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Research Article

Staying sheltered: geographical variation in nestbox use by a nocturnal raptor outside the breeding season

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Tree cavities and nestboxes are crucial resources for cavity-nesting birds. While cavities are essential for reproduction, their importance outside the breeding season remains poorly understood, with most existing evidence focusing on nestbox use by small birds to reduce heat loss during winter. Whether non-breeding cavity use varies geographically along latitudinal gradients is also largely unknown. Here, we conducted a three-year study on tawny owl *Strix aluco* to investigate nestbox use during autumn and winter using trail cameras in four populations located at different latitudes (Finland, Sweden, Slovenia, Italy). We predicted non-breeding nestbox use to be a daytime behaviour, and to be more common under colder climatic conditions, in more deciduous habitats and in areas with higher predator (both avian and mammalian) and mobber abundance. We indeed find that tawny owls primarily use nestboxes during the day and in winter, but use nestboxes rarely outside the breeding season, except in Italy. PCA-based analyses of population differences in climate, forest habitat and bird community provides some support for the notion that tawny owl nestbox use outside the breeding season is mainly associated with deciduous forest, possibly because these provide less cover in winter. In addition, tawny owl nestbox use is mainly observed in active territories and winter nestbox use is associated with the probability of starting to breed in the subsequent breeding season. Our findings imply nestboxes, and presumably also natural cavities, have multiple ecological functions for tawny owls outside their breeding season. A better understanding of year-round nestbox use is important for developing effective wildlife conservation strategies in forest ecosystems.

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Keywords: cavity use behaviour, geographic variation, non-breeding season, population monitoring, roosting behaviour, tawny owl

Introduction

Numerous bird species rely on cavities for different purposes such as nesting, food-hoarding, roosting and shelter (Gibbons and Lindenmayer 2002, Aitken and Martin 2007, Goldingay 2009, Cockle et al. 2010, 2011, van der Hoek et al. 2017, Yatsiuk 2024). Secondary cavity-nesting birds, in particular, rely strongly on cavities, whether natural or human-provided, for survival and reproduction. Cavities can also represent safe roosting sites, providing protection from both harsh weather conditions (Kendeigh 1961, Cooper 1999) and predators (Sunde et al. 2003, Bock et al. 2013), thus being important also outside the breeding period (Mainwaring 2011, Bock et al. 2013).

However, suitable natural cavities are often scarce, especially in forest ecosystems, where cavity availability is further reduced by habitat loss and fragmentation (Newton 1994, Gibbons and Lindenmayer 2002, Souter et al. 2004, Tews et al. 2004, Aitken and Martin 2008, 2012). In particular, logging and removal of cavity-bearing trees contribute significantly to this decline (Bunnell 2013, Edworthy and Martin 2013). Given this shortage, many secondary cavity-nesting birds use alternatives such as barns, abandoned buildings and nestboxes (Mainwaring 2011). Nestboxes are widely installed for wildlife research, conservation or public interest and primarily serve to provide breeding sites. However, they can also function as important roosting sites, improving overwintering survival and benefiting population dynamics, which is especially well documented for small passerine birds (Newton 1998, Pinowski et al. 2006, Dhondt et al. 2010, Veľký et al. 2010, Mainwaring 2011). In contrast, nestbox use outside the breeding season remains poorly studied in larger birds, including raptors.

Many raptors, including owls, rely on cavities for breeding but also use them for other purposes and readily adopt nestboxes as substitutes for natural sites (Davis et al. 2017). For example, pygmy owls *Glaucidium passerinum* use nestboxes to hoard food during winter (Masoero et al. 2018, 2020a), and their cavity use varies depending on climatic and habitat conditions (Masoero et al. 2020b, Baroni et al. 2021). Similarly, little owls *Athene noctua* were found to roost in cavities throughout the year (Nieuwenhuyse et al. 2008, Bock et al. 2013). In tawny owl *Strix aluco*, a nocturnal raptor mainly active at night, populations inhabiting landscapes with abundant cavities but relatively sparse forest cover, such as the western part of the Netherlands, individuals are known to use cavities year-round (Koning and Baeyens 1990). However, apart from these few observations, non-breeding cavity use remains an understudied behavioural trait, lacking a comprehensive quantification. In particular, little is known about how biotic factors (e.g. abundance of avian and mammalian predators or mobbers) or abiotic factors (e.g. temperature, rainfall and other climate variables) influence cavity or nestbox use outside the breeding season. Moreover, previous studies have largely focused on single populations, limiting comparisons across a species' ranges and across different environmental and climatic contexts (e.g. Dhondt et al. 2010, Masoero et al. 2018, 2020a, Baroni et al. 2021).

