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Urban permeability for birds: An approach combining mobbing-call experiments and circuit theory

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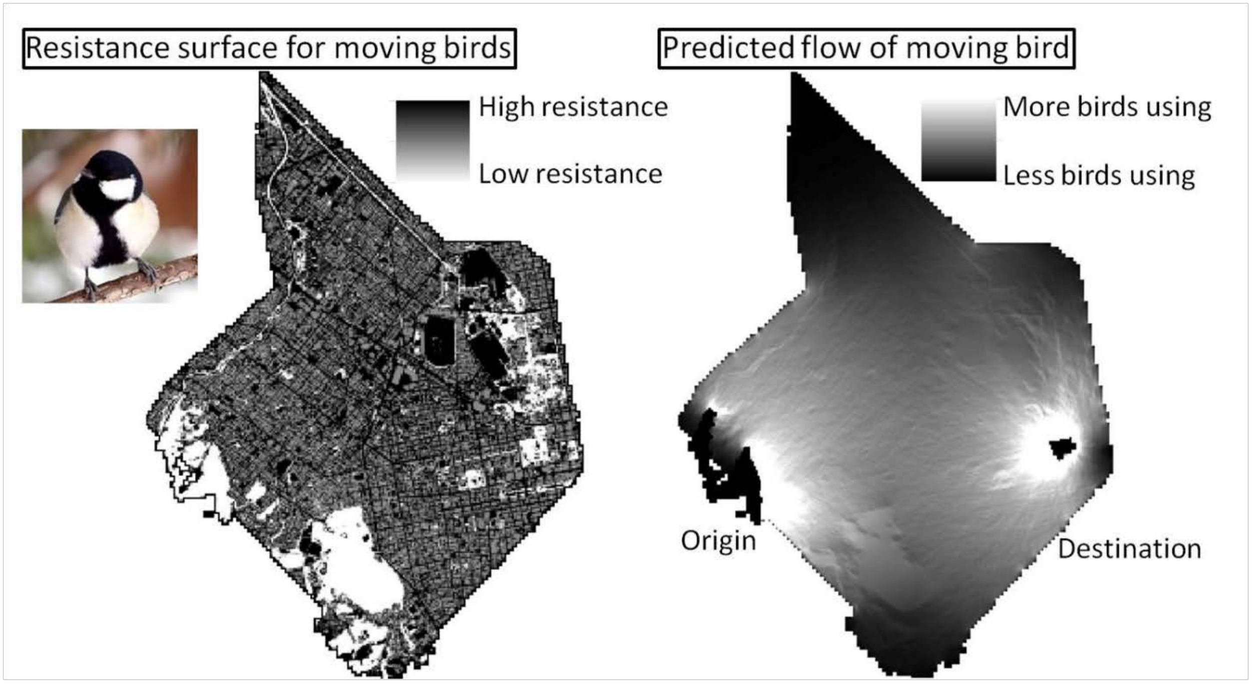
Abstract

The urban matrix was recently shown to be a mosaic of heterogeneous dispersal habitats. We conducted a playback experiment of mobbing calls to examine the probabilities of forest birds to cross a distance of 50 m over urban matrix with different land-cover types in an urban area. We treated the reciprocal of the crossing probabilities as a movement resistance for forest birds. We drew resistance surfaces based on the land-cover maps of urban XXX. We applied a circuit theory to examine the relative role of a detour route consisting of a riparian corridor and urban matrix for dispersing forest bird individuals from continuous forest to an isolated green space in the midst of an urban area. Our results showed that wood cover had the highest crossing probability, while open land (grassland and pavement) had the lowest probabilities. Buildings and water surface displayed an intermediate probability. Resistance surfaces and flow maps at 25- and 50-m resolutions were very similar and suggested that dispersing individuals are likely to use the intervening building areas that dominate the urban matrix rather than detour through riparian corridors. Our results showed the useful combination of experimental approaches and circuit theory, and the importance of the spatial configuration of corridors, as well as the composition and management of dispersal habitats, to landscape connectivity.

Keywords Corridor・Dispersal habitat・Field experiment・Isolated tree・Matrix・Moving cost

Graphical abstract



Highlight

- Tree planting in open spaces can facilitate forest bird movements in urban area.
- Buildings can be a permeable landscape component for forest birds due to the existence of vertical structure.
- Building matrix dominating the urban landscape is likely to contribute to bird movements more than a detour riparian corridor.

1. Introduction

Urban areas are currently expanding worldwide (Grimm et al. 2008), and the value of biodiversity conservation in urban areas has been increasing, not only because of its importance for urban biodiversity, but also in a global biodiversity context (Savard et al. 2000; Miller 2005). In urban areas, green spaces such as parks and shrines provide suitable breeding habitats for many species (e.g., Dallimer et al. 2012; Soga et al. 2014), and green spaces well connected with other green spaces and continuous forests maintain higher species richness and abundance of varied taxa (e.g., Natuhara and Imai 1999; Soga and Koike 2013; Myczko et al. 2014). Therefore, restoration and conservation of urban green spaces and their connectivity are of prime importance for biodiversity conservation in urban areas.

In urban areas, however, conservation actions to create new large green spaces are often not feasible due to high land prices (Naidoo et al. 2006). On the other hand, restoring and preserving connectivity is a more realistic and potentially cost-effective conservation option (Baguette et al. 2013). Urban landscapes have recently been shown to be mosaics of various “dispersal” habitats (Cline and Hunter 2014) with different resistances to bird movements, such as rivers and pavements (Tremblay and St. Clair 2009). Therefore, bird movements are a function of not only straight-line distances between breeding habitats, but also the composition and configuration of dispersal habitats (Adriaensen et al. 2003). Hence, understanding and predicting movements of organisms across heterogeneous landscapes is crucial to the development of an effective conservation strategy (Lima and Zollner 1996; Bélisle 2005).

