

# 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, Maicas & 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, Maicas & 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/km<sup>2</sup>, while northern densities dropped to 0.1 pair/km<sup>2</sup> (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 (Maicas & 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 km<sup>2</sup> 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).

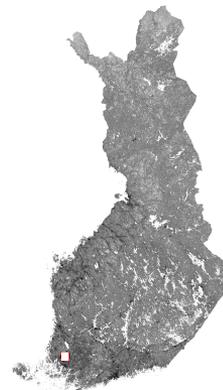
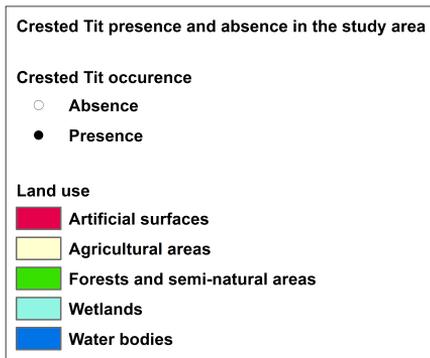
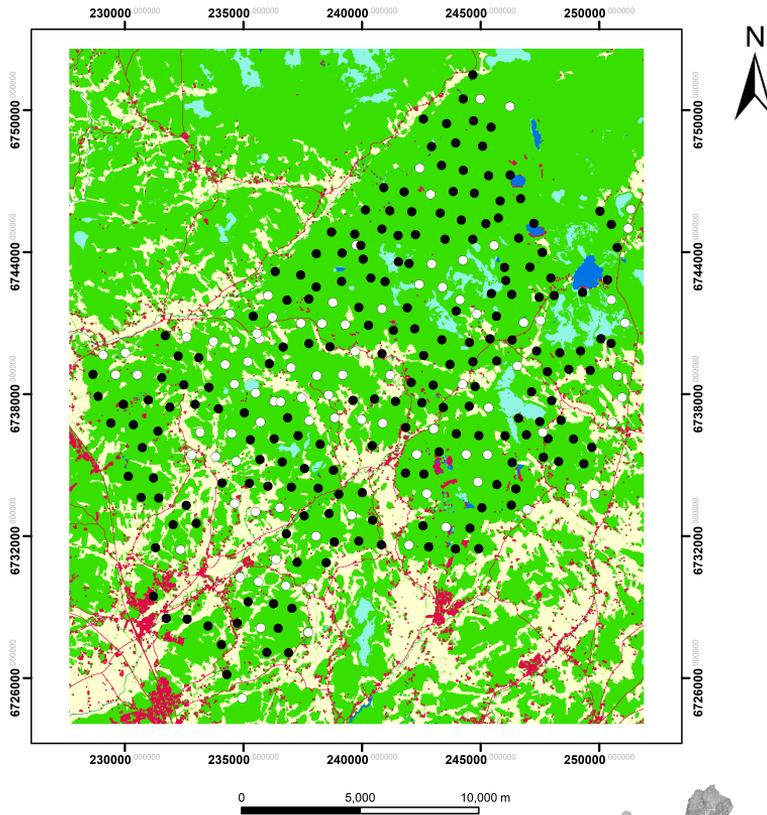
The distance calculation was performed by overlaying the site locations with a map of residential structures. Using the QGIS platform, we calculated Euclidean distances from each site to the closest house. This method is well-documented in GIS literature for its accuracy in spatial analysis (QGIS Development 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 <i>et al.</i> 2023)	Present in 63 sites (22%)
Sum pine foliage	Sum of pine foliage biomass	Multi-source National Forest Inventory	30–2.79 × 10 <sup>4</sup> kg/ha (mean = 1.55 × 10 <sup>4</sup> )
Sum spruce foliage	Sum of spruce foliage biomass	Multi-source National Forest Inventory	361–1.33 × 10 <sup>6</sup> kg/ha (mean = 4.06 × 10 <sup>4</sup> )
Sum deciduous foliage	Sum of deciduous foliage biomass	Multi-source National Forest Inventory	84–1.65 × 10 <sup>4</sup> kg/ha (mean = 4.05 × 10 <sup>3</sup> )
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>i.e.</i> , 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>i.e.</i> , forest >15 years old, Area of agricultural areas, Area of peatbogs, Total area of the raster layers included in the buffers		

A



B



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).

