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Year-round multi-scale habitat selection by Crested Tit (*Lophophanes cristatus*) in lowland mixed forests (northern Italy)

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A R T I C L E I N F O

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A B S T R A C T

Determining how animals respond to resource availability across spatial and temporal extents is crucial to understand ecological processes underpinning habitat selection. Here, we used a multi-scale approach to study the year-round habitat selection of the Crested Tit (*Lophophanes cristatus*) in a semi-natural lowland woodland of northern Italy, analysing different habitat features at each scale. We performed Crested Tit censuses at three different spatial scales. At the macrohabitat scale, we used geolocalized observations of individuals to compute Manly's habitat selection index, based on a detailed land-use map of the study area. At the microhabitat scale, the trees features were compared between presence and absence locations. At the foraging habitat scale, individual foraging birds and their specific position on trees were recorded using focal animal sampling. Censuses were performed during both the breeding (March to May) and wintering (December to January) seasons. At the macrohabitat scale, the Crested Tits significantly selected pure and mixed pine forests and avoided woods of alien plant species, farmlands and urban areas. At the microhabitat scale, old pine woods with dense cover were selected, with no significant difference in the features of tree selection between the two phenological phases. At the foraging habitat scale, the species was observed spending more time foraging in the canopies than in the understorey, using mostly the portion of Scots Pine (*Pinus sylvestris*) canopies closer to the trunk in winter, while during the breeding period, the whole canopy was visited. Overall, breeding and wintering habitats largely overlapped in the Crested Tit. Based on our findings, lowland Crested Tits can be well defined as true habitat specialists: they are strictly related to some specific coniferous woodland features. Noteworthily, compared to other tit species, which normally show generalist habits during winter, the Crested Tit behaves as a habitat specialist also out of the breeding season. Our study stressed the importance of considering multi-scale (both spatial and phenological) habitat selection in birds.

1. Introduction

The habitat of a population encompasses the biotic and abiotic resources and conditions that govern the presence, survival and reproduction of individuals (Caughley and Gunn, 1996). Animals may use habitats disproportionately to availability, resulting in active ‘habitat selection’ i.e., the set of a species’ positive or negative behavioural responses to environment, with an asymmetrical use of resources (Block and Brennan, 1993; Manly et al., 2004). Habitat selection studies shed light on the mechanisms of natural selection since the ability to select

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proper resources may be related to fitness (Brown, 1984; Manly et al., 2004; Jones, 2022). Habitat selection can be extended at different spatial and temporal scales. For instance, the strength of selection may vary according to habitat availability and different site-specific characteristics: in this case a so-called 'functional response' to habitat availability may occur (Holbrook et al., 2019). Different functional responses may result from different climatic conditions, ecological interactions (predation and competition with different species depending on the biogeographic area), and context-dependent changing anthropogenic impacts (Raynor et al., 2017).

Indeed, habitat selection is a scale-sensitive process. In a multi-scale approach, habitat selection can be approached at different spatial and temporal scales in order to provide an ecologically realistic understanding of animal ecological needs (Mayor et al., 2009). Hence, some studies on habitat use and selection (Johnson, 1980) rely on a hierarchical approach at different spatial scales (Jedlikowski and Brambilla, 2017), while others compare habitat selection at different temporal stages, e.g., seasonally (for breeding, wintering, migration) or across years (Hernández, 2021). However, detecting the most informative level for a species may not be trivial (Dayton and Tegner, 1984) and, unfortunately, the choice towards as specific spatial or temporal dimension is often determined by logistical constraints rather than ecological questions (Bowyer and Kie, 2006; Brambilla et al., 2006; Djorgova et al., 2021). Actually, species use different environmental factors that belong to different spatial scales: their estimation in a single scale approach may lead to conflicting results due to lack of knowledge at other scales (Chalfoun and Martin, 2007; Berlusconi et al., 2022). Hence, habitat selection measured at a given scale is often insufficient to predict habitat selection at other scales: each conclusion is potentially correct, but none provides a 'full picture' (Wiens, 1989), if considered *per se*. Indeed, multiple-scale studies provide a more accurate and ecologically realistic evaluation of the habitat needs, describing adaptive features in-depth than single-scale studies (Mayor et al., 2009; Paolini et al., 2019; Assandri et al., 2022).