To consider movements in heterogeneous landscapes, a movement cost map is required for a focal landscape (Richard and Armstrong 2010). However, measuring the movement or travel costs (e.g., energy consumption, predation risk: Bélisle 2005) of varied land-cover types and drawing the corresponding cost maps are often difficult. Therefore, movement costs or resistances (i.e., the antonym of permeability) are usually estimated based on expert opinion, or approximated by the habitat quality based on the species distribution models (Beier et al. 2011; Zeller et al. 2012). Nevertheless, because habitat quality is not always correlated with movement resistances (Rosenberg et al. 1998; Haddad and Tewksbury 2005), directly measuring movement costs or resistances is preferable.

Circuit theory has been adapted for ecological studies to predict landscape connectivity and simulate animal movements in heterogeneous landscapes as a flow of an electrical current in a circuit (McRae et al. 2008; McRae and Shah 2009). In circuit theory, electrical resistance and voltage are comparable to “movement resistance” and “random walk probability” and the value of the current density corresponds to the number of individuals moving through parts of the landscape (McRae et al. 2008). Typically, landscapes are divided into equally sized grid cells, and a movement resistance can be assigned to each cell. The theory enables us to evaluate the possible movement routes in the landscape by predefining the start (departure) and end nodes. The advantage of circuit theory relative to the other methods of connectivity evaluation (e.g., least-cost method, graph theory) is that it integrates all of the possible pathways into connectivity calculations and offers a measure of isolation assuming a random walk (McRae et al. 2008).

It seems usual in urban landscape that a riparian forest corridor performing movement path of forest wildlife and connecting habitats makes a detour and the urban matrix between habitats consists primarily of buildings and roads (e.g. Fig. 1). In such case, one can straightforwardly hypothesize, given the high moving resistances of the urban matrix, that forest birds moving between two habitats use a detour route consisting of the riparian corridor (corridor hypothesis; cf. Bélisle and Desrochers 2002; Gillies and St. Clair 2008). An alternative hypothesis is that forest birds directly move from one greenspace to another, given that forest birds are not especially reluctant to enter the urban matrix (matrix hypothesis), as shown by Hodgson et al. (2007). In this study, we compared the likelihoods of two hypotheses introduced above using field experiments and the application of circuit theory. First, we quantified the probabilities of forest bird individuals to cross a distance of 50 m over heterogeneous dispersal habitats (wood cover, water surface, building, pavement and grassland) in urban landscapes using the playback of mobbing calls (Desrochers and Hannon 1997; Bélisle and Desrochers 2002). We conveniently treated the reciprocal of the probabilities as a movement resistance (i.e., the substitution of moving cost), and drew resistance surfaces by assigning resistances to each grid cell according to the respective land cover types at resolutions of 50-m. We also constructed a 25-m resolution resistance surface to accurately represent the fine-grained distribution of urban structure such as roads and rivers. We applied circuit theory to the resistance surfaces to predict the relative contribution of the riparian corridor and urban matrix to the movement of forest birds from forests surrounding the urban area to a green space in the midst of the urban area. To our knowledge, this is the first study that applied circuit theory to the resistance surface based on directly measured movement resistances.

2. Methods

2.1. Study area and plots

The study was conducted in the cities of Sapporo (43 3N, 141 20E), Ebetsu and Ishikari, Hokkaido, northern Japan. Sapporo is the fourth largest city in Japan, with a population of 1.93 million. Continuous forest, which acts as a source habitat for many forest species, spreads across the southeast parts of Sapporo (Fig. 1). The campus of XXX and its botanical garden contains native woodlands that exist as forest remnants and also have extensive tree plantings. The large number of forest birds has been observed in these woodlands (xxx). A riparian forest corridor extends from the continuous forest to the botanical garden, making a detour to the north (Fig. 1). The urban matrix between the continuous forest and the botanical garden consists primarily of buildings and roads. Yamanote is located at the east end of the continuous forest, and was used as the source node in the application of circuit theory while the botanical garden of XXX was treated as the end node (Fig. 1).

Color aerial photographs taken after 2007 and provided by the Geographical Survey Institute of Japan were used to select survey plots. Based on the aerial photographs, we categorized the landscape into five land-cover types (wood cover, grassland, pavement, buildings and water surface) which are common in this urban landscape. Grassland included farmland that was covered by herbaceous vegetation. We selected 71 plots which were 50 ×

30 m in the extent and differed in the ratio of five land-cover types (wood cover: 0 - 100.0 %; grassland: 0 - 100.0 %; pavement: 0 - 92.9 %; buildings: 0 - 69.0 %; water surface: 0 - 99.5 %; Appendix A). These ratios were not correlated each other ($|r| < 0.41$). Because forest birds cross non-forest gaps in straight lines to reach mobbing calls (Desrochers and Hannon 1997), we assumed that land-cover types more than 15 m from lines did not greatly influence the gap-cross decision of birds. We confirmed such behavior in our experiments. We tried to establish the plots to be at least 400 m apart. The mean, minimum, and maximum distances between nearest neighbor plots were 760 m, 71 m, and 6,416 m respectively ($n = 71$). Each plot was composed of a 50-m × 30-m rectangle, and we examined the probability of forest bird individuals to cross these rectangles embedded in a complex of the land-cover types. We chose 50 m because gap-cross probabilities can be clearly differentiated at around this distance (e.g., Tremblay and St. Clair 2009). Each plot met the following two conditions (Fig. 2): (i) A woodland larger than 2 ha (which we call the starting point) and a tree (goal point) were spaced apart by 50 m (except for plots in the woodland [>80% wood cover plots]). (ii) No land-cover types were found to clearly enhance forest bird movements (e.g., wood cover) within 50 m on long side of the rectangles (except for the plots in the woodland).

