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Research Paper

Mobbing call experiment suggests the enhancement of forest bird movement by tree cover in urban landscapes across seasons

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ABSTRACT. Local scale movement behavior is an important basis to predict large-scale bird movements in heterogeneous landscapes. Here we conducted playback experiments using mobbing calls to estimate the probability that forest birds would cross a 50-m urban area during three seasons (breeding, dispersal, and wintering seasons) with varying amounts of tree cover, building area, and electric wire density. We examined the responses of four forest resident species: Marsh Tit (*Poecile palustris*), Varied Tit (*Sittiparus varius*), Japanese Tit (*P. minor*), and Eurasian Nuthatch (*Sitta europaea*) in central Hokkaido, northern Japan. We carried out and analyzed 250 playback experiments that attracted 618 individuals. Our results showed that tree cover increased the crossing probability of three species other than Varied Tit. Building area and electric wire density had no detectable effect on crossing probability for four species. Seasonal difference in the crossing probability was found only for Varied Tit, and the probability was the highest in the breeding season. These results suggest that the positive effect of tree cover on the crossing probability would be consistent across seasons. We therefore conclude that planting trees would be an effective way to promote forest bird movement within an urban landscape.

Expérimentation de cris de houspillage suggère une augmentation des mouvement d'oiseaux selon le couvert forestier dans des paysages urbains en toutes saisons.

RÉSUMÉ. Les comportements de déplacements à l'échelle locale sont importants car ils servent de base afin de prédire les déplacements à grande échelle d'oiseaux dans des paysages hétérogènes. Nous avons utilisé des enregistrements de cris de houspillage afin d'estimer la probabilité que des oiseaux forestiers traversent une zone urbaine de 50-m lors de trois saisons (reproduction, dispersion, ainsi que hivernage) avec différent couvert forestier, zones de bâtiments, et densité de fils électriques. Nous avons examiné les réponses de quatre espèces résidentes : mésange nonette (*Poecile palustris*), mésange variée (*Sittiparus varius*), mésange de Chine (*P. minor*), ainsi que la sitelle de Naga (*Sitta europaea*) en Hokkaido Centrale, au nord du Japon. Nous avons effectué et analysé 250 enregistrements qui ont attiré 618 individus. Nos résultats démontrent que le couvert forestier augmente la probabilité d'une traverse pour trois espèces, autre que la mésange variée. Les zones de bâtiments ainsi que la densité des fils électriques n'ont pas d'effet détectable sur la probabilité de traverse des quatre espèces. Une différence saisonnière fut discernée seulement pour la mésange variée, et la probabilité la plus élevée est durant la saison de reproduction. Ces résultats suggèrent que l'effet positif d'un couvert forestier pour une traverse serait consistant durant toutes les saisons. Nous concluons donc que planter des arbres serait une mesure effective pour favoriser le mouvement des oiseaux forestiers en milieu urbain.

Key Words: *breeding season; building area; dispersal season; Hokkaido; wintering season*

INTRODUCTION

Movement, or a change in the spatial location of an organism, is a fundamental ecological process that determines the distribution, population dynamics, and community structure of organisms (Clobert et al. 2001, Nathan et al. 2008). As fragmentation of habitats proceeds, movement of individuals between habitats becomes impeded (Bélisle et al. 2001, Creegan and Osborne 2005), and the risk of extinction of regional and local populations increases (Fahrig 1998, Ferraz et al. 2007). Rapid changes in land use cause habitat loss and degradation as well as habitat fragmentation (Haddad et al. 2015, Newbold et al. 2015). Thus, how the movement of organisms among habitats can be enhanced is a matter of great concern.

Urban areas, which are among the most intensely used land, are often characterized by fragmented landscapes consisting of various dispersal habitats and a variety of factors that limit the movement of organisms, such as residential areas and pavement (Hodgson et al. 2007, Tremblay and St. Clair 2009, 2011). Thus, connectivity between isolated breeding habitats is a function of distance between them and the configuration of the elements comprising urban landscapes (Adriaensen et al. 2003). It also has been suggested that the density of the tree canopy (Gillies et al. 2011), building areas (Hodgson et al. 2007), and electric wire density (Shimazaki et al. 2016) can affect bird movement in urban landscapes. In addition, bird movement behaviors (Krebs 1971, Ekman et al. 1981, Siffczyk et al. 2003) as well as urban environments vary among seasons in urban environments.