While cavities and nestboxes can provide substantial benefits, they may also entail some costs. Cavities can increase predation risk if predators are able to access them. Martens *Martes martes/foina*, in particular, are important predators of cavity-nesting owls, as they can efficiently climb trees and access both natural cavities and nestboxes (Sonerud 1985b, Sasvári and Hegyi 2011, Karell et al. 2020). Martens prey on eggs and nestlings and may revisit previously discovered nest sites in subsequent years (Sonerud 1985a, Sorace et al. 2004), potentially forcing owls to shift roost or nesting sites to reduce the risk of repeated predation. Predator activity and accessibility of nestboxes may therefore influence their attractiveness as roosting sites during the non-breeding season. Nestbox characteristics such as box dimensions, entrance size, placement height, orientation and tree species on which boxes are installed may further influence roosting decisions and nestbox use (Caro 2005).

Cavity and nestbox use may also provide thermal benefits. Roosting in enclosed spaces can reduce heat loss and energy expenditure through thermal insulation (Kendeigh 1961, Cooper 1999, Nord et al. 2011). However, heat loss is influenced not only by ambient temperature but also by wind and precipitation, which can substantially increase energy costs (McCafferty et al. 1997a, 1997b). Roosting in cavities or nestboxes may therefore provide significant energetic savings during winter (McCafferty et al. 2001), suggesting that their use may be more closely linked to short-term local microclimate conditions rather than to temperature alone. Variation in habitat composition and climate across a species' range may consequently lead to population-level behavioural differences, with individuals adopting different life-history strategies to maximize their fitness in the habitat where they live.

To fill this knowledge gap, we conducted a large-scale, three-year monitoring study of four tawny owl populations spanning a latitudinal gradient across the species' European range. Nestbox use during the non-breeding season may have important implications for survival and behaviour (Sonerud 1985b, Galeotti et al. 2004), potentially providing protection from predators (both avian and mammalian) and mobbers, as well as shelter from harsh winter conditions. As tawny owls are nocturnal, we expect they primarily use the nestboxes in the non-breeding season during the day. Benefits from using the nestbox in the non-breeding season may also align with subsequent breeding-site selection. The putative factors affecting nestbox use during the non-breeding season are not mutually exclusive and lead to a set of specific predictions

(Table 1), leading to an expectation to find differences in nestbox use among populations according to local biotic and abiotic conditions. For example, if harsher climate conditions drive nestbox use, we predicted higher use in winter than in autumn and greater use at higher latitudes in northern Europe. If tawny owls use nestboxes to reduce predation or mobbing risk, we expected higher nestbox use in populations with greater densities of mobbers and avian or mammalian predators' densities. With respect to habitat composition, we predicted more frequent nestbox use in deciduous than in coniferous forests, as winter leaf reduces cover and increases exposure during daytime roosting. To test these predictions, we used bird censuses conducted in autumn and spring to quantify avian predators and mobbers at study sites, combined with GIS-derived habitat data and weather variables (temperature, rainfall, wind speed, snow depth and photoperiod). Based on these variables, we first formulate specific predictions and quantified nestbox use in each population and compare the results with these predictions.