Since habitat selection is a hierarchical process that acts at multiple spatial scales, several authors distinguish four main scale-dependent habitat types (Morris, 1987; Block and Brennan, 1993): 1) global-scale habitat: selection of the geographical and climate range of a species; 2) macrohabitat: identifiable units whose minimum area corresponds to an average individual home range; 3) microhabitat: environment-specific physical and biological characteristics that influence an individual location within the area (i.e., home range core area); 4) foraging habitat, such as the choice of feeding patches.

In specialist species it is important to study habitat selection at several scale levels, or in different biological periods. Identifying the crucial level(s) at which they exploit particular depending resources to maximise their fitness is crucial for correct conservations plans (Domínguez et al., 2017; Morganti et al., 2021).

In the present work, we explored habitat selection at different spatial and temporal scales, providing a comprehensive picture of year-round habitat selection by Crested Tit (*Lophophanes cristatus*), a small cavity-nesting woodland passerine. We studied habitat selection at three different spatial scales (macrohabitat scale, microhabitat scale and foraging habitat scale; see Hinsley et al., 2007), and comparing it between breeding and wintering periods. Earlier research on this species, overall poorly studied compared to Great (*Parus major*) and Blue Tits (*Cyanistes caeruleus*), focused on various aspects of its biology and ecology, such as the effects of anthropogenic food provisioning (Jansson and Bromssen, 1981), habitat fragmentation (Lens and Dhondt, 2008), timing of breeding and nesting-site on breeding success (Denny and Summers, 1996) and the costs and benefits of male cooperation in nest building (Lens et al., 1994b). Only a few studies analysed habitat selection of the species, always in woodland patches, often focusing on pine plantations (Summers et al., 1993; Maícas and Fernández Haeger, 2004), or natural environments (Hartley, 1987; Summers et al., 1999; Atiénzar et al., 2009; Cutini et al., 2009). However, all these studies addressed the topic at a single spatial scale and single phenological period. Our study is the first unravelling the habitat use and selection of this poorly studied species in a semi-natural lowland area of northern Italy. The multi-scale analysis of habitat selection was carried out with regards to the tree species composition and vegetation structure, which are regarded as crucial traits for site selection of Crested Tit (Anderson and Shugart, 1974; Denny and Summers, 1996; Summers et al., 1999; Atiénzar et al., 2009). Specifically, at the macrohabitat scale we studied the selection of broad land-use categories, while at the microhabitat scale we studied the influence of forest structure and tree-species composition on Crested Tit occurrence. Eventually, at the foraging habitat scale, we observed the position of the birds on the trees and shrubs on which they were foraging. Data were collected during a breeding and two wintering periods.

2. Methods

2.1. Target species and study area

The Crested Tit (*Lophophanes cristatus*) is a small, hole-nesting woodland passerine widespread in Europe, where it inhabits conifer and mixed woodlands (Cramp and Perrins, 1993). The Crested Tit is both a resident and short-migrant species: lowland individuals are regarded as year-round territorial, defending exclusive group ranges also during non-breeding period (Ekman, 1979), while Alpine individuals are often short-migrant, reaching lower altitudes in winter (Brichetti and Fracasso, 2011). In winter, the species often forms flocks, generally consisting of an adult pair and a varying number of non-kin (Lens and Dhondt, 1992). In other Europe, the species is typically linked to coniferous forests, also pine plantations, but several studies highlight differences in macro and micro-habitat use among different geographical areas (Collette, 1987; Mingozzi et al., 1988; Lens and Dhondt, 1993; Summers et al., 1993, 1999; Estrada et al., 2004; Atiénzar et al., 2009), probably due to context-dependent functional responses (Holbrook et al., 2019). Crested Tit breeds uncommonly in Italian lowlands since it is linked to mountain spruce or fir forests, mostly between 800 m and 1800 m a.s.l. (Cutini et al., 2009; Brichetti and Fracasso, 2011).