In this study, we conducted playback experiments using mobbing calls (Desrochers and Hannon 1997, B  lisle and Desrochers 2002, Clair 2003) in experimental plots with different amounts of three urban elements (tree cover, buildings, and electric wire) during three seasons (breeding, dispersal, and wintering) and estimated the effects of these elements and seasons on the probability of forest birds to cross 50-m distances embedded in the urban area. This can be an important step to predict large-scale bird movements in heterogeneous landscapes based on the empirically measured movement data (Haddad 1999, Shimazaki et al. 2016) because habitat quality cannot be a reliable indicator of movement resistances (Haddad and Tewksbury 2005, Keeley et al. 2016, Zi  lkowska et al. 2016).

METHODS

Mobbing call and its recording

Our focal species were Marsh Tit (*Poecile palustris*), Varied Tit (*Sittiparus varius*), Japanese Tit (*P. minor*), and Eurasian Nuthatch (*Sitta europaea*), which are resident forest generalist species (hereafter: focal species). We recorded the mobbing calls of focal species (5 Marsh Tits, 2 Varied Tits, a Japanese Tit, and 2 Eurasian Nuthatches) and two other species, a Great Spotted Woodpecker (*Dendrocopos major*) and a Eurasian Treecreeper (*Certhia familiaris*), for 30 sec using a perched stuffed Ural Owl (*Strix uralensis*), which is one of the dominant predators for our focal species in our study region, in mid-April 2013 at the Tomakomai Experimental Forest of Hokkaido University (Shimazaki et al. 2016). Although it is better to use different recordings in each playback experiment to capture potential variations of mobbing calls in different locations or seasons, because the recording included definitive types of mobbing calls by focal species, we used this single mobbing call recording in all playback experiments (see Appendix 1).

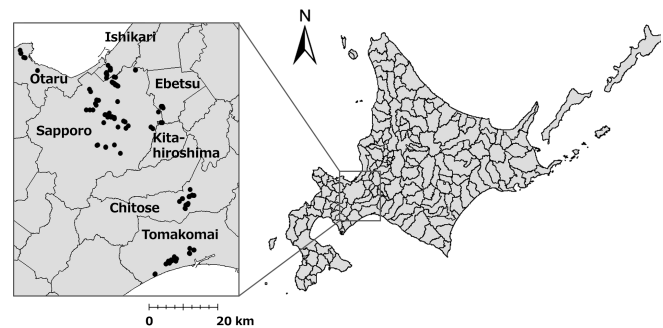
Study area and experimental plots

We conducted experiments in Sapporo, Hokkaido, Japan (43  3' N, 141  20'E) and six adjacent cities (Otaru, Ebetsu, Ishikari, Kitahiroshima, Chitose, and Tomakomai; Fig. 1) to examine the effects of three elements included in the urban landscape on bird movement. Sapporo is the fourth largest city in Japan, with a population of 1.93 million. Sapporo and the six adjacent cities are home to 2.57 million people and form a large urban area in the middle of Hokkaido.

We established 121 50  50-m experimental plots in the study area (Fig. 1). The center of one side of each plot (called the starting point) was positioned at the edge of woodlands > 2 ha in area, and the center of the opposite side (goal point) was located at a tree. The plots were 50  50-m square so that the gap crossing probabilities of the birds could be clearly differentiated (Creegan and Osborne 2005, Tremblay and St. Clair 2009). We tried to place the plots at least 400 m from each other (Tremblay and St. Clair 2009). We used Fundamental Geospatial Data (Geospatial Information Authority of Japan) to measure the ratio of building area (0–35.8%) within plots. We used color aerial photographs to manually identify individual tree canopies, and measured the ratio of tree cover (0–100%) with Quantum GIS ver. 1.8.0. The photographs were provided by the Geospatial Information Authority of Japan (<http://maps.gsi.go.jp/>). We visually checked

in the fields if buildings and/or tree cover were still present as they were in the past, because at least six years had passed since the data were generated and the photographs taken. We did not use a plot after tree cover and/or building area had been altered during the experimental periods as a consequence of tree felling or a building being demolished. We measured the total length of electric wire in each plot, and treated it as the wire density. The absolute values of Pearson's correlation coefficient of those variables were ≤ 0.55 .