Material and methods

Study populations

Monitoring of nestbox use was conducted over three consecutive autumn–winter periods, (September–February 2021/2022, 2022/2023 and 2023/2024) in four nestbox breeding populations of tawny owls. Two populations were located at the northern limit of the species' range: Finland (central point Siuntio: 60°15′N, 24°15′E; hereafter FI) and Sweden (central point Undenäs: 58°39′N, 14°25′E; hereafter SW). The other two populations were located in central/southern Europe: Slovenia (central point Mt Krim: 45°58′N, 14°25′E; hereafter SI) and Italy (central point Rocca dell'Adelasia: 44°21′N, 8°19′E; hereafter IT). These populations were situated in different European regions, each characterized by distinct habitat compositions and bird and predator communities. In FI and SW, tawny owls occupy in spruce-dominated forests interspersed by agricultural areas. Winters are cold and snowy, with long periods of sub-zero temperatures. In SI, the habitat consists of mixed mountain forests, where beech *Fagus sylvatica* and fir *Abies* and *Picea* are the dominant tree species (Vrezec and Tome 2004). The climate is temperate continental, with moderately cold winters and significant snowfall due to elevation. In IT, the study area is mainly covered by broadleaf forests, with chestnut *Castanea sativa* and beech as the most common species. The temperature is higher and winters are wetter than in the other sites.

Data collection

We installed infrared trail cameras (Victure model HC200) in 117 nestboxes (FI n = 30; SW n = 30; SI n = 30; IT n = 27) to investigate tawny owl nestbox use during the non-breeding period. In 2021 a camera was mounted in nestboxes where tawny owls had nested at least once in either year 2019 or 2020. Cameras were mounted on the inner face of the nestbox roof to minimize disturbance to the birds and were set to take a picture every two hours throughout autumn and winter (September to February), allowing the detection of roosting individuals. The total number of pictures collected and analysed per country, including daylight observations, is summarized in Table 2. Although this study focuses on the non-breeding period, cameras remained active year-around as part of a parallel study on breeding behaviour. Accordingly, pictures were downloaded from SD cards twice per year: in February (prior to breeding season onset) and in July/August (after the breeding season, as most young have already fledged in mid–late summer). Nestboxes differed slightly among the study populations in design and dimensions, reflecting locally established monitoring protocols. However, all boxes were suitable for tawny owl occupancy and were installed following standard practices within each region.

Since tawny owls may occupy a territory without breeding or entering a nestbox, we complemented camera data with playback surveys to assess owl presence. At each site (n = 117), surveys were conducted twice per year, in October and February. During the first hours of the night, we played a tawny owl call for 15 min, and recorded responses from nearby individuals. Tawny owls are year-round territorial, with strong site tenacity and mate fidelity (Francis and Saurola 2004, Sunde 2011, Passarotto et al. 2023). Hence, combining playback records with camera images allowed us to detect owls within their territories even when they did not enter the nestboxes. A territory was considered occupied if a positive playback was recorded or if breeding occurred during the subsequent breeding season.

To assess the effect of climate and photoperiod on nestbox use, we collected average autumn and winter values of temperature, rainfall (i.e. precipitation of rain, not considering snow precipitation), wind speed, snow depth and photoperiod (hours of daylight) for the autumn–winter periods 2021/2022, 2022/2023 and 2023/2024 from the meteorological station closest to each study area. For Finland, Slovenia

Table 1. Summary of predictions based on abiotic (climate) and biotic (mobbers and habitat type) variables putatively affecting the use of nestboxes by tawny owl outside the breeding season. For each type of variable, the expected increasing (+) or decreasing (–) use of nestboxes outside the breeding season by tawny owls is provided. Possible mechanisms, as well as country-specific expectations, are also provided (Finland = FI, Sweden = SW, Slovenia = SI, Italy = IT).

		Expected	Expectation			
Variable	Direction	Possible mechanism	FI	SW	SI	IT
Temperature	–	Thermoregulation	+	+	–	–
Mobbing	+	Reduce disturbance	–	+	+	+
Prop. of coniferous trees	–	Provide cover	+	+	+	–

Table 2. Total number of trail camera images and tawny owl detections during the non-breeding season in each study population. For each population, we report 1) the total number of images recorded across the entire study period, 2) the total number of images recorded in autumn and winter, 3) the number of images containing a tawny owl in autumn and winter, 4) the number of daylight images recorded in autumn and winter, and 5) the number of daylight images containing a tawny owl in autumn and winter. In IT, 27 cameras were deployed, compared to 30 cameras in the other populations. In addition, intermittent camera failures (e.g. battery depletion or technical issues) resulted in variation in the number of camera-trap images among populations. Finland = FI, Sweden = SW, Slovenia = SI, Italy = IT.