Pineta Regional Park of Appiano Gentile and Tradate (northern Italy, mean latitude 45°44′ N, mean longitude 8°56′ E) is possibly one of the lowest elevation sites in Italy where a large Crested Tit population breeds and winters (mean elevation 325 m a.s.l.; Gagliardi et al., 2007). The 4821 ha of the protected area is composed of about 70% of forests and woodlands. The dominant vegetation is constituted by acidophilous forests of coniferous (Scots Pine, *Pinus sylvestris*) and broad-leaved trees (chestnut, *Castanea sativa*), while a lesser extent is represented by mesophilic forests (dominated by oak species, *Quercus* spp.) and woods composed by alien tree species (mostly Black Locust, *Robinia pseudoacacia*); important to note is also the presence of pioneer vegetation and heathland (Bianchi, 2002). The particular continuous abundant presence of Scots Pine represents an ideal habitat for the Crested Tit in the area: in fact, the Pineta Regional Park is located in the typical landscape context of glacial terraces in the Italian sub-Alpine lowlands, surrounded by large urban areas and open farmlands. For this reason, we defined our study area including a 1 km buffer strip outside the administrative borders of Pineta Regional Park to consider all the typical sub-Alpine lowlands habitats, either natural, semi-natural or urban.

2.2. Habitat selection at the macro-scale

2.2.1. Crested Tit occurrence locations collection

Occurrence locations of single birds were collected during the 2021 breeding season (10 March – 20 May) and the 2020–2021 and 2021–2022 wintering seasons (1 December – 10 February). We collected all the occurrence locations investigating the study area through a series of opportunistic transects mostly along trails (i.e., paths and roads), with a considerable number of off-road tracks. All the transects were 5–8 km long, balanced to cover the whole study area. The transects were travelled in the morning (after sunrise) to maximise the detection. A total of 41 transects during the breeding season and a total of 50 during the two wintering seasons were covered. Random opportunistic observations in the area were also used. We defined as 'occurrence location' any point where the individual was observed foraging, preening, or singing. We got the GPS coordinates of every location with Google Maps Android application, with an accuracy of $\pm$10 m. A total of 154 occurrence locations were recorded during the breeding season, while 232 were recorded in the two wintering seasons.

2.2.2. Habitat characteristics at the macro-scale

At the macro-scale, we started from land-use data of Lombardy Region DUSAF (Dusaf 6.0, 2018), where forest patches were remapped more precisely. Forest habitats were classified by the dominant species (canopy cover >50%) and by a sub-type (canopy cover >25%) at a 30 m spatial resolution (Bianchi, 2002). Habitats were mapped during the 2020 and 2021 vegetative seasons (starting from June to October). Then, we pooled the forestry maps with urban and agricultural. Eventually, we obtained an exhaustive map of the land-use study area. Overall, 87 land-use categories were identified at first, subsequently merged into 8 major habitat classes in order to favour the ecological interpretability of the findings based on both macro-scale structure and typology (see Appendix Table S1 in Online Resource): acidophilic conifer woods, acidophilic mixed woods, acidophilic broadleaves woods, mesophilic broadleaves woods, pioneer vegetation, alien plant species woods, open farmlands, urban areas.

2.2.3. Habitat-specific selection ratios

We adopted a 'use vs availability' approach obtaining Manly's selection ratios for each habitat class within the study area, based on occurrence locations, for each phenological period (Manly et al., 2004). We used as 'availability' measure for a given habitat class the habitat extent/study area extent ratio. Habitat 'use' was calculated as the ratio of the number of locations falling into the habitat class on the total number of locations. Finally, we derived the selection ratios of each habitat class for each phenological period as the ratio between the 'use' and the 'availability' measures (Manly et al., 2004). Selection ratios with their relative 95% confidence intervals (95% CI) were estimated using the Koopman's score method, as recommended in Aho and Bowyer (2015). Selection ratios (including the associated 95% CI intervals) > 1 indicate a habitat preference, whereas values < 1 indicate avoidance (Manly et al., 2004). All the analyses were run in QGIS version 2.18.28 (QGIS Development Team, 2018) and R 4.0.2 (R Core Team, 2020) using 'asbio' R package (Aho, 2014).

2.3. Habitat selection at the micro-scale

2.3.1. Survey locations

We randomly distributed 100 survey locations within the study area, with the condition that they were at least 200 m away from each other to avoid repeated individual counts. Each survey location was covered twice in the 2019–2020 wintering period (December and January) and twice in the 2021 breeding period (first repetition 15 March – 15 April, second repetition 16 April – 17 May). All the survey sessions were carried out for 10 min in the morning. We reported the presence or the absence of Crested Tit within a 100-m-radius area around the survey location (Bibby, 2000). Each survey point was classified as positive in each phenological period if the species was detected at least once. Overall, the presence of Crested Tit was recorded in 41 survey locations during the breeding period, and in 40 survey locations during the wintering period. All the Crested Tit presences were recorded in survey locations within forested areas, except for one location in winter (located in urban area).