2.2. Playback experiment

We conducted experiments from 09:00 to 15:00 on days without heavy rain and/or strong winds (Bélisle and Desrochers 2002; Creegan and Osborn 2005) from 25 June to 29 August 2013 for 55 plots in the urban matrix and from 6 to 15 August 2014 for 16 woodland plots. In total, we conducted 84 experiments in 71 plots by two surveyors. When we used the same plots multiple times or plots less than 400 m distant from the nearest plots, we spaced two successive trials at least 2 weeks apart to prevent habituation of birds to the mobbing call (Tremblay and St. Clair 2009).

We examined the responses of the following six bird species to the mobbing call: Marsh Tit (*Poecile palustris*), Willow Tit (*Poecile. montanus*), Coal Tit (*Periparus ater*), Varied Tit (*Poecile. varius*), Japanese Tit (*Parus minor*), and Eurasian Nuthatch (*Sitta europaea*). These species are forest dwellers and are frequently observed in Sapporo throughout the year. The mobbing call lasted 30 s and contained the call patterns of various species of tits and was recorded in mid-April 2013 with a stuffed Ural Owl (*Strix uralensis*) at the Tomakomai Experimental Forest (TOEF) of XXX. The recorded calls contained calls of Marsh Tit, Varied Tit, Eurasian Nuthatch, Great Spotted Woodpecker (*Dendrocopos major*), and Treecreeper

(*Certhia familiaris*).

We positioned one portable speaker (EUROPORT EPA40, Behringer, Germany) connected to the player (Apple iPhone4S, Apple, USA or NW-S760, Sony, Japan) at each of the start (S) and goal (G) points within 1 m from the ground, and oriented to the woodland and S points, respectively (Fig. 2). After positioning of the speakers, the surveyor at the S points played the calls and recorded the attracted birds within 10 m of the S points. We stopped the playbacks when no new individuals were attracted for a duration of 1 min after the last new individual had been attracted. The longest playback period was 6 min. The volume of the playback was adjusted to 60 dB at 5 m distant from the speaker (also at the G points). As soon as we stopped the playback at the S points, we turned on the playback at the G points. We presumed that birds at the S points heard the mobbing calls played back at the G points, given that the surveyor at the S points heard the mobbing calls from the G points (Tremblay and St. Clair 2009). The playback was continued until either 6 min had passed or all bird individuals attracted to the S points had reached the G points. The surveyor at the S points recorded whether each individual crossed, and the surveyors at the G points assisted in the identification of bird individuals. If multiple individuals of the same species formed a flock or pair, we treated them as one individual. We stopped and did not conduct further experiments when we judged that tits formed multispecies flocks. All recorded individuals comprising the same flock made the same crossing decisions. When we lost the track of the individuals after the playback at the G points was turned on and could not judge whether individuals came to G point was ones we observed at S point or not, we excluded these individuals from our records. We also excluded individuals from our records when we could not judge clearly whether they had joined the same group (e.g., when large time lapses occurred between individuals departing at the S points.)

2.3.Calculating crossing probabilities

We estimated the matrix-crossing probability per individual using logistic regression analysis. We treated six tit species as the same because the sample size was not large enough for analysis when they were treated separately. We treated the number of individuals attracted to the S points as the number of trials, the number of individuals crossing the matrix (i.e., reaching the G points) as the number of successes, and the matrix-crossing probability as a success probability, which can depend on the ratio of five land-cover types, in a binomial distribution. We treated the ratios of five land-cover types as continuous explanatory variables and omitted an intercept in the linear predictor (cell means method: Kéry 2010). Hence, the individual coefficients means the matrix-crossing probability (at logit scale) given that grid cells were totally covered by the respective land cover types (we call this model as ‘five variables model’). The analyses were performed using R version 3.0.1 (R Development Core Team 2013).

2.4. Resistance surfaces and circuit theory

Because the estimates of the pavement and the grassland were similar (see results), we treated them as a single land cover type (open land). Therefore, we extracted four land cover types in Sapporo urban area (Fig. 1), and constructed the logistic regression model with four land-cover types (four variables model). We used the color aerial photographs taken after 2007 provided by the Geographical Survey Institute of Japan to manually identify individual tree canopies with Quantum GIS version 1.8.0 at 1:2,000-scale. The water area and the buildings were extracted using the data provided by the Geographical Survey Institute of Japan (http://fgd.gsi.go.jp/download/). We treated the rest of the urban area as open land.

We gridded this land-cover map by 25- and 50-m resolution cells, and predicted the matrix-crossing probabilities of individual cells based on the ratios of four land cover types with the constructed logistic regression model at two resolutions. We then calculated the moving resistances of each grid cell as the reciprocal of the crossing probabilities (P_i):1/P_i, because the probability of movement between the pair of nodes corresponds to the conductance in a circuit, and the conductance is the reciprocal of the resistance (McRae et al. 2008). We applied circuit theory to these maps with CircuitScape version 3.5 (McRae and Shah 2009), in which Yamanote and the botanical garden were used as the source and end nodes, respectively, of the circuit (Fig. 1). The interiors of the botanical garden and Yamanote were assumed to be no resistance (i.e., forest birds could move freely within these areas and could exit in any direction). We calculated the effective resistance of a whole circuit and obtained current flow map throughout the study area (Fig. 3). We compared the total amounts of current density (the amount of current flow summed across the grid cells) and mean current density between the riparian corridor and whole study area of 25-m resolution map which identified resistance heterogeneity better than 50-m resolution map.