Population	Total images	Season		Images with owl		Daylight images		Daylight images with owl	
		Autumn	Winter	Autumn	Winter	Autumn	Winter	Autumn	Winter
FI	113 687	46 282	67 405	54	37	13 608	9690	21	7
SW	86 115	29 448	56 667	54	183	8837	11 475	29	72
SI	88 738	41 575	47 163	93	175	16 965	15 336	76	94
IT	72 731	30 565	42 166	642	1933	11 993	14 200	469	1274

and Italy climate variables were obtained from the Finnish Meteorological Institute (https://en.ilmatieteenlaitos.fi/), the Slovenian National Meteorological Service (https://meteo.arso.gov.si/met/en/weather/) and the Historical Weather API (Free Open-Source Weather API | Open-Meteo.com), respectively. For Sweden, climate variables were obtained from the European Climate Assessment and Dataset project (www.ecad.eu). Photoperiod data were extracted from www.timeanddate.com for all study areas.

To quantify the abundance of potential mobbers and avian predators, we conducted bird census twice per year (October and February) at each nestbox site. During each census, we recorded all species (when identifiable) of small passerines (e.g. tits, finches), thrushes, corvids, woodpeckers and avian predators (e.g. Eurasian goshawk *Accipiter gentilis* and common buzzard *Buteo buteo*) and the number of individuals heard or observed (approximately 30–50 m around the nestbox) for each species observed for 10 min.

Finally, to explore whether habitat influenced nestbox use, we calculated the percentage cover of forest type within 1000 m buffer around each nestbox, corresponding to the typical home range size of tawny owls (based on observed movement patterns, Passarotto et al. 2023). Forest cover data were extracted from CORINE Land Cover data (land.copernicus.eu), and differentiated between coniferous, mixed and deciduous forests to assess their potential influence on owl behaviour.

Statistical analysis

Analyses were conducted in R 4.4.2 (www.r-project.org). To explore differences in abiotic and biotic conditions among study populations, we performed a principal component analysis (PCA) using the *PCA* function from the 'FactoMineR' package (ver. 2.11) on centered and scaled variables. The PCA included population-level autumn and winter climatic variables (mean temperature, rainfall, wind speed, snow depth and photoperiod averaged over the autumn–winter period for each population), site-level forest composition (percentage of deciduous, coniferous and mixed forest), and bird community metrics derived from site-level census data (i.e. number of small passerines, corvids, thrushes, woodpeckers and diurnal raptors per site). The first two principal components (PC1 and PC2) were used to interpret the main gradients in habitat and climate structure between the study populations.

GLMMs were implemented using the 'glmmTMB' package (ver. 1.1.10; 38). The response variable was nestbox use by tawny owls during the non-breeding season, defined as autumn (September–November) or winter (December–February), modelled with a binomial distribution (0 = owl absent; 1 = owl present) with each camera image treated as separate observation. Fixed effects included country (FI, SW, SI and IT), season (autumn or winter), year, light period at the time of observation and territory occupancy (binary variable indicating whether a territory was occupied or not, regardless of nest box use; Data collection). Nestbox identity (Box ID) was included as a random factor to account for repeated observations of the same nestbox. Model assumptions and potential overdispersion were evaluated using simulation-based diagnostic in the 'DHARMa' package (ver. 0.4.7), and no evidence of substantial overdispersion was detected. Model stability and random-effect structure were further assessed by checking for singularity, which was not indicated in the final model. Light period was classified based on the solar elevation angle calculated from the geographic coordinates of the study area's central point and observation time using the 'suncalc' package (ver. 0.5.1). Observations were categorized into four periods: dawn (sun elevation –6° to 0°), day (sun elevation > 6°), dusk (sun elevation 0° to 6°) and night (sun elevation ≤ −6°), following standard astronomical definitions. To evaluate whether nestbox use patterns differed when considering only daytime roosting behaviour, we additionally repeated the analyses using only daylight observations. Because nestbox use was strongly concentrated during the daylight period (Supporting information), the main analyses and figures presented in the results focus on daylight observations only.

