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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 Sapporo. 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.

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

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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 Hokkaido University 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 (Namba et al., 2010). 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 Hokkaido University 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 B). 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 6416 m respectively ($n = 71$). Each plot was composed of a 50-m $\times$ 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 Osboren, 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 Hokkaido University. 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,