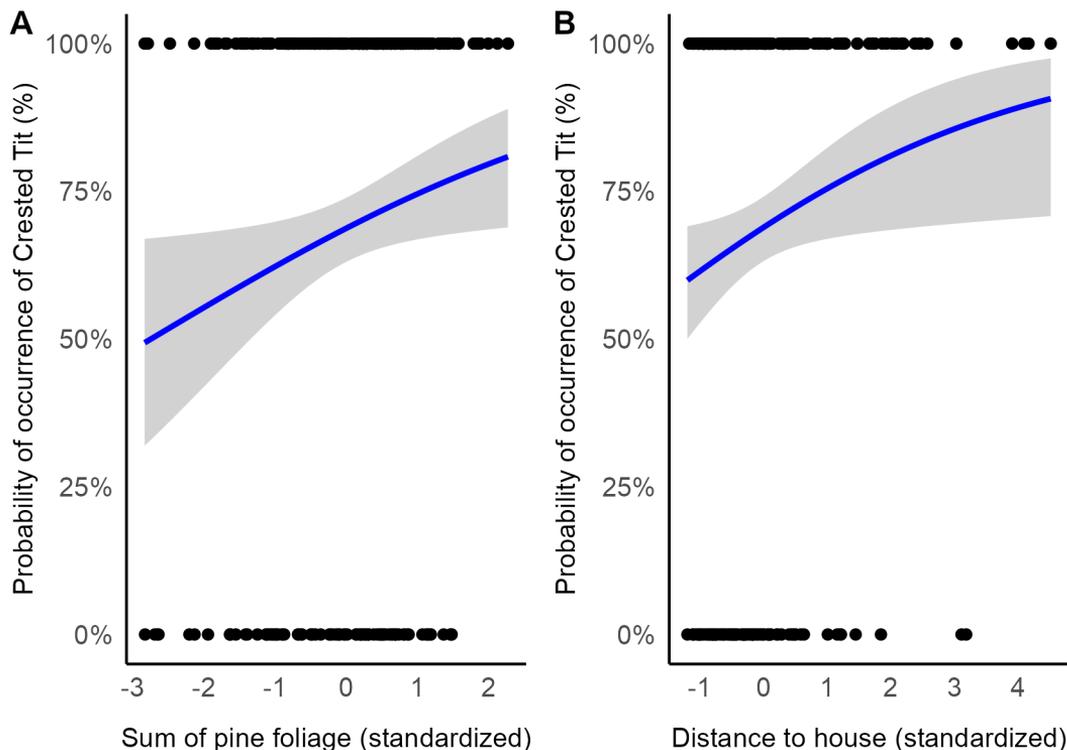


Fig. 2. Probability (expressed as a percentage) of Crested Tit presence in relation to A: Sum of pine foliage and B: Distance to the nearest house, within a 100 m radius buffer around the detector. In both graphs, the variables were standardized to a mean of zero and a unit standard deviation to allow 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 km<sup>2</sup> 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
<b>A</b>					
(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>B</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.

### **Töyhtötiäisten 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 ihmis-toiminnan aiheuttaman paineen ja elinympäristöjen heikentymisen vuoksi.

Tutkimme töyhtötiäisen 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 töyhtötiäisen 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 töyhtötiäiskanta on Suomessa yleisesti taantumassa, havaitsimme lajin esiintyvän 68 %:ssa kartoituspisteistämme, mikä vahvistaa passiivisen akustisen seurannan luotavuutta hyödyllisenä menetelmänä lintujen elinympäristövaatimusten ja populaatioiden seurannassa. Tulokset parantavat ymmärrystämme töyhtötiäisen 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., Wischniewski, 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>
- Atiënzar, 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>
- Brottons, 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., Votka, E., Orell, M. & Rytönen, 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 maaintujen 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>
- Maicas, 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](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>