An initial full model including climate variables, forest composition and bird community metrics was tested. Although some predictors were significant in simpler or univariate models, they became non-significant when included simultaneously in more complex models. Multicollinearity was assessed using variance inflation factors (VIFs) with the 'performance' package (ver. 0.13.0) in R. Several predictors, particularly country, season and climatic variables such as average temperature, photoperiod and wind speed showed high VIFs (up to ~ 275), reflecting strong geographical and seasonal structuring of climatic conditions across study areas. Because climatic conditions are intrinsic to country identity

and seasonality in this system, we decided to retain country and season as proxies for spatial and temporal environmental differences, and excluded highly collinear climatic variables from the final model. The final model included only predictors with acceptable collinearity (VIF < 4; 39) and biologically relevant effects.

To test whether nestbox use during the non-breeding season was more frequent with proximity to the following breeding season, and therefore potentially nestbox use could be associated with prospecting behaviour, we constructed a dataset linking autumn and winter nestbox use to breeding occupancy in the subsequent breeding season. Nestbox use in autumn and winter was summarised per box and year and matched to breeding status in the following spring. Breeding occupancy (0/1) was modelled using binomial GLMMs, with autumn and winter nestbox use included as predictors and nestbox identity included as a random factor to account for repeated observations of the same box across years.

Results

Differences in abiotic and biotic factors between study populations

A total of 361 271 camera-trap images was analysed across all study populations during the non-breeding season, of which 3171 showed tawny owls inside the nest box (Table 2). Tawny owls were hence rarely inside the nest box in the non-breeding season, particularly in FI, SW and SI, whereas they used the nest boxes in the non-breeding season more commonly in IT.

Climatic conditions, forest composition and bird communities differed among the four study populations (Supporting information). Variation among populations was more pronounced for climatic and habitat variables than for bird community composition.

The PCA integrating population-level climatic variables, site-level forest composition and bird community metrics showed differences between populations (Supporting information). The first two principal components (PC1: 32.5 and PC2: 22.4%) together explained 54.9% (Supporting information) of the total variance.

PC1 primarily represented a broad climatic gradient, contrasting colder sites with greater snow depth and wind speed against warmer sites characterised by higher mean temperature and longer photoperiods. Along this axis, northern populations (FI and SW, Fig. 1; Supporting information) clustered at the colder end of the gradient, whereas IT was at the warmer end, with SI in an intermediate position (Fig. 1; Supporting information). PC2 was mainly associated with variation in precipitation and forest composition, particularly rainfall and the relative contributions of mixed and deciduous forest, with secondary contributions from wind speed and bird community composition. This axis highlighted fine-scale ecological differences among sites that were not strictly aligned with latitude or climate alone.

Tawny owl nestbox use

Tawny owls used nestboxes during the non-breeding season mainly during the daytime with lower use at dawn, dusk and night (Supporting information). Focusing on daylight observations, nestbox use varied significantly among study populations and seasons (Fig. 2a and Table 3), with nestbox use being highest in IT (Fig. 2a). Post hoc comparisons confirmed significantly higher nestbox use in IT compared to SW ($z = 3.39$, $p = 0.0039$) and SI ($z = 3.47$, $p = 0.0030$). Post hoc comparisons involving FI were not significant, reflecting