3. Results

3.1. Mobbing call experiments

In the experiments, we observed 95 Japanese tits, 46 willow tits and marsh tits (distinguishing these two species was difficult in field observations), 30 varied tits, 18 Eurasian nuthatch, 6 coal tits and 2 unspecified individuals of tit family. Since we treated multiple individuals of the same species coming together as one individual, the above numbers were reduced to 93 Japanese tits and 45 willow and marsh tits (the numbers of other species didn't change); totally 194 individuals at S points in 84 experiments conducted in 71 plots. The focal species showed the similar relative frequencies to five land-cover types (Appendix B). In total, of 194 individuals attracted to the S points, 115 individuals (59 %) reached G points. In five variable model, wood cover had the highest crossing probability, and its 90% CI did not overlap with that of grassland and pavement (Table 1; Appendix C). Grassland and pavement had similar crossing probabilities. Building and water surface had the intermediate crossing probabilities. We then next constructed models with four explanatory variables by treating pavement and grassland as a single land cover type (four variable models), and obtained similar results; however, 95% CI of crossing probability for wood cover did not overlap with that of open land (Table 1).

3.2. Predicted moving routes

Although a resistance surface of 25-m resolution identified a larger amount of high resistance grid cells dominated by open land than a land-cover map at 50-m resolution (Fig. 1), the resultant flow maps were similar (Fig. 3). Current flows were concentrated in an ellipse-shaped area, in which the major axis of the ellipse was matched with the straight line between Yamanote and the botanical garden. A higher current density existed inside the riparian corridor than in the adjacent cells, but it was equal or lower than in the ellipse-shaped area. The riparian corridor covered about 5% of the total study area and the cumulative current density for the riparian corridor was also about 5% of the total current density for the total area (Table 2). So, the mean current density for the riparian corridor was nearly equal to that of the total area. The circuit theory results were not largely altered if we used the complements of the crossing probabilities ($1 - P_i$) instead of the reciprocal as the moving resistance (data not shown).

4. Discussion

4.1. Crossing probabilities of heterogeneous urban matrix

Forest birds are well known to be reluctant to cross open spaces (Desrochers and Hannon 1997; Bélisle and Desrochers 2002; Tremblay and St. Clair 2009). Grassland and pavement tended to show lower crossing probabilities, and when they were treated as a single land cover type (open land), their crossing probabilities were significantly different from that of wood cover. This result is consistent with previous reports, and showing that the existence of trees increased the crossing probabilities in urban area. It is also indicated that tree planting in open spaces can facilitate forest bird movements across whole landscapes. This finding could be expected because forest birds frequently use isolated trees as stepping stones when crossing open habitats (Gillies et al. 2011).

Hodgson et al. (2007) observed bird movements at forest edges adjoining residential housing. They found that 30–50% of bird individuals entered the housing matrix. We motivated forest birds to cross urban matrix using the mobbing call and similarly found that around 60% of forest birds crossed the building matrix (mainly composed of houses). The results of these two studies suggest that buildings do not constitute an impenetrable barrier to the movement of forest birds. The vertical structures of buildings would be expected to play a role similar to that of isolated trees and enhance forest bird movements. Indeed, we observed frequently that birds crossing the building matrix used artificial structures, such as the Yagi antennas and electric cables, as perches (Appendix D).

Contrary to previous work in North America showing that water surface impeded bird movements (St. Clair 2003; Tremblay and St. Clair 2009), our results demonstrated that the crossing probability of water surface could be comparable to that of wood cover. The reason for this discrepancy is not clear, but our study area may have low densities of predators and predation risks.

4.2. Predicted bird movements in the heterogeneous urban landscape

Compared with a resolution of 50 m, a 25-m-resolution resistance map identified larger amounts of high-resistance grid cells dominated by pavement and grassland (Figs. 1, 3). However, little difference was observed in the current flows between the maps. Because buildings with intermediate crossing probabilities dominated the urban matrix in our study area, a slight increase in the number of impenetrable land-cover types would not be expected to greatly affect the current flows. We predicted that forest birds would move through the urban matrix in heterogeneous urban landscapes using multiple pathways (extensively elongated ellipse-shaped areas) rather than a single route. Furthermore, mean current density of the riparian corridor was nearly equal to that of total area irrespective of its high crossing probability. This suggests that a detour route consisting of a riparian corridor may play a minor role in the movement of forest birds from continuous forests to isolated forests in the urban matrix; thus the spatial configuration of the corridors, as well as the composition and management of the dispersal habitats, are important for enhancing landscape connectivity.

Because habitat quality is not always a reliable indicator of moving resistances (Rosenberg et al. 1998; Haddad and Tewksbury 2005), the measurement of the moving resistances of varied matrix of land-cover types using easily conducted experimental approaches (e.g., playback of mobbing calls) should be encouraged. Our conclusion that forest birds are likely to reach urban green spaces using the housing matrix was derived by summing the movements of small scales over large scales. This type of prediction of movement behavior at the landscape scale from local movements can be a promising scale-up approach due to its efficiency and the control for motivations to cross gaps and locations where data collection was conducted. (Desrochers et al. 1999; Haddad 1999). However, our conclusion is a prediction at the smaller scale, and needs to be tested by other approaches (e.g., radio tracking, recently developed modeling approach: Gillies and St. Clair 2008; Graves et al. 2014), because animal movement and behavior can differ at different scales (Johnson et al. 2002) and experimentally motivated birds are expected to have a different temperament than naturally dispersing individuals (Bélisle 2005). Although we treated the six species of tit as being the same because of their similar life histories and the small sample size (a tentative analysis showed similar responses among the species), differences may exist in the responses to different types of land cover among species. Thus, further studies are required to identify the differences among species.

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List of tables

Table 1 Result of logistic regression for two models.

We first constructed the logistic regression model with five explanatory variables, and next constructed the model with four explanatory variables by treating grassland and pavement as a single land cover type (open land).

[1] Coefficients of logistic regression analysis to represent crossing probabilities (at logit scale).

[2] Estimated crossing probabilities derived from the mean estimates of regression parameters (β): = 1/(1+exp(-β)).

[3] 95% confidence intervals (CIs) of the crossing probabilities derived from the CIs of regression parameters.

[4] 90% confidence intervals (CIs) of the crossing probabilities derived from the CIs of regression parameters.