Fig. 1. Study area and experimental plots. We conducted the experiments in Sapporo and six adjacent cities. Dots mean experimental plots.



Mobbing call playback experiment

The first author (A.S.) conducted the experiments with one assistant from 08:30 to 16:00 on days without heavy rain and/or strong winds (B  lisle and Desrochers 2002, Creegan and Osborne 2005) during three distinct periods: (1) breeding (6 May–17 June 2014); (2) dispersal (1 August–30 September 2014); and (3) wintering (10 December 2014–16 February 2015). We stratified the time of day at which the individual experiments were conducted to avoid the confounding of the effects of covariates and time of day.

We positioned a portable speaker (EUROPORT EPA40; Behringer, Willich, Germany) connected to a player (iPhone4S; Apple, Cupertino, California, USA or NW-E083, Sony, Tokyo, Japan) at the starting (S) and goal (G) points within 1 m from the ground and oriented the speakers to the woodland and S points, respectively. After positioning the speakers, we started playbacks at the S points and recorded the birds attracted within 10 m of the S points. We continued to play the call for 6 min unless 1 min had passed since the last new individual was attracted. Immediately after we stopped playing the call at the S points, the speaker at the G points was turned on to play the call. Then we recorded birds crossing the plots from the S to the G points. If multiple individuals of the same species formed a flock or pair, they were treated as one individual to avoid the problem of pseudoreplication. We ceased the experiment and did not collect the data when tits formed a flock ambiguously (e.g., large time lag between individuals of the same flock crossing the plot) or multispecific flocks formed. The call was stopped when 6 min had passed or all birds had crossed the plots from the S to the G points. We did not record individuals flying from anywhere other than the S to the G points. Playback volume was adjusted to 60 dB (= environmental quality standards for noise in Sapporo city) at 5

Table 1. Number of experiments and individuals attracted to start and goal points of each seasons and species.

Species	Season	Number of experiment [†]	Number at start point [‡]	Number at goal point [§]	Crossing probability
Japanese Tit	Breeding	55	83	46	0.55
	Dispersal	46	59	27	0.46
	Wintering	40	70	27	0.39
Marsh Tit	Breeding	42	58	29	0.50
	Dispersal	48	70	29	0.41
	Wintering	33	47	21	0.45
Varied Tit	Breeding	29	34	29	0.85
	Dispersal	47	60	38	0.63
	Wintering	32	53	25	0.47
Nuthatch	Breeding	14	14	9	0.64
	Dispersal	29	36	17	0.47
	Wintering	24	34	11	0.32

[†]Number of experiments when focal species were successfully attracted to start point.

[‡]Number of individuals attracted to start point.

[§]Number of individuals attracted to goal point from start point.

^{||}Crossing probability obtained by dividing number of individuals at goal point by number of individuals at start point.

m from the speaker, and we confirmed that surveyor at the S points heard the playbacks from the G points (Tremblay and St. Clair 2009). We did not conduct a survey if mobbing calls played at the G point could not be heard at the S point (Tremblay and St. Clair 2009).

Statistical analysis

We estimated the effects of tree cover, building area, electric wire density, and season on the probabilities that focal species crossed the plots (crossing probability) using logistic regression analysis. We treated the number of individual birds that were attracted to the S point in one experiment as the number of trials, and then the number of individuals crossed the plots from the S to the G points among them as the number of successes, and the crossing probability as a success probability of the binomial distribution. We then examined the effects of the predictor variables (tree cover, building area, electric wire density, and season) on the crossing probability. We constructed models for all possible combinations of variables, ranked them using Akaike's information criterion (AIC), and considered significant variables in the best model as meaningful predictor variables. However, we averaged the models if there were multiple well-supported models whose delta AIC scores were < 2, and significant variables in the averaged model were considered meaningful predictor variables. We calculated support for each model as Akaike weight (w_i) and computed a single coefficient using the w_i weighted average and the coefficient of each model. We assumed that all variables were included in every model, so the coefficient corresponding to a variable that was not selected was set to zero in some models. We used R (ver. 3.2.0) and 'MuMIn' R package (ver. 1.15.1) for the model selection and averaging.