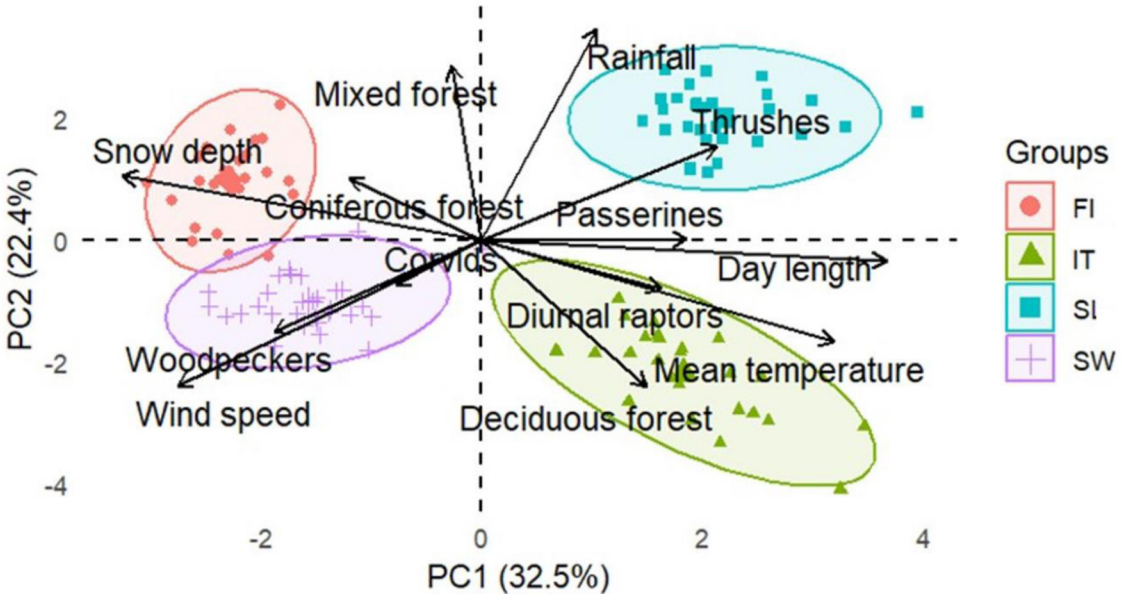

Figure 1. PCA biplot showing the study populations' positions according to Dim.1 (PC1) and Dim.2 (PC2), based on bird community composition, climate variables and forest types. Finland = FI, Sweden = SW, Slovenia = SI, Italy = IT.

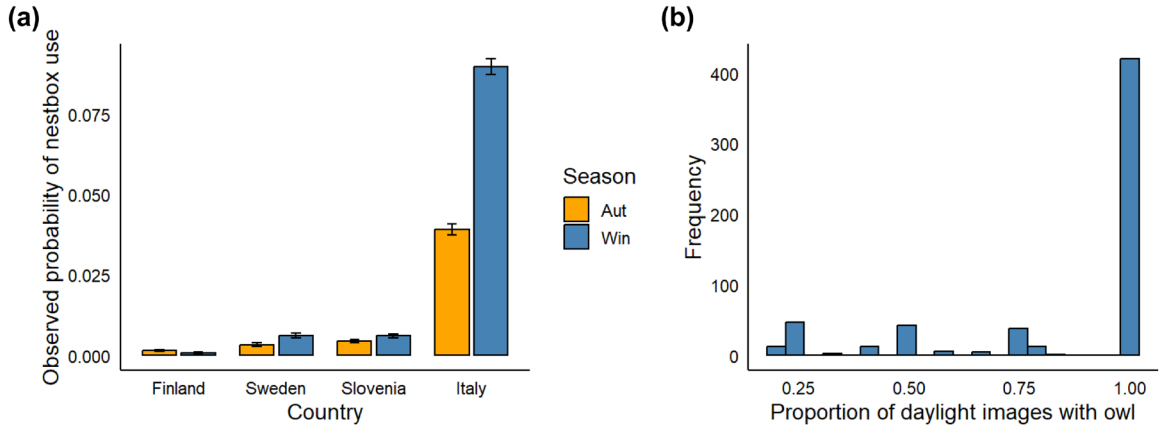

Figure 2. (a) Bar plot showing observed probability of tawny owl nestbox use during the non-breeding season across study populations and seasons during daylight observations. Bars represent mean values ± SE. (b) Histogram showing the distribution of the proportion of daylight images containing tawny owls per nestbox-day (all populations combined), considering only days with at least one owl detection. Values close to 1 indicate more continuous daytime nestbox occupancy within a given day.

inconclusively high uncertainty around the Finnish estimates, despite hardly any owls roosting in nestboxes in Finland. Across all populations, nestbox use in the non-breeding season was significantly higher in winter than in autumn (Fig. 2a and Table 3). Nestbox use in the non-breeding season was higher in active territories (Table 3). Furthermore, winter nestbox use was positively associated with breeding occupancy in the subsequent breeding season (β ± SE = 1.906 ± 0.554, z = 3.44, p = 0.0006; Supporting information). Boxes used during winter had a significantly higher probability of being occupied for breeding, whereas autumn use showed no detectable effect (β ± SE = 1.166 ± 0.713, z = −1.64, p = 0.102; Supporting information). Additionally, if a tawny owl used the nestbox during the day, it frequently stayed inside the nestbox the whole day (70.1% of all days, Fig. 2b), particularly in IT, although short-term daytime visits were also observed in all populations (Supporting information).