[5] Movement resistance (1 / crossing probability).

[6] In four variables model, the grassland and the pavement were integrated into the open.

Table 2. Current densities flowing thorough a whole study area and riparian corridor.

[1] Number of grid cells within the whole study area and riparian corridor in the 25 m resolution resistance surface.

[2] Total amounts of current density.

[3] Mean current density per grid cell.

Note that riparian corridor was included in the total area.

Table 1 Result of logistic regression for two models.

	Variable	Coefficients[1]	SE	Crossing probability[2]	95% CI[3]	90% CI[4]	Movement resistance[5]
Five variables model	Wood cover	1.38	0.46	80	63-91	66-90	1.25
	Grassland	-0.04	0.35	49	32-66	35-63	2.04
	Pavement	-0.23	0.50	44	23-68	26-64	2.27
	Buildings	0.44	0.61	61	32-84	36-81	1.64
	Water surface	0.98	0.74	73	41-93	46-91	1.37
Four variables model	Wood cover	1.38	0.46	80	63-91	66-90	1.25
	Open land[6]	-0.11	0.28	47	34-61	56-59	2.13
	Buildings	0.35	0.54	59	33-81	37-78	1.69
	Water surface	0.98	0.74	73	41-93	46-91	1.37

We first constructed the logistic regression model with five explanatory variables, and next constructed the model with four explanatory variables by treating grassland and pavement as a single land cover type (open land).

[1] Coefficients of logistic regression analysis to represent crossing probabilities (at logit scale).

[2] Estimated crossing probabilities derived from the mean estimates of regression parameters (β): = 1/(1+exp(-β)).

[3] 95% confidence intervals (CIs) of the crossing probabilities derived from the CIs of regression parameters.

[4] 90% confidence intervals (CIs) of the crossing probabilities derived from the CIs of regression parameters.

[5] Movement resistance (1 / crossing probability).

[6] In four variables model, the grassland and the pavement were integrated into the open.

Table 2. Current densities flowing thorough a whole study area and riparian corridor.

	Number of grid cells[1]	Cumulative current density[2]	Mean current density[3]
Total area	42346	218.18	0.0052
Riparian corridor	2242	11.75	0.0052

[1] Number of grid cells within the whole study area and riparian corridor in the 25 m resolution resistance surface.

[2] Total amounts of current density.

[3] Mean current density per grid cell.

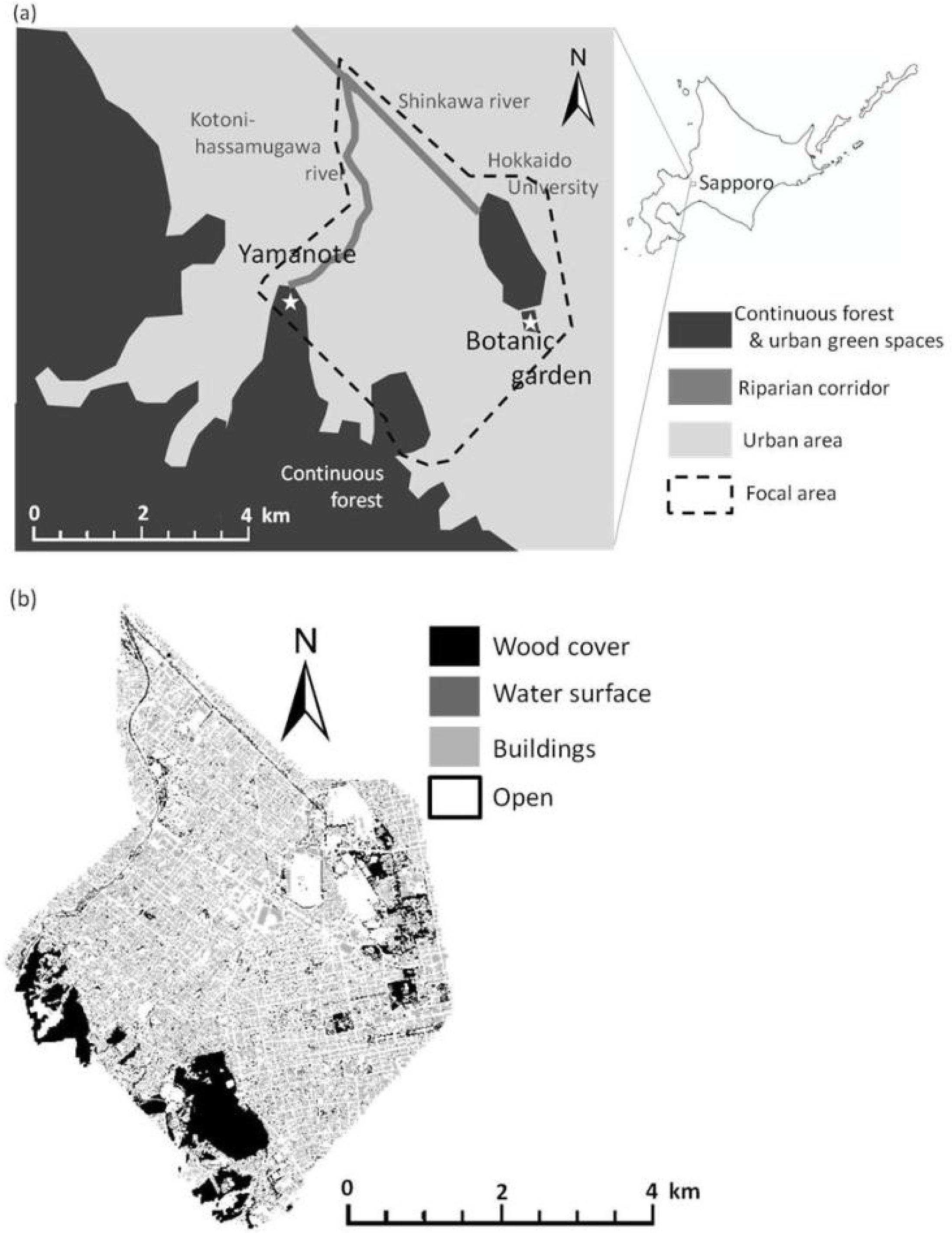
Note that riparian corridor was included in the total area.