RESULTS

We carried out the playback experiments 250 times and observed 618 individuals for the analysis (Table 1). The model selection result showed several models that were well supported, with delta AIC scores < 2 for all focal species (Japanese Tit: six models; Marsh Tit: four models; Varied Tit: five models; and Eurasian nuthatch: six models: Appendix 2). Crossing probability was

estimated to be the highest in the breeding season among the three seasons for Varied Tit (Table 2). The building area and electric wire density were not associated with the crossing probability of any of the focal species, and the RVI (Relative Variable Importance) of these variables was mostly low. The crossing probabilities of three focal species other than Varied Tit were significantly positively associated with the tree cover (Fig. 2; Table 2). When the interaction between the tree cover and season was added as a variable in the averaged model for focal species, no significant interaction terms were detected (Appendix 3).

Fig. 2. Relationship between the ratio of tree cover and crossing probability of four focal species. The continuous variable other than the tree cover were set to average and the season was set to dispersal season.

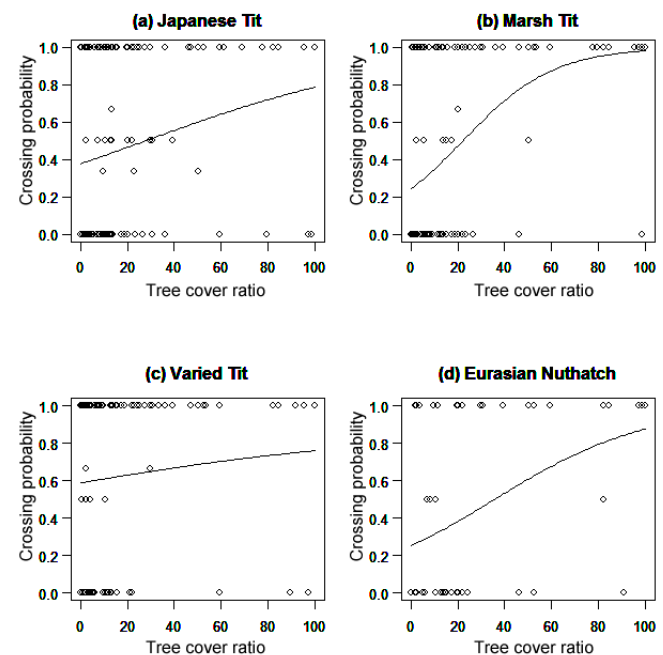


Table 2. Results of model averaging for four species in three seasons.

Species	Parameter	Estimate	SE	z-value	p-value		RVI
Japanese tit	Intercept	-0.43	0.41	1.05	0.29		
	Electric wire [†]	0.0016	0.0016	0.98	0.33		0.68
	Tree [‡]	0.018	0.008	2.34	0.02	*	1.00
	Building [§]	-0.005	0.013	0.39	0.70		0.26
	Dispersal	-0.24	0.34	0.69	0.49		0.53
	Wintering	-0.35	0.41	0.85	0.40		
Marsh tit	Intercept	-1.32	0.47	2.78	0.01	**	
	Electric wire [†]	-0.0003	0.0011	0.28	0.78		0.31
	Tree [‡]	0.052	0.011	4.57	0.00	***	1.00
	Building [§]	0.016	0.022	0.72	0.47		0.51
Varied tit	Intercept	1.67	0.60	2.78	0.01	**	
	Electric wire [†]	0.0002	0.0008	0.22	0.82		0.16
	Tree [‡]	0.009	0.010	0.91	0.36		0.64
	Building [§]	-0.005	0.014	0.36	0.72		0.30
	Dispersal	-1.27	0.56	2.24	0.03	*	1.00
	Wintering	-1.86	0.56	3.27	0.00	**	
Nuthatch	Intercept	-0.83	0.79	1.03	0.30		
	Electric wire [†]	0.0008	0.0019	0.44	0.66		0.32
	Tree [‡]	0.031	0.010	3.11	0.00	**	1.00
	Building [§]	0.001	0.015	0.07	0.94		0.19
	Dispersal	-0.39	0.63	0.61	0.54		0.50
	Wintering	-0.69	0.86	0.80	0.43		

*** < 0.001, ** < 0.01, * < 0.05.

[†]Effect of electric wire density.