2.3.2. Habitat characteristics at the micro-scale

Since all the observations of Crested Tits occurred in forested sites, we used a restricted dataset including only survey points within forested areas ($N = 67$) to measure the forest composition and structure at the micro-scale. All trees within a 15-m-radius sample circle cantered to the survey point were counted, identified and the diameter at breast height (DBH hereinafter) was measured. In addition, the average height and canopy cover were estimated using 25-m-radius sample circles. We assumed the homogeneity of micro-scale characteristics for the 100-m-radius plot in which we recorded presence/absence of the species (see Hinsley et al., 2007). Forest habitats were mapped during the 2020 vegetative season (starting from June to October). Eventually, we calculated tree density, average DBH and the proportion of conifers at survey stations.

2.3.3. Statistical analyses

We compared habitat characteristics between presence and absence survey points. For each phenological period, two different models were developed, analysing: 1) the effect of proportion of coniferous trees and 2) the micro-scale vegetation structure of tree layer on the probability of presence (see Atiénzar et al., 2009). Pearson's correlation coefficients were used to test for independence between variables, with a threshold value of $r = 0.60$ (see Appendix Table S2 in Online Resource). A logistic regression (GLM) was used to estimate the effects of the proportion of coniferous trees and the final set of vegetation structure predictors (average DBH, tree height, canopy cover) on the probability of presence. All the analyses were run R 4.0.2 (R Core Team, 2020) using 'asbio' R package (Aho, 2014).

2.4. Foraging habitat selection

2.4.1. Observations of foraging individuals

The foraging habitat selection and behaviour of Crested Tits was studied adapting existing methods to our specific needs (Lens et al., 1994a; Hinsley et al., 2007). Crested Tit observations were carried out covering the same transects of the macro-scale habitat analysis. Bird behaviour was recorded using an instantaneous sampling technique (Altmann, 1974; Martin and Bateson, 2018); for each contact, only the first observation of each bird following detection was used. Location was recorded as 'tree canopy' or 'understorey', then we identified the tree species as 'conifer' or 'broadleaf'. If Crested Tit was foraging in tree canopy, we assigned the vertical location within canopy as top, middle third or lower third, and the horizontal location as inner, middle, or outer third. Birds' behaviour was recorded as foraging, vigilance, maintenance (e.g., preening, scratching) or communication; for foraging birds, gleaning (rapid, repeated pecking) from trunks/branches/twigs or gleaning from leaves/needles/buds was recorded. A total of 94 observations were recorded during the breeding period and 118 observations were recorded during both wintering periods.

2.4.2. Statistical analyses

Differences between the foraging behaviour, use of tree canopy or understorey, use of conifer or broadleaf trees and were investigated using Pearson chi-square tests. Chi-square test was also used to compare independently vertical and horizontal locations observations with hypothetical equipartition of observations among vertical and horizontal thirds respectively. When the chi-square test was significant, the standardized residuals and their p-values were analysed by post-hoc tests based on residuals with Bonferroni adjustment method. Data from the two different phenological periods were analysed separately. All the analyses were run R 4.0.2 (R Core Team, 2020).

3. Results

3.1. Habitat selection at the macro-scale

The Manly's selection ratios showed that Crested Tit selected the same macrohabitat typologies both in breeding and wintering period (Fig. 1). Acidophilic conifer woods (with more than 50% of Scots Pine canopy