List of figures

Fig. 1. Study area and its land-cover types.
(a) Location of study area, Sapporo, Hokkaido, northern Japan. (b) Land-cover maps.

Fig. 2. Details of study plot.
The matrix of five land-cover types. See main text for details.

Fig. 3. Resistance surface (a, b) and the predicted flow of moving bird individuals (c, d).
Maps (a, c) at 25 m resolution and (b, d) at 50 m resolution



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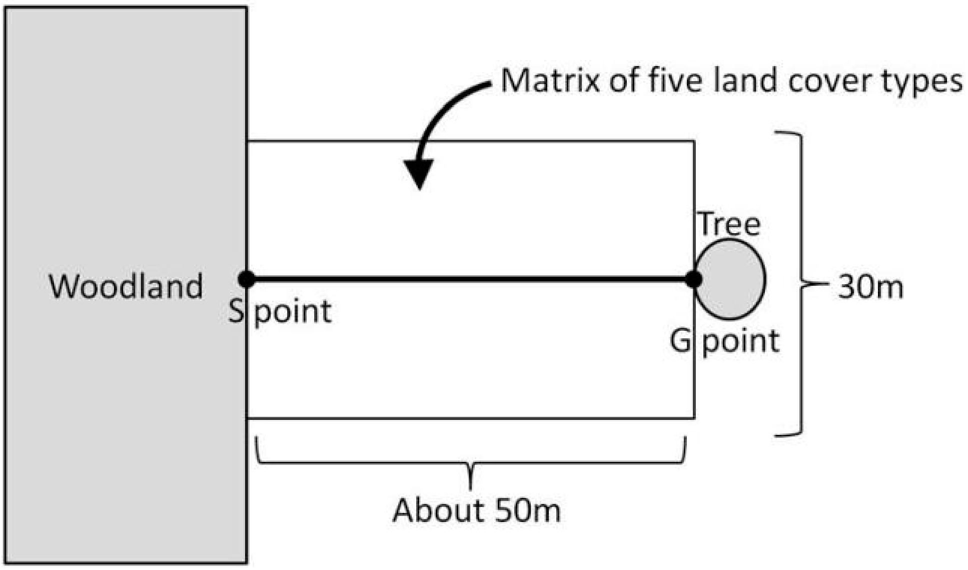
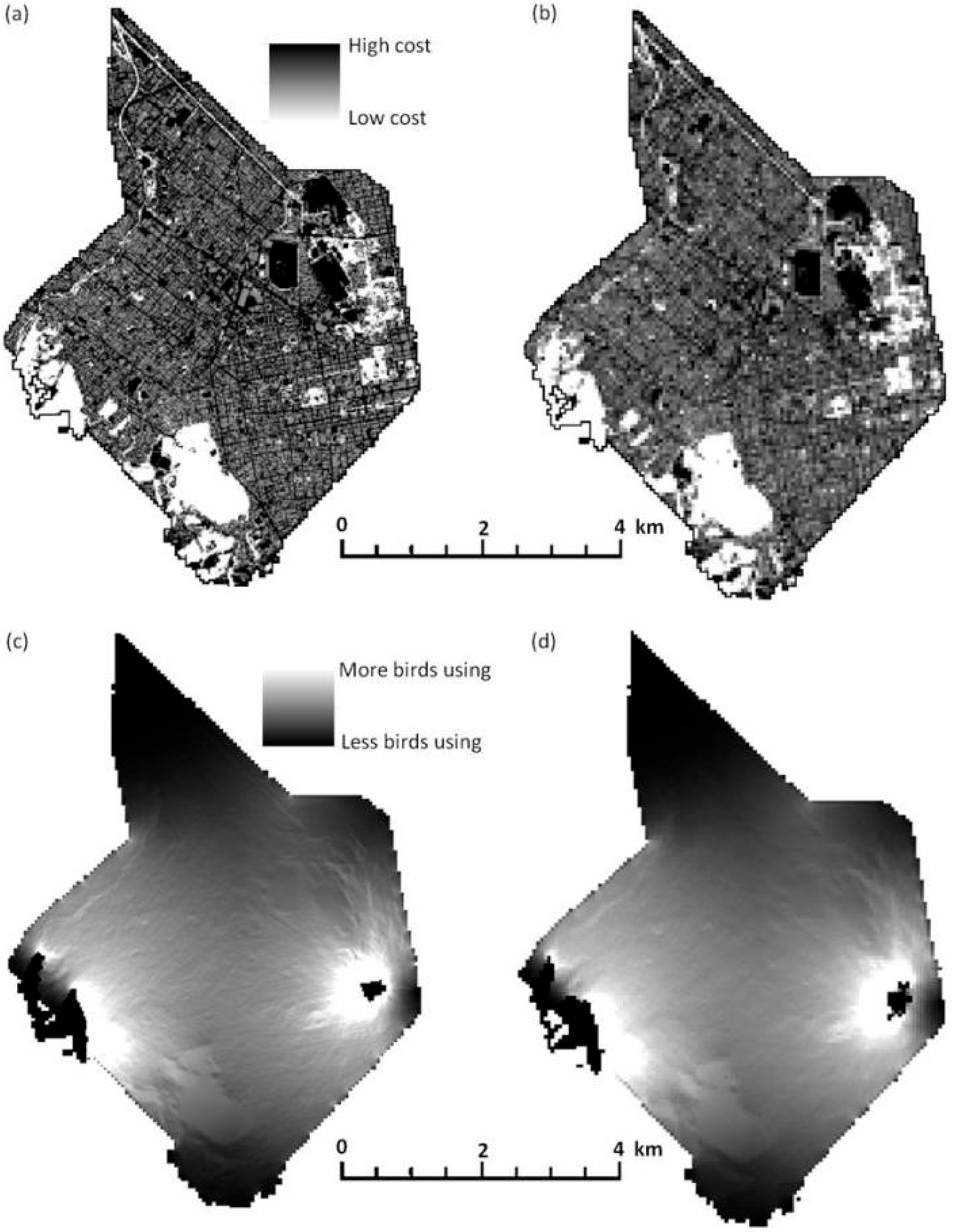


Fig. 2. Details of study plot.