[‡]Effect of tree cover.

[§]Effect of building area.

^{||}Effect of dispersal and wintering seasons compared with breeding season.

^{||}Relative variable importance (single values were obtained for two terms of seasonal effects).

DISCUSSION

The tree cover had a positive effect on the crossing probabilities of the focal species other than Varied Tit, suggesting that planting trees effectively would promote forest bird movement in urban landscapes (Fig. 2), fitting well with previous studies showing that forest birds use individual trees or small patches as stepping stones in agricultural landscapes (Gillies et al. 2011) and our previous study in the same urban area (Shimazaki et al. 2016). Although we did not formally identify the tree species in the study area, broad-leaved tree species dominated the trees in the urban area. We observed that individual birds used coniferous trees as the perches during the experiments (A. Shimazaki, *personal observation*). However, forest birds can have preferences in tree species (Holmes and Robinson 1981, Yoshii et al. 2015), and what tree species are planted may be important for the gap-crossing behavior as well as bird movements in urban area. For example, in Japan, Coal Tit (*Periparus ater*) and Goldcrest (*Regulus regulus*) are known as specialists of coniferous trees, and their abundance is higher in conifer plantations than in natural forests dominated by broad-leaved forests, though abundance of most species and therefore bird species richness are higher in natural forests (Yamaura et al. 2008, 2009). These suggest that planting broad-leaved trees may be beneficial for many bird species.

The result showing that the building area was not significant in the models for any of the focal species indicates that building density has only minor effects on the crossing probabilities of forest birds. However, our previous study found that increasing building area facilitates movement of tits and nuthatches

compared to open areas (Shimazaki et al. 2016), and Hodgson et al. (2007) showed that omnivores and nectarivores are more likely to penetrate edges adjoining high-density housing than those adjacent to low-density housing. In our previous study, we did not measure the electric wire length as we did here, and in this study wire density was the second most important variable for Japanese Tit (Table 2). Thus, the effect of building on bird movement might be confounded with that of electric wire. It seems that Psittaciformes and Passeriformes, which were the focus of Hodgson et al. (2007) and are distributed in the southern hemisphere, had different behavioral traits from our focal species, so they responded differently to increased building density.

The crossing probabilities of Varied Tit during the dispersal and wintering seasons were significantly lower than those during the breeding season. Other species also showed the similar seasonal effects though their effects were not significant (Table 2). Because the focal species form and defend territories during the breeding season (Krebs 1971), the strong response to our mobbing playback may be due to territorial aggression of respondents toward perceived intruders. Therefore, the seasonal effect on gap crossing behavior may not be due entirely to a change in gap permeability as much as to a change in testosterone levels. This is where the scale of studies like ours must be extrapolated carefully to larger scale connectivity, given that playback studies in general only test within-territory movement behavior (e.g., Sieving et al. 1996). The interaction between the tree cover and season was not supported in any of these focal species, suggesting that the positive effect of tree cover on the movement of forest birds was consistent across seasons.

We conducted a playback experiment and inferred bird movements at a 50-m scale. Although these small-scale behavioral decisions can be easily measured as the basis of the large-scale predictions (Lima and Zollner 1996, Haddad 1999, Bélisle and Desrochers 2002), large-scale movements may be driven by different motivations and cues, and cannot be extrapolated from small-scale behavioral studies (Desrochers et al. 1999, Zollner 2000, Bélisle 2005, Abrahms et al. 2017). Therefore, our results should be used alongside those generated by other approaches including large-scale translocations (Bélisle et al. 2001, Castellón and Sieving 2006, Gillies and St. Clair 2008), observation of spontaneous movements of birds (Grubb and Doherty 1999, Lees and Peres 2009), and species distributions (Watling et al. 2011).

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/1013>

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Appendix 1. Details of the mobbing call recording in the playback experiments.

