

## SHORT NOTES

## Bird foraging is influenced by both risk and connectivity in urban parks

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Submitted: 13 July 2018; Received (in revised form): 5 September 2018; Accepted: 9 September 2018

### Abstract

Animal behaviour is increasingly seen as an integral component in maintaining connectivity within landscapes. Perceived predation risk causes changes in behaviour, differentially distributing individuals across landscapes, resulting in patchy habitat use. While intuitively these two ecological processes must be linked, they are often investigated in isolation. Here we investigate these two processes in a feeding experiment of small birds in semi-natural urban parks during winter. Using an information theoretic model selection approach, we found that adding connectivity measures to variables reflecting birds' perception of risk significantly improved our understanding of foraging and use in urban landscapes. Our results demonstrate the importance of accounting for both perceived risk and connectivity when measuring resource use.

**Key words:** foraging, connectivity, predation risk, trade-off, urban park

### Introduction

Animal behaviour is a fundamental process in landscape ecology. Understanding why animals are motivated to move to a new patch, and the degree to which landscapes facilitate or impede animal movement among resource patches, is required to determine connectivity among patches (With et al. 1997; Belisle 2005; Visscher et al. 2017; Visscher and Merrill 2018). Animals distribute themselves across the landscape based on their perception and behavioural response to potential predation risk (Lima and Dill 1990). The spatial representation of predation risk is a conceptual framework that has been coined the 'landscape of fear' (sensu Laundré et al. 2001). By differentially distributing individuals on the landscape, the consequences of connectivity and predation risk directly influence individual foraging success, population growth and trophic dynamics and are critical for conservation and management of animal populations (Lima and Dill 1990; Lima 1998; Chetkiewicz et al. 2006; DeWitt et al. 2017).

The ecology of urban ecosystems and wildlife present an interesting case for the role of connectivity in highly fragmented landscapes (Forman 2014; Pickett and Cadenasso 2017), in part, because the relative roles of food availability and risk (both predation or human disturbance) is not clear and may be species specific (Shochat 2004; Tsurim et al. 2008; Goddard et al. 2010; Lowry et al. 2013). The configuration of patches and cover characteristics in fragmented urban landscapes can influence bird species diversity and movement (Tremblay and St. Clair 2009, 2011; de Castro Pena et al. 2017), while local measures related to a bird's perception of risk are correlated with foraging effort (Lee et al. 2005; Tsurim et al. 2008, 2010; Valcarcel and Fernández-Juricic 2009).

Since their formulation, giving-up density (hereafter GUD) experiments have become an important tool for measuring organisms' perception of risk and have been successfully applied to rodents, birds and ungulates (Brown 1988; Altendorf et al. 2001; Lee et al. 2005; van der Merwe and Brown 2008). GUDs predict that the harvest rate and food remaining at a site

is representative of the cost of foraging (C), predation risk (P) and missed opportunity cost (MOC) of alternative behaviours (given as  $H = C + P + MOC$ ; Brown 1988). Often GUD studies compare risky to safe sites and implicitly assume that the entire landscape is equally accessible and attribute differences in harvest rates or food remaining to predation solely. However, because connectivity can degrade over relatively small inter-patch distances (With and Crist 1995), this assumption may be problematic in heterogeneous landscapes such as increasingly fragmented urban landscapes (Marzluff and Ewing 2001). Therefore, in certain situations it may be statistically unclear whether the observed GUD is due to perceived risk (P) or an inability to reach the specified location as a result of insufficient landscape connectivity (subsumed within C). Indeed, it may be difficult to untangle the effects of risk and access through connectivity, which we define here as a landscape characteristic that facilitates the movement of individuals to suitable foraging locations.

Ecologists have made great strides incorporating predation (reviewed in McLoughlin et al. 2010) and connectivity (reviewed by Chetkiewicz et al. 2006) effects into resource selection studies using a combination of use and movement data; however, these methods may be cost prohibitive and unnecessary in studies of small organisms. Here we use the amount of seeds eaten in artificial food patches to investigate resource use by over wintering birds in a semi-natural urban parks. Specifically, we use model selection procedures to evaluate inferential models incorporating risk and connectivity alone as well as the combination of risk and connectivity for describing patch use by songbirds in urban parks.

## Methods

We established feeding sites (total  $n = 101$ , unique sites = 62) in three semi-natural urban parks, namely, Capilano park (CAP,  $n = 20$ ), Goldbar park (GBP,  $n = 18$ ) and Tiger Goldstick park (TGP,  $n = 24$ ) in Edmonton, Alberta, Canada. All three parks are connected to the North Saskatchewan River Valley park system that bisects the city with a total of 18 000 hectares of urban parks (Fig. 1). Feeding sites within each park were selected to represent different landscape fragmentation configurations and contexts, including potential risk. The first set of sites ('continuous',  $n = 24$ ) was located within a fairly continuous conifer or mixedwood patches that extended from the contiguous river valley cover. These sites comprised of both planted and natural shrubs and coniferous trees (*Pinus* and *Picea* spp.). The second group of sites ('open',  $n = 18$ ) were located almost entirely in open fields (or city maintained lawn) devoid of cover. The last set of sites ('diffuse',  $n = 20$ ) were located throughout scattered and defoliated (for winter) deciduous elm (*Ulmus* × *hollandica*) or aspen (*Populus tremuloides*) trees. Each feeding site supported a tray approximately 150 cm above the ground from which we measured the amount of food eaten by birds during week long trials throughout the winter (winters of 2011/2012 and 2016/2017). At the beginning of each week, we filled each feeder with 500 g of mixed wild bird seed. We did not mix the seed into a substrate (i.e. sand) as pilot field work suggested that the substrate would often freeze solid in extremely cold conditions (including daytime temperatures of  $-37^{\circ}\text{C}$  during this study; D.R. Visscher