The matrix was composed of five land-cover types. See main text for details.



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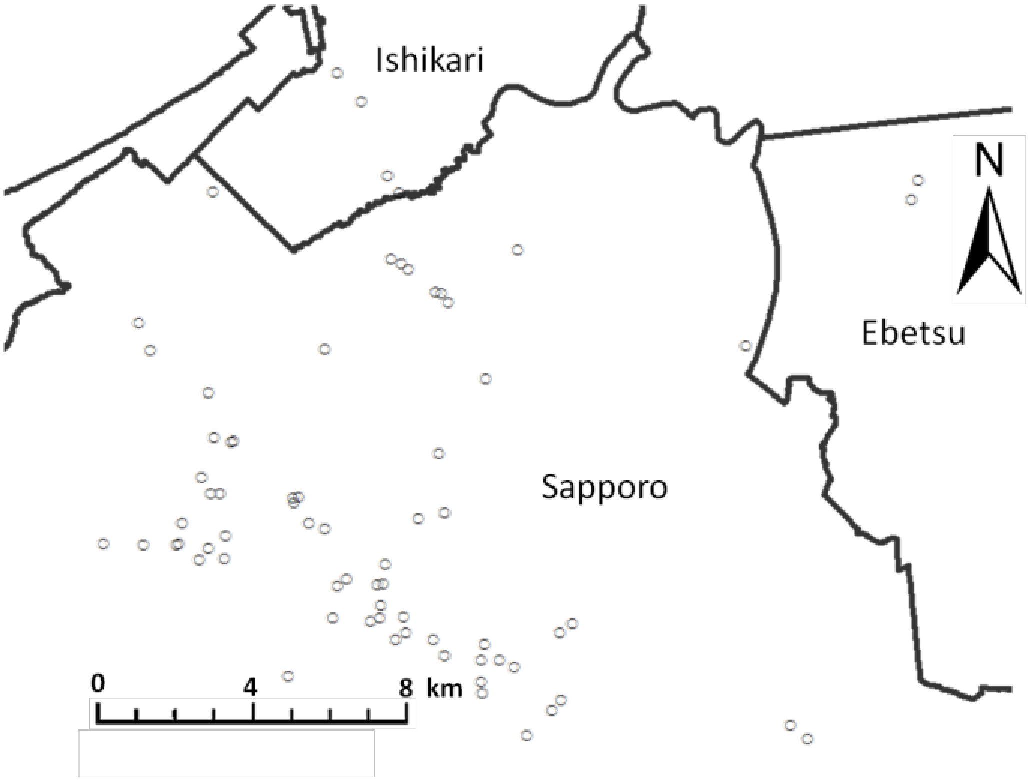
List of appendices

Appendix A. 71 survey plots located in Sapporo, Ebetsu and Ishikari.

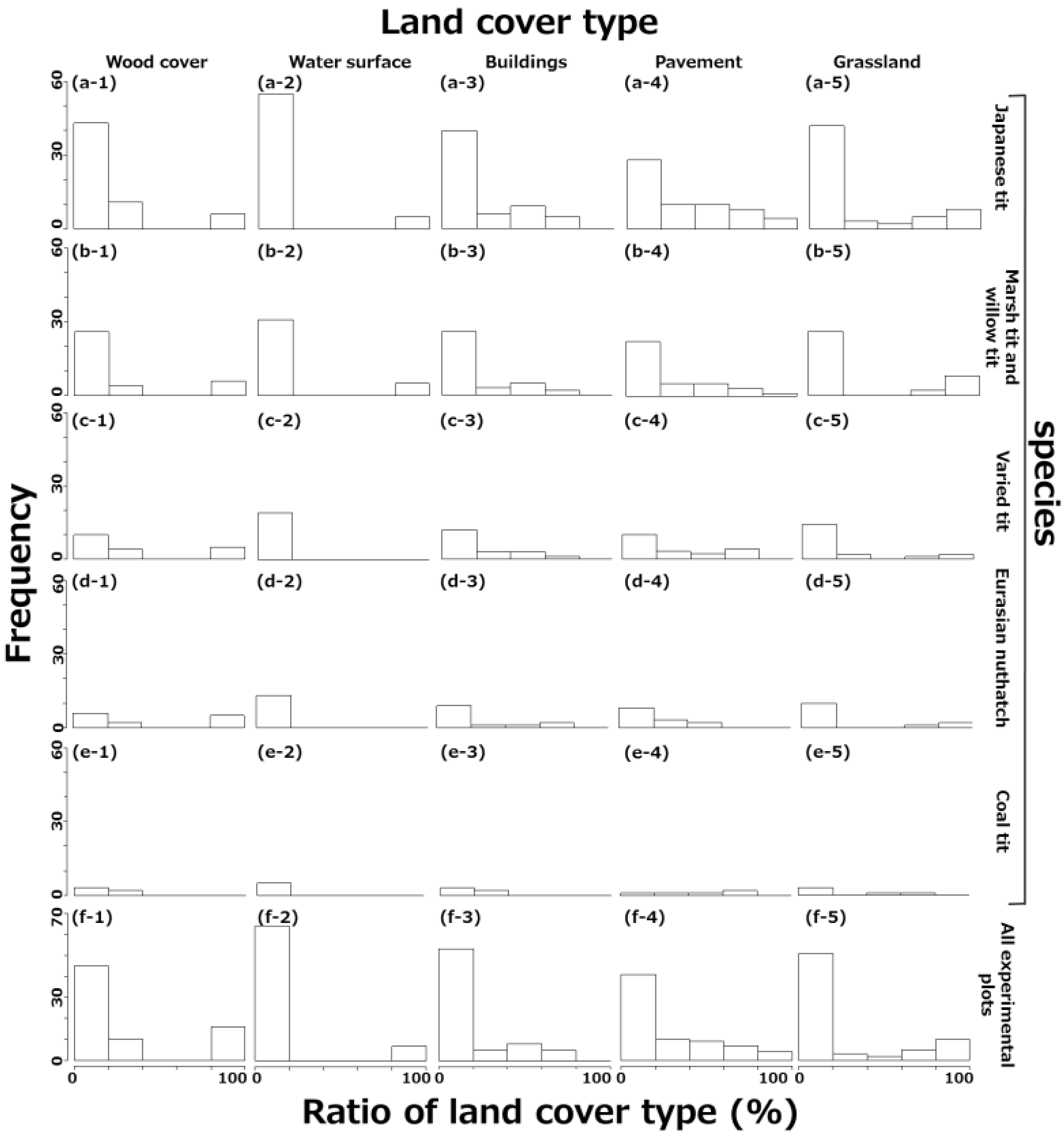
Appendix B. Histograms showing the frequency of the number of individuals occurred in the start (S) points separated by the ratio of land cover type in which individual species appeared and species. (f) Histograms of the number of experiment plots (totally 71) separated by the ratio of land cover type.