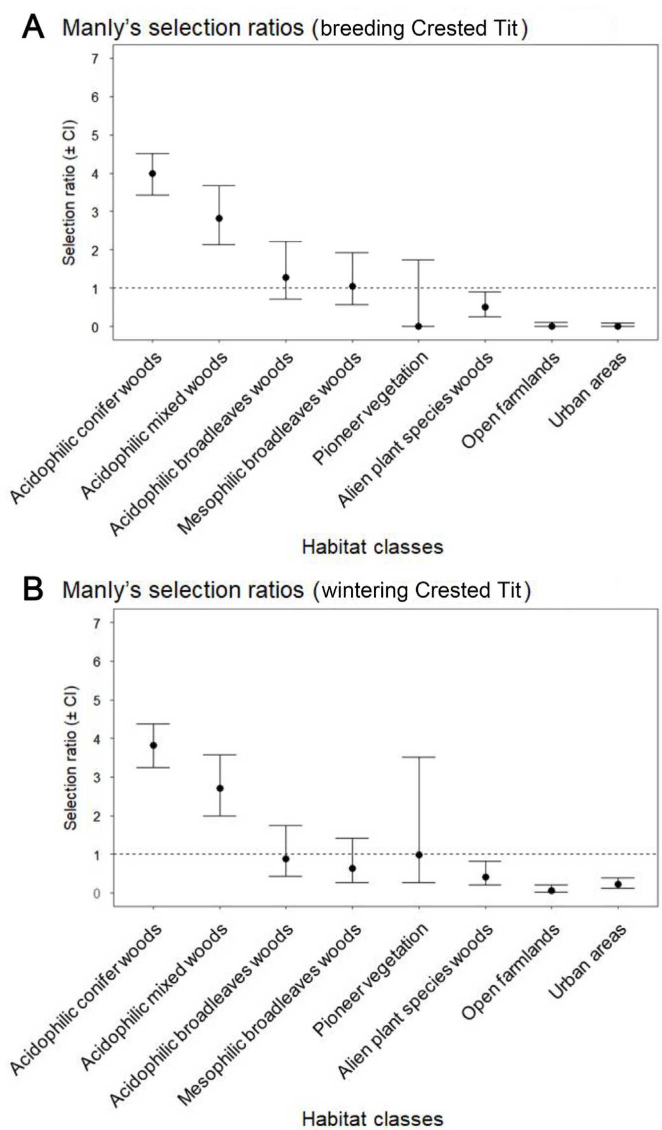

Fig. 1. Manly's selection ratios based on single locations for habitat selection at the macro-scale, for (A) breeding and (B) wintering period. Whiskers represent 95% confidence intervals (CI). A selection ratio of 1 (or CI crossing the 1 dashed line) indicates that the habitat was used in proportion to its availability. > 1: the habitat is significantly selected. < 1: the habitat is significantly avoided.

cover) and acidophilic mixed woods (with at least 25% of Scots Pine canopy cover). Acidophilic broadleaves woods (dominated by Chestnut *Castanea sativa*) and mesophilic broadleaves woods (dominated by Common Oak *Quercus robur*) were used proportionally to their availability; pioneer vegetations also showed this pattern. Woods composed of alien plant species (mainly dominated by Black Locust *Robinia pseudacacia* or Red Oak *Quercus rubra*), urban areas and open farmlands were avoided (Fig. 1). See also Appendix Table S3 in Online Resource.

3.2. Habitat selection at the micro-scale

The presence of Crested Tits at micro-habitat scale was positively related to the proportion of conifers in the sampling area ($p < 0.05$; Table 1) and to tree canopy cover and average DBH ($p < 0.05$), while there was no effect of tree layer height on the probability of occurrence ($p > 0.05$; Table 2). This pattern was similar in the breeding and in the wintering period (Tables 1 and 2).

Table 1
Logistic regression models exploring the effects of the proportion of coniferous trees on the probability of presence of Crested Tit in each phenological period: breeding and wintering.

Variable	Coefficient ± S.E.	*z*	*p*
Breeding period			
Intercept	1.03 ± 0.44	2.36	0.002
Proportion coniferous trees	2.24 ± 0.62	3.56	>0.001
Wintering period			
Intercept	0.76 ± 0.34	2.25	0.024
Proportion coniferous trees	1.45 ± 0.45	3.25	0.001

The effect of coniferous trees had a significantly positive effect in both models.

Table 2
Logistic regression models exploring which predictor, among the tree structural variables, affected the probability of presence of Crested Tit in each phenological period (breeding and wintering).

Variable	Coefficient ± S.E.	*z*	*p*
Breeding period			
Intercept	0.69 ± 0.32	2.15	0.032
Canopy cover	1.34 ± 0.38	3.52	>0.001
Tree height	0.10 ± 0.34	0.30	0.762
Average DBH	0.74 ± 0.36	2.06	0.040
Wintering period			
Intercept	−4.68 ± 1.95	−2.4	0.016
Canopy cover	0.03 ± 0.01	2.22	0.026
Tree height	0.03 ± 0.08	0.45	0.656
Average DBH	0.12 ± 0.06	2.03	0.042

Canopy cover and average DBH had a significantly positively effect in each model.