Discussion

We used trail cameras mounted inside tawny owl nestboxes taking pictures at regular intervals to study the use of nestboxes outside the breeding season. We studied this behaviour in four populations, two northern (FI and SW) and two southern populations (SI and IT). Not surprisingly for a nocturnal owl, we find that tawny owls use the nestboxes outside the breeding season primarily during the day, often staying in the box during the whole day. We further find clear seasonal and geographical differences in nestbox use by tawny owls during the non-breeding season: nestbox use is higher in winter compared to autumn across all study populations. Strikingly, we find that in most populations tawny owls rarely use the nest boxes outside the breeding season, except in the Italian population where we show tawny owls are much more prone to use the nestbox in the non-breeding season compared to the other populations. Thus, population-specific factors appear to underlie variation in this behaviour. We find clear population differences in terms of climate, forest habitat and bird community. While information on nestbox use in more populations is required for stronger inferences, we here speculate which population-specific differences could underlie the observed behavioural differences in tawny owl nestbox use outside the breeding season.

Tawny owl nestbox use outside the breeding season is concentrated during the daylight period, whereas use during dawn, dusk and especially nighttime is comparatively lower. As tawny owls are primarily nocturnal, the predominance of daylight detections – as well as our finding that they typically stay inside the box the whole day – is consistent with

Table 3. Binomial GLMM analysing nestbox use by tawny owl during daylight-only observations in the non-breeding season according to populations, season (autumn or winter) and territory activity. Values in bold are statistically significant (p < 0.05). Monitoring was conducted over three consecutive autumn–winter periods (2021/22, 2022/23 and 2023/24) in each population, with cameras installed in 117 nestboxes: FI n = 30, SW n = 30, SI n = 30 and IT n = 27. Finland = FI, Sweden = SW, Slovenia = SI, Italy = IT.

Ind. variables	Estim. Beta ± SE	Z	p (Z)	χ^2(ANOVA)	df	p (ANOVA)
Country FI	−25.23 ± 198.14	−0.13	0.899	149.86	4	**< 0.001**
Country IT	−9.02 ± 1.91	−4.73	**< 0.001**			
Country SI	−15.46 ± 1.55	−10.01	**< 0.001**			
Country SW	−15.18 ± 1.46	−10.37	**< 0.001**			
Season (Winter)	0.90 ± 0.06	15.88	**< 0.001**	252.25	1	**< 0.001**
Territory active	1.23 ± 0.15	8.09	**< 0.001**	65.47	1	**< 0.001**

the interpretation that nestboxes are mainly occasionally used as diurnal roosting sites during the non-breeding season. Roosting inside enclosed spaces during daylight hours may reduce exposure to mobbers and to visually oriented avian predators, which pose a threat during daylight hours. Daytime use may also reduce disturbance-related energetic costs and provide indirect energetic benefits under colder conditions. In contrast, nestbox use at night was comparatively rare. During the nighttime, tawny owls are actively foraging and therefore spend most of their time outside nestboxes, which may also reduce predation risk from mammalian predators such as pine/beech martens through increased vigilance and mobility (Mikkola 2014). Inspection of camera images revealed only few instances of pine martens inside nestboxes during autumn and winter, recorded in Finland and Slovenia. While this observation is anecdotal and does not allow inference about actual predation rates, it suggests that direct intrusion of mammalian predator into nestboxes may occur relatively infrequently. Overall, this diel pattern suggests that non-breeding cavity use is more associated with daytime roosting and avoidance of diurnal harassment or predation than with concealment during nocturnal activity.