Objectives

Although it is desired to use different recording in each playback experiment (Kroodsmma et al., 2001), we used a single mobbing call recording recorded in the breeding season in all playback experiments. To justify this, we assessed whether the recording can be considered a representative of mobbing calls of our focal species. Specifically, using many available mobbing call recordings in xeno-canto (<http://www.xeno-canto.org/>, accessed at 0130-2017), we compared the number of discrete mobbing calls of our focal species in our recording with those in other regions because the Paridae species has several types of mobbing calls that might convey different information (Hailman, 1989). In addition, we examined whether the number of discrete mobbing calls differs between breeding and non-breeding seasons. In these assessments, we focused on one of our focal species (the marsh tit) for following reasons: 1) it is known that various species including the family Paridae respond to not only conspecific mobbing calls but also interspecific ones (e.g., Bélisle and Desrochers, 2002). 2) The marsh tit has wide distribution range across the old world as well as is one of the most common Paridae species in our study region. The following analyses were performed using Adobe Audition 3.0 software and R software (ver. 3.2.0) with “tuneR” and “seewave” packages.

Compiling mobbing call recordings from xeno-canto

In available recordings of the marsh tit in xeno-canto, we compiled 43 mobbing call recordings which were originally categorized as “alarm call” or “aggression call”. Of these, we excluded recordings with high levels of background noise (e.g., wind noise, other bird calls) from further analyses. We also excluded recordings that accompanied with marsh tits’ songs because “alarm calls” uttered in such situation might convey different information compared to those uttered to predators. As a result, we used 30 mobbing call recordings (mean recording times (sec) $\pm$ Standard Deviation = 60.40 ± 39.78) recorded in several countries (14 in Germany, 9 in Poland, 3 in France,

2 in Netherlands, 1 in Czech and Sweden) in the following analyses.

Comparisons of the number of discrete mobbing calls in different locations and seasons

Based on the sound spectrograms, we counted the number of spectrally discrete mobbing calls for our single recording, all xeno-canto recordings (hereafter the xeno-canto recordings, $n = 30$), and subsets of the xeno-canto recordings in the breeding season (March to August, hereafter the nonbreeding recordings, $n = 8$) and in the non-breeding season (September to February, hereafter the nonbreeding recordings, $n = 22$).

We identified four spectrally different types of mobbing calls of the marsh tit in all recordings we assessed (Fig A1.1). Hereafter, we referred to each type of mobbing calls as type I, II, III, and IV calls, respectively. Among them, our 30-sec recording included three types of mobbing calls (types I, II and III). Specifically, the recording included 20 type I calls, 13 type II calls and 6 type III calls. The type I calls consisted of a single “tiii” note (Fig A1.1a). The type II calls consisted of a single “chicka” note and various number of “dee” notes (Fig A1.1b), which is an important metric of Paridae’s mobbing call quality (Courter and Ritchison, 2010). The number of “dee” notes in type II calls (mean $\pm$ SD) was 2.31 ± 1.18 (Range: 0-5). The type III calls consisted of multiple “jee” notes (Fig A1.1c) and the number of “jee” notes (mean $\pm$ SD) was 9.50 ± 3.27 (Range: 5-13). The xeno-canto recordings, the nonbreeding recordings and the breeding recordings had four different types of mobbing calls (types I, II, III and IV). The mean numbers of different types of mobbing calls ($\pm$ SD) were 1.30 ± 0.47 in the xeno-canto recordings ($n = 30$), 1.26 ± 0.49 in the breeding recordings ($n = 8$) and 1.30 ± 0.47 in the nonbreeding recordings ($n = 22$). The seasonal difference (breeding vs. non-breeding seasons) was not significant (t-test; $p = 0.77$). The type IV calls consisted of multiple “pi” or “picho” notes (Fig A1.1d) and were included in only two recordings, suggesting that this type of mobbing call would be rare. Thus, these results suggest that our single recording includes almost all types of mobbing calls of the marsh tit and there are no seasonal variations of their mobbing calls, indicating that our 30-sec recording can be considered a representative mobbing calls of our focal species.

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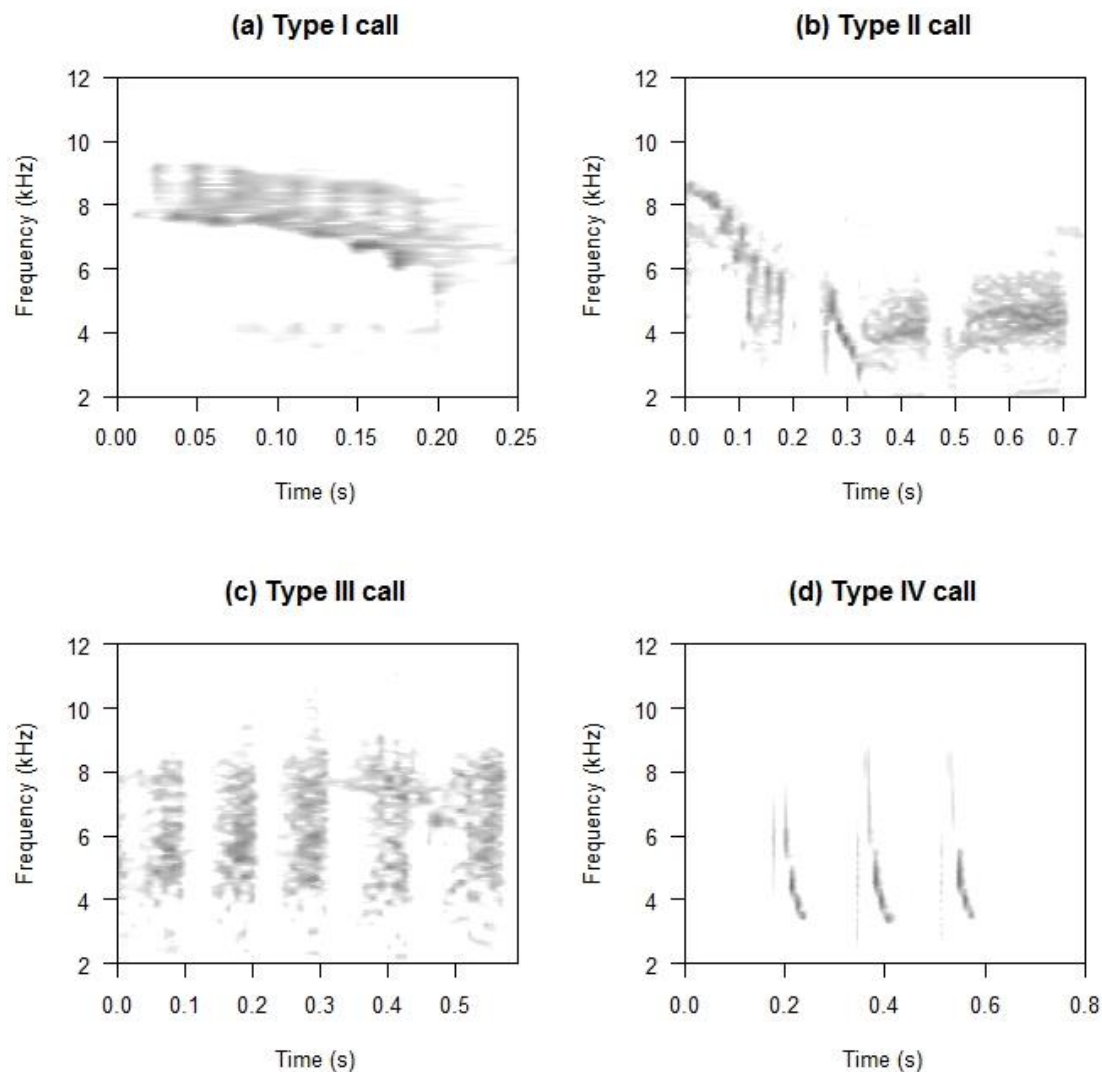


Fig. A1.1. Examples of sound spectrograms of the mobbing calls of the marsh tit. We draw spectrograms of the type I, II, III calls using the recording used in the playback

experiments. The sound spectrogram of the type IV call was drawn using one of xenocanto recordings (XC127377).

Appendix 2. Results of model selection for four species.

Appendix A2.1. Results of model selection for four species. Models with delta AIC <2 are shown.

Japanese Tit	Intercept	Electric wire †	Tree ‡	Building §	Season	AIC	ΔAIC ¶	Weight
	-0.47	0.0022	0.020		+	267.7	0	0.17
	-0.80	0.0021	0.020			267.9	0.22	0.15
	-0.07		0.017		+	268.2	0.51	0.13
	-0.42		0.017			268.4	0.71	0.12
	-0.21	0.0027	0.017	-0.020	+	268.6	0.96	0.10
	-0.54	0.0027	0.017	-0.020		268.9	1.17	0.09
Marsh Tit	Intercept	Electric wire †	Tree ‡	Building §	Season	AIC	ΔAIC ¶	Weight
	-1.07		0.049			195.3	0	0.30
	-1.62		0.055	0.029		195.4	0.07	0.29
	-1.50	-0.0014	0.054	0.035		196.7	1.42	0.15
	-1.00	-0.0004	0.048			197.2	1.92	0.11
Varied Tit	Intercept	Electric wire †	Tree ‡	Building §	Season	AIC	ΔAIC ¶	Weight
	1.54		0.014		+	175.6	0	0.27
	1.76				+	176.6	1.01	0.16

	2.13			-0.023	+	177.1	1.53	0.13
	1.35	0.0011	0.015		+	177.2	1.56	0.12
	1.73		0.012	-0.010	+	177.4	1.77	0.11

Nuthatch	Intercept	Electric wire †	Tree ‡	Building §	Season	AIC	ΔAIC ¶	Weight
	-1.08		0.029			97	0	0.22
	-0.22		0.029		+	97.1	0.06	0.21
	-0.71	0.0027	0.034		+	97.9	0.9	0.14
	-1.56	0.0026	0.033			98	0.94	0.14
	-0.44		0.032	0.012	+	99	1.95	0.08
	-1.09		0.029	0.000		99	2	0.08

† Effect of electric wire density. ‡ Effect of tree cover. § Effect of building area.

|Effect of season (indicating that whether the terms were included or not). ¶

Differences in AIC with the model having the smallest AIC. ||Akaike weights showing the likelihood that the individual model is the best model.

Appendix 3. Statistical analysis with an interaction between season and the tree cover.

We averaged the models with interaction terms for individual species to consider the possible season-specific effects of tree cover.

Table A3.1. Results of model averaging with interaction between the tree cover and seasons.

Species	Parameter	Estimate	SE	z value	p value
Japanese tit	Intercept	-0.31	0.46	0.67	0.50
	Electric wire †	0.0016	0.0016	0.97	0.33
	Tree ‡	0.014	0.012	1.19	0.23
	Building §	-0.005	0.013	0.39	0.70
	Dispersal	-0.42	0.49	0.85	0.39
	Wintering	-0.56	0.55	1.02	0.31
	Tree × Dispersal ¶	0.007	0.014	0.47	0.64
	Tree × Wintering ¶	0.008	0.016	0.47	0.64
Marsh tit	Intercept	-1.32	0.47	2.78	0.01 **
	Electric wire †	0.000	0.001	0.28	0.78
	Tree ‡	0.052	0.011	4.57	0.00 ***
	Building §	0.016	0.022	0.72	0.47

Varied tit	Intercept	1.72	0.61	2.78	0.01	**
	Electric wire †	0.0002	0.0008	0.21	0.84	
	Tree ‡	0.006	0.013	0.47	0.64	
	Building §	-0.004	0.013	0.34	0.74	
	Dispersal	-1.34	0.62	2.15	0.03	*
	Wintering	-1.92	0.60	3.13	0.00	**
	Tree × Dispersal ¶	0.004	0.013	0.31	0.76	
	Tree × Wintering ¶	0.003	0.012	0.28	0.78	
Nathatch	Intercept	-0.78	0.83	0.93	0.35	
	Electric wire †	0.0008	0.0019	0.43	0.67	
	Tree ‡	0.034	0.018	1.86	0.06	.
	Building §	0.001	0.013	0.06	0.95	
	Dispersal	-0.33	0.74	0.44	0.66	
	Wintering	-0.94	1.03	0.90	0.37	
	Tree × Dispersal ¶	-0.006	0.019	0.32	0.75	
	Tree × Wintering ¶	0.002	0.017	0.11	0.91	

‘***’ < 0.001, ‘**’ < 0.01, ‘*’ < 0.05, ‘ · ’ < 0.1

The interactions were not included in model of marsh tit (models with interaction terms

had >2 delta AIC).

† Effect of electric wire density. ‡ Effect of tree cover. § Effect of building area. |
Effect of dispersal and wintering seasons compared with breeding season. ¶ Effect of
interaction between tree cover and dispersal/wintering seasons.

Appendix 4. Source data and R code to analyze the data.

Please [click here](#) to download file 'appendix4.zip'.