3.3. Foraging habitat selection

Crested Tit foraged almost exclusively in the tree canopy: both in breeding (96.7% of observations, $N = 94$, $\chi^2 = 82.4$, df = 1, $p < 0.001$) and in wintering (98.3% of observations, $N = 118$, $\chi^2 = 110.1$, df = 1, $p < 0.001$) period. The species spent more time foraging in Scots Pine or other conifers than in broadleaf trees both in breeding (75.3% of observations, $N = 91$, $\chi^2 = 33.2$, df = 1, $p < 0.001$) and wintering period (92.2% of observations, $N = 116$, $\chi^2 = 82.8$, df = 1, $p < 0.001$). During breeding period, Crested Tit foraged using the canopy as whole, without selecting a specific portion neither in vertical ($\chi^2 = 0.15$, df = 2, $p = 0.95$) nor in horizontal locations ($\chi^2 = 3.58$, df = 2, $p = 0.13$; Fig. 2); moreover, the species foraged gleaning both trunks/branches/twigs and leaves/buds ($N = 24$, $\chi^2 = 0.67$, df = 1, $p = 0.414$). Conversely, during wintering period, the locations of Crested Tit in the canopy differed from the expected homogeneous distribution, both along vertical ($\chi^2 = 14.6$, df = 2, $p < 0.001$) and horizontal portions ($\chi^2 = 11.6$, df = 2, $p = 0.003$): analysing residuals, on the vertical dimension the species selected the middle third and avoided top third, while horizontally it avoided the outermost portion (Fig. 2). Moreover, during this period, the species significantly preferred foraging by gleaning trunks/branches/twigs than leaves/buds (66.7% of observations, $N = 63$, $\chi^2 = 7.00$, df = 1, $p = 0.008$).

4. Discussion

Our findings describe the habitat selection exerted by a poorly studied passerine species over its entire yearly cycle, finding support of a true habitat specialism year-round, an unusual condition in this group of insectivorous birds. Our census methods are robust and well representative of the surveyed area. The replication of the surveys in years with exceptional ecological conditions, as could be for instance a winter with extreme snow cover, may result in different selection ratios.

At the macro-scale, the species selects pure and mixed pine forests, while avoids woods composed by alien plants, farmlands and urban areas. At the micro-scale, old pine woods with dense cover are selected.