Appendix C. Mean (dots), 90 % confidential interval (dot lines) and 95% confidential intervals (solid lines) of crossing probabilities in the model with land cover of five variables model (a) and four variables model (b).

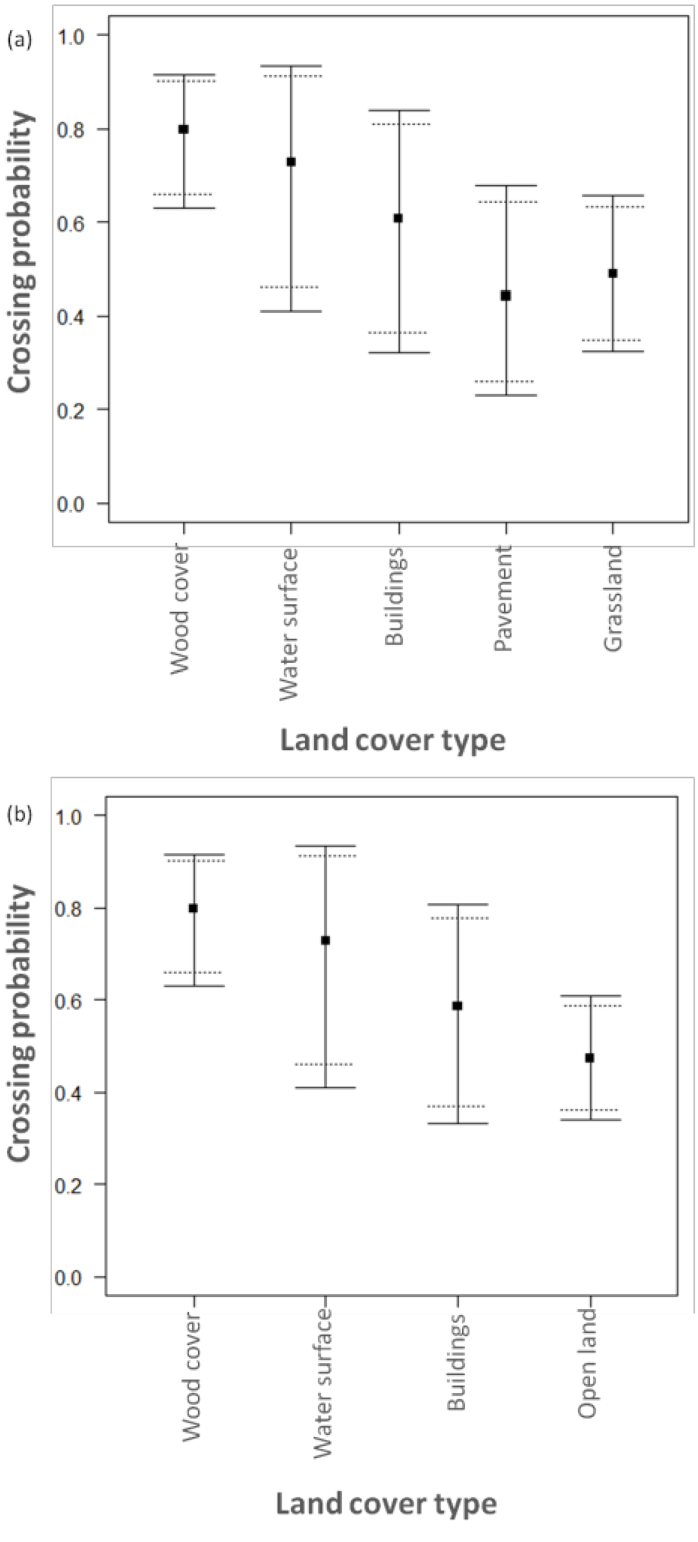
Appendix D. A male Japanese tit (*Parus minor*) used an electric cable as a perch to cross the building matrix.



Appendix A. 71 survey plots located in Sapporo, Ebetsu and Ishikari.



Appendix B. (a-e) Histograms of the mobbing call experiments in which individual species appeared separated by the ratio of land cover type and species. (f) Histograms of the number of experiment plots (totally 71) separated by the ratio of land cover type.



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