Previous studies have shown that roosting in enclosed spaces can increase survival by providing thermal insulation and reducing energy expenditure (Kendeigh 1961, McCafferty et al. 1997b, Cooper 1999, Nord et al. 2011, Bock et al. 2013). However, our results do not support the notion that nestboxes are primarily used as thermal shelters during winter, as our population comparison shows that Finland and Sweden, where nest boxes are rarely used outside the breeding season, have the lowest temperatures (often below zero). Thus, while nestboxes may provide some thermal benefits, other ecological factors are likely more influential. Similar conclusions have been drawn for cavity-using species, for which thermal insulation represents only one of several potential advantages, and its relative importance depends on habitat conditions and species-specific adaptations (McCafferty et al. 1997b, Bock et al. 2013).

Our results also show that outside the breeding season, a nestbox is used primarily in active territories (where tawny owls responded to playback and/or were breeding). Winter nestbox use is furthermore associated with subsequent breeding occupancy. This finding indicates that nestbox use outside the breeding season may reflect early breeding site selection and be part of the reproductive cycle, and hence does not only reflect roosting solely for thermoregulation or avoiding mobbers and predators (both avian and mammalian). It has also been shown in other studies that owls often inspect cavities ahead of the breeding season (Sonerud 1985a, Galeotti et al. 2004).

The PCA-based comparison across study populations indicates that the study areas differed substantially in forest composition, climate and bird community structure. Northern study areas (FI and SW) clustered together along gradients characterized by lower temperatures and coniferous-dominated forests, whereas IT stood apart, characterized by higher temperatures and higher proportions of deciduous and mixed forests. These environmental gradients may contribute to the observed geographical differences in nestbox use. In particular, in Mediterranean deciduous forests (i.e. IT), seasonal leaf loss may expose roosting owls to increased predation and mobbing risk, thereby promoting the use of enclosed roosting sites (Sonerud 1985b). This interpretation is consistent with the higher nestbox use observed in IT. Coniferous habitats (i.e. FI, SW, SI) may therefore offer sufficient natural shelter, diminishing the relative importance of nestboxes during the non-breeding season.

Differences in predator and mobber communities between study areas could drive owls to use nest boxes more frequently in areas with higher mobbing pressure or predation risk (Mainwaring 2011). Although predator and mobber abundance varied between study areas and showed significant effects in univariate models, these effects were not retained in the full model. This likely reflects collinearity with other habitat or climatic variables, suggesting that these factors may interact and jointly shape nestbox use.

Our findings have important implications for conservation, as they highlight the need to account for multiple ecological factors when assessing the importance of cavities for wildlife. The fact that nestbox use was not solely temperature-driven underscores the importance of maintaining suitable cavity availability in forests, regardless of climate conditions. Retaining cavity-bearing trees in managed forests can provide crucial shelters for tawny owls and other secondary cavity users (Gibbons and Lindenmayer 2002, Bunnell 2013). However, the importance of tree cavities as shelters is likely context-dependent and may vary with landscape configuration and the availability of alternative roosting sites such as caves, barns and abandoned buildings. Furthermore, while artificial nestboxes are often used to support breeding populations, our study suggests they may also serve as important refuges outside the breeding season, particularly in areas where natural cavities are limited and where biotic pressures are elevated.

Overall, this study highlights the complexity of nestbox use in tawny owls during the non-breeding season, suggesting that factors beyond thermal benefits, such as habitat composition, predator and mobbing pressure, may be important factors underlying this behaviour, while it is at the same time linked to the reproductive cycle of the tawny owls. As we find marked population differences, regional differences (e.g. in forest composition and structure) may influence nestbox use outside the breeding season. Additionally, the availability of suitable cavities could be a key factor shaping this behaviour. Observed differences in nestbox use may therefore reflect variation in the availability of suitable alternative roosting sites, rather than absolute availability of cavities per se. Future research should aim to disentangle the relative importance of these factors using a combination of direct observation and experimental approaches that explicitly test cavity use. Additionally, analysing variation in cavity use as a function of day-to-day-variation in weather parameters would provide a more explicit test of its potential thermoregulatory function. From a conservation perspective, ensuring high availability of

natural cavities is crucial for supporting tawny owl populations and other cavity-dependent species across forest landscapes, especially those where human pressure is high and habitat quality is low.

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Supporting information

The Supporting information associated with this article is available with the online version.

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