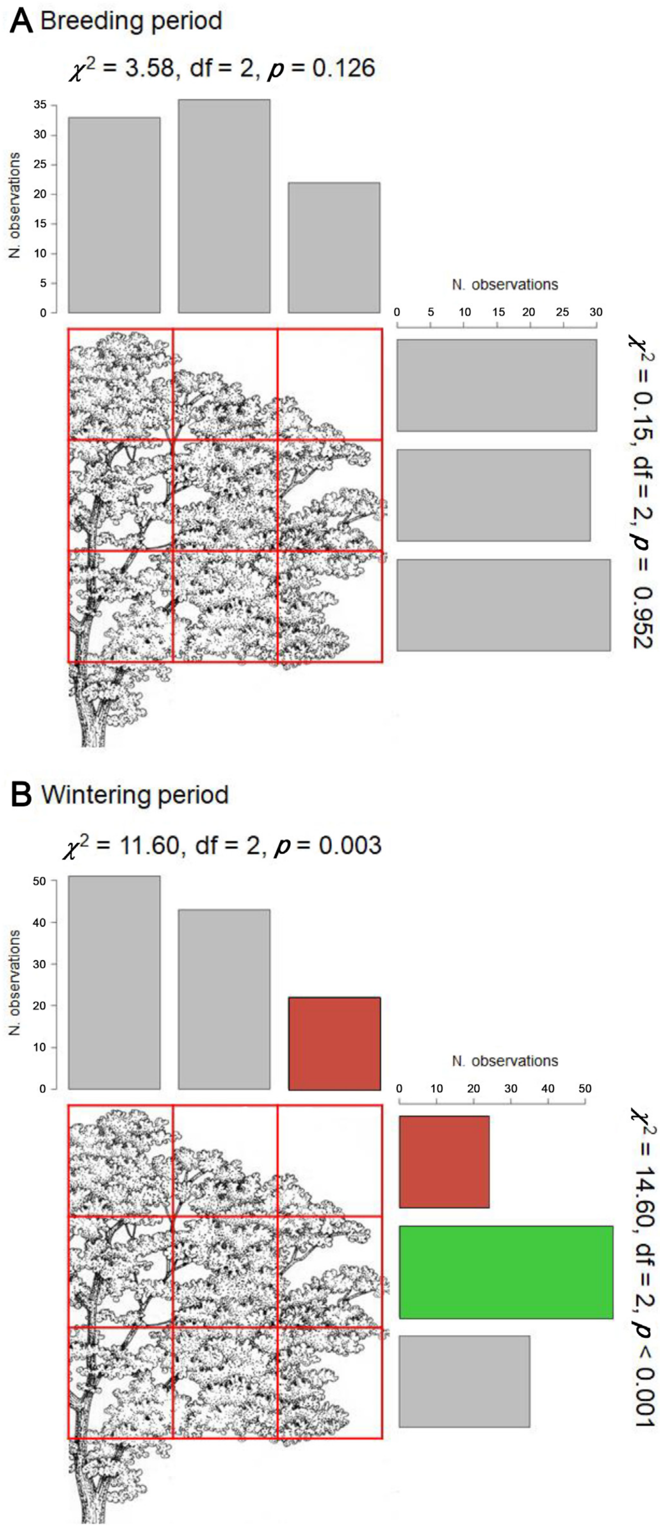

Fig. 2. Bar diagrams showing the partitioning zones of foraging individual locations in vertical and horizontal thirds (separately) in tree canopy, for (A) breeding and (B) wintering period. *Y* axes indicate number of observations. Overall significance is expressed by χ^2 scores and *p* values. During breeding period, Crested Tit foraged using the canopy as whole, without selecting a specific portion neither in vertical nor in horizontal locations. Conversely, during wintering period, the locations of Crested Tit were not equipartited neither in vertical nor in horizontal portions. Analysing residuals, only in winter, the species significantly selected middle vertical third (green bar), avoiding top third (red bar), and significantly avoided outside horizontal third (red bar).

Overall, the breeding and the wintering habitats qualitatively overlapped. At the foraging scale, the species was observed spending more time foraging in the canopies than in the understorey, using mostly the inner and middle canopies of Scots Pine in winter, gleaning trunks/branches/twigs, while during breeding period the species used the canopy as a whole, gleaning both trunks/branches/twigs and leaves/buds.

According to literature, conifers (specifically Scots Pine) were found to be important for Crested Tit at different spatial and phenological scales (Ekman, 1979; Cramp and Perrins, 1993; Summers et al., 1999; Cutini et al., 2009). At the macro-scale, the species was strictly linked to coniferous habitats occurring in the landscape but also mixed acidophilic formations (with at least 25% of Scots Pine canopy cover) were selected. As far as micro-scale selection is concerned, the likelihood of both breeding and wintering occurrence of Crested Tit increased with the increase in Scots Pine presence, even in mainly broadleaves patches. Hence, Crested Tits resulted also able to use broadleaves forest, with single Scots Pine trees, at the micro-scale, as demonstrated by other studies (Maícas and Fernández Haeger, 2004; Díaz et al., 2008; Atiénzar et al., 2009). Moreover, almost all of the birds both in breeding and in wintering period were observed foraging in Scots Pine. Crested Tits have their biology and behaviour adapted to coniferous forests (Hartley, 1987; Lens and Dhondt, 1992; Lens et al., 1994a), thus choosing Scots Pine in habitat selection may be a useful strategy to maximise their food availability (Tremblay et al., 2003; Díaz et al., 2008) and quality (Blondel et al., 1993).

