon arrival, would be required to test this hypothesis directly.

In short, our study offers rare empirical evidence of migratory protogyny in the Icelandic population of Red-necked Phalaropes. We found no support for condition-dependent arrival, highlighting instead the likely importance of intrasexual competition and sex-specific migratory strategies in shaping arrival phenology. With its unusual combination of polyandry, reversed sexual dimorphism, and long-distance migration, the Red-necked Phalarope is an exceptional model for exploring the causes and consequences of sex-biased migration. We encourage future research to integrate fine-scale tracking, particularly at the departure of non-breeding areas, and physiological assessment to uncover the mechanisms driving this pattern. Understanding how sex shapes migration in this species will broaden our understanding of the evolution of movement, mating, and adaptation.

Muutoltapaluun protogynia ja paluuajan riippuvuus kunnosta islantilaisilla vesipääskyillä

Monien muuttolintujen naaraat ja koiraat palaavat pesimäalueille eri aikaan. Tätä ilmiötä on usein selitetty siten, että varhainen saapuminen hyödyttää sukupuolta, johon kohdistuu vahvempi sukupuolivalinta, koska se parantaa mahdollisuutta vallata reviiri ja siten löytää lisääntymiskumppani. Tämä selitys on kuitenkin riittämätön niiden lajien osalta, joilla naaraat saapuvat ensin eivätkä valtaa reviiriä. Yksi vaihtoehto on, että aikaisin saapuvat naaraat ovat

Table 1. Morphometric measurements and leukocyte profiles of Red-necked Phalaropes (*Phalaropus lobatus*) from northern Iceland. Values represent means ± standard deviations; sample sizes are reported in separate columns. Sexual differences in morphometric traits were tested using one-tailed t-tests. Leukocyte data are expressed as proportions of the total leukocyte count; statistical comparisons were not conducted for leukocyte parameters due to limited sample sizes. H = heterophils, L = lymphocytes.

	Male		Female		*p*
	N	Mean ± SD	N	Mean ± SD	
Wing (mm)	9	109.8 ± 3.7	9	117.4 ± 2.7	<0.001
Body mass (g)	9	35.4 ± 3.7	9	44.2 ± 4.9	<0.001
Scaled mass index (g)	9	40.1 ± 5.4	9	39.5 ± 5.2	0.81
Heterophils	6	0.342 ± 0.217	5	0.275 ± 0.188	-
Lymphocytes	6	0.641 ± 0.213	5	0.699 ± 0.21	-
H/L ratio	6	0.761 ± 0.859	5	0.478 ± 0.361	-
Total leukocyte count	6	15.87 ± 5.50	5	15.18 ± 5.35	-

paremmassa kunnossa. Tässä artikkelissa esitämme ensimmäisiä todisteita muutoltapaluun protogyniasta vesipääskypopulaatiossa (*Phalaropus lobatus*) Islannissa. Vesipääsky on kahlaaja, jolla naaraat ovat koiraita kookkaampia eli sukupuolidimorfismi on käänteistä. Testaamme myös ensimmäistä kertaa hypoteesia paluuajan kuntoriippuvuudesta protogynisellä lajilla käyttämällä saapumisaikoja, morfometrisiä mittauksia ja leukosyyttiprofiileja. Vaikka naaraat palasivat muutolta merkittävästi koiraita aiemmin, emme havainneet, että varhainen saapuminen olisi yhteydessä parempaan kuntoon. Leukosyyttiprofiilit eivät myöskään viitanneet merkittäviin eroihin sukupuolten välillä, vaikka aineisto ei sallinut tilastollista testaamista. Tuloksemme viittaavat pikemminkin sukupuolikohtaisten muuttostrategioiden ja sukupuolen sisäisen kilpailun rooliin saapumisajan määräytymisessä. Ainutlaatuisen elämänkaarensa ansiosta vesipääsky on erinomainen kohdelaji tutkittaessa sukupuolen osalta vinoutuneen muuton evoluutiota. Jotta ymmärrettäisiin paremmin muuton protogynian ekologisia ja evolutiivisia ajureita, tarvitaan lisää tutkimuksia, joissa yhdistetään yksityiskohtaista paikannusta, lisääntymisen seurantaa ja fysiologista aineistoa.

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References

Bennett, G. F. 1970: Simple techniques for making avian blood smears. — Canadian Journal of Zoology 48: 585–586. https://doi.org/10.1139/z70-098

Coppack, T. & Pulido, F. 2009: Proximate control and adaptive potential of protandrous migration in birds. — Integrative and Comparative Biology 49: 493–506. https://doi.org/10.1093/icb/icp029

Davis, A. K., Maney, D. L. & Maerz, J. C. 2008: The use of leukocyte profiles to measure stress in vertebrates: a review for ecologists. — Functional Ecology 22: 760–772. https://doi.org/10.1111/j.1365-2435.2008.01467.x

Deakin, J. E., Guglielmo, C. G. & Morbey, Y. E. 2023: Covariation between protandry and sexual size dimorphism is age specific in songbirds. — Journal of Ornithology 165: 157–167. https://doi.org/10.1007/s10336-023-02082-8

Eikenaar, C., Hessler, S. & Hegemann, A. 2020: Migrating birds rapidly increase constitutive immune function during stopover. — Royal Society Open Science 7: 192031. https://doi.org/10.1098/rsos.192031

Eikenaar, C., Ostolani, A., Hessler, S., Ye, E. Y. & Hegemann, A. 2023: Recovery of constitutive immune function after migratory endurance flight in free-living birds. — Biology Letters 19: 20220518. https://doi.org/10.1098/rsbl.2022.0518

Gätke, H. 1895: Heligoland as an ornithological observatory; the result of fifty years' experience. — David Douglas, Edinburgh. https://doi.org/10.5962/bhl.title.28887 URL: https://www.

biodiversitylibrary.org/bibliography/28887

Harvey, C., Baliga, V. B., Wong, J. C. M., Altschuler, D. L. & Inman, D. J. 2022: Birds can transition between stable and unstable states via wing morphing. — Nature 603: 648–653. https://doi.org/10.1038/s41586-022-04477-8

Hatch, M. I., Smith, R. J. & Owen, J. C. 2010: Arrival timing and hematological parameters in Gray Catbirds (*Dumetella carolinensis*). — Journal of Ornithology 151: 545–552. https://doi.org/10.1007/s10336-009-0487-y

Jehl, J. R. 1986: Biology of red-necked phalaropes (*Phalaropus lobatus*) at the western edge of the great basin in fall migration. — The Great Basin Naturalist 46: 185–197. URL: https://www.jstor.org/stable/41712210

Kissner, K. J., Weatherhead, P. J. & Francis, C. M. 2003: Sexual size dimorphism and timing of spring migration in birds. — Journal of Evolutionary Biology 16: 154–162. https://doi.org/10.1046/j.1420-9101.2003.00479.x

Krietsch, J., Cragnolini, M., Kuhn, S., Lanctot, R. B., Saalfeld, S. T., Valcu, M. & Kempenaers, B. 2022: Extrapair paternity in a sequentially polyandrous shorebird: limited evidence for the sperm storage hypothesis. — Animal Behaviour 183: 77–92. https://doi.org/10.1016/j.anbehav.2021.10.021

Lindström, Å. 2020: Migration tracks of waders: avoiding the pitfalls of speed estimates and inferred strategies. — Wader Study 127: 2–3. DOI: 10.18194/ws.00181 URL: https://www.waderstudygroup.org/article/13504/

Morbey, Y. E., Coppack, T. & Pulido, F. 2012: Adaptive hypotheses for protandry in arrival to breeding areas: a review of models and empirical tests. — Journal of Ornithology 153: 207–215. https://doi.org/10.1007/s10336-012-0854-y

Morbey, Y. E. & Hedenström, A. 2020: Leave earlier or travel faster? Optimal mechanisms for managing arrival time in migratory songbirds. — Frontiers in Ecology and Evolution 7: 492. https://doi.org/10.3389/fevo.2019.00492

Nebel, S., Bauchinger, U., Buehler, D. M., Langlois, L. A., Boyles, M., Gerson, A. R., Price, E. R., McWilliams, S. R. & Guglielmo, C. G. 2012: Constitutive immune function in European starlings, *Sturnus vulgaris*, is decreased immediately after an endurance flight in a wind tunnel. — Journal of Experimental Biology 215: 272–278. https://doi.org/10.1242/jeb.057885

Peig, J. & Green, A. J. 2009: New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. — Oikos 118: 1883–1891. https://doi.org/10.1111/j.1600-0706.2009.17643.x

Reynolds, J. D., Colwell, M. A. & Cooke, F. 1986: Sexual selection and spring arrival times of Red-Necked and Wilson's Phalaropes. — Behavioral Ecology and Sociobiology 18: 303–310. https://doi.org/10.1007/BF00300008

Rubega, M. A., Schamel, D. & Tracy, D. M. 2020: Red-necked Phalarope (*Phalaropus lobatus*). — In Birds of the World. Billerman, S. M., Keeney, B. K., Rodewald, P. G. & Schulenberg, T. S. (eds.) Cornell Lab of Ornithology. https://doi.org/10.2173/bow.renpha.01

Sullivan, T., N., Meyers, M. A. & Arzt, E. 2019: Scaling of bird wings and feathers for efficient flight. — Science Advances 5: 4269. 10.1126/sciadv.aat4269

van Bemmelen, R. S. A., Kolbeinsson, Y., Ramos, R., Gilg, O., Alves, J. A., Smith, M., Schekkerman, H., Lehikoinen, A., Petersen, I. K., Þórisson, B., Sokolov, A. A., Välimäki, K., van de Meer, T., Okill, J. D., Bolton, M., Moe, B., Hanssen, S. A., Bollache, L., Petersen, A., Thorstensen, S., González-Solís, J., Klaassen R. H. G. & Tulp, I. 2019: A migratory divide among Red-Necked Phalaropes in the Western Palearctic reveals contrasting migration and wintering movement strategies. — Frontiers in Ecology and Evolution 7: 86. https://doi.org/10.3389/fevo.2019.00086

Online supplementary material

Supplementary materials available in the online version of the article include Figures S1–S2 and a PDF containing the R code.