Both during breeding and wintering period, the species exhibited a similar pattern in habitat selection at multi-scale level. At the macro-scale level, Crested Tit is strictly related to woodlands, avoiding open farmlands and urban areas. Previous evidence of Crested Tits using large ornamental conifer trees (chiefly cedars and fir) in urban areas, which are found in our study area, may be partially mislead by anecdotal observation (Cramp and Perrins, 1993; Brichetti and Fracasso, 2011). Indeed, woods composed of invasive alien plant species were significantly avoided: in our study area, forestry management practices have promoted dramatic changes in tree species composition in the past, so that harvested stands are dominated by pioneer invasive alien trees, such as Black Locust or high-density American Red Oak saplings, which have become established at the expense of native plant communities (Bianchi, 2002). These pure broadleaves formations had an altered vegetation structure and composition, resulting an unsuitable habitat for the species. Several studies have demonstrated that changes in after logging in forest habitats, with the entering of alien plant species, can lead to changes in avian community composition and abundance of many bird species, including tits, also for reducing in food availability (Welsh, 1987; Thompson et al., 1999; Laiolo et al., 2003; Li et al., 2020).

At the micro-scale level, habitat selection of Crested Tit was also coherent between the two different phenological periods. Wood patches with large DBH trees (i.e., old trees) were selected. Large old trees provide more ecological niches available for insects (Horák, 2017), the main prey of Crested Tit (Atiénzar et al., 2009). Moreover, Crested Tits nest in old rotten stumps, usually over 22 cm in diameter at the nest cavity (Summers et al., 1993). High canopy cover was also positively selected: greater canopy cover offers more protection from predators (Lens and Dhondt, 1993; Lens et al., 1994a), as well as a continuous, dense layer in which to forage for more abundant food resources (Lens and Dhondt, 2008).

Our results are similar to those in other parts of the species' range (Collette, 1987; Summers et al., 1993, 1999; Maícas and Fernández Haeger, 2004; Lens and Dhondt, 2008; Atiénzar et al., 2009), but also several differences emerged. This is not unexpected, since habitat selection is a context-dependent process: it varies among populations and individuals of the same species according to different local conditions, habitat availability and different features within the studied area, (the so-called 'functional response'; Holbrook et al., 2019). Hence, functional responses in habitat selection are important outcomes that characterize phenotypic plasticity for a given species, particularly in specialized ones such as Crested Tit, and thus the ability of a population to respond to spatial changes in the landscape (Mitchell et al., 2020). Multi-spatial-scale approach sheds light on habitat characteristics for context-dependent habitat selection (Robinson and Holmes, 1982; Denny and Summers, 1996; Broughton et al., 2012).

Our results reveal a difference in foraging habitat selection between breeding and wintering period: while breeding Crested Tit used the coniferous tree canopy as a whole, during winter the species selected the inner parts of the canopy. Previous studies carried out in wintering flocks also showed this behaviour, explaining how Crested Tit chose to forage in high-quality food trees and at predator-protected sites (Hartley, 1987; Lens et al., 1994a; Krams, 1996). These previous studies only concerned individuals in wintering flocks, where the dominant Crested Tit individuals usually defend the best predator-protected sites against subordinates (Lens and Dhondt, 1992, 1993). However, our results showed wintering Crested Tit foraging by gleaning trunks and branches, probably looking for overwintering insects under bark corks (Jansson and Bromssen, 1981), and therefore we found the individuals in those parts of the canopy with trunks and larger branches (i.e., the innermost parts). Conversely, the species was observed to forage in the canopy as whole during breeding by collecting pine needles, located in the most exposed canopy parts, thought the best predator-protected sites are assumed to be the inner parts of the canopy (Krams, 1996). Thus, in both periods, high-quality food sites resulted to be the main driver in foraging habitat selection, rather selecting predator-protected parts of the canopy (see Jansson et al., 1981).

Overall, we can say that Crested Tit is a specialist species associated with a sufficiently high availability of Scots Pine in the lowland mixed forests of northern Italy. The same tree species and forest-structure characteristics are selected throughout the year, with small differences occurring only on the foraging scale. These results should be used when making forest management plans. Sufficient patches of unharvested old forest with a good amount of Scots Pine must be maintained in natural parks especially in lowlands, and the forest management for species conservation must prevail over purely economic-based felling.

Authors' contribution

AB, LAW, GP, AM and AM conceived and designed this study. AB, GT, SM, EC and GG performed the study. AB, LAW, GT, SM and AM analysed the data. AB, LAW, DR, MM and AM wrote the paper. All authors read and approved the final manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Ethics statement

This research and the experiments comply with the current laws of the country in which they were performed (Italy). It was based on simple field observation without any experimental manipulation or damage to the studied birds.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.avrs.2022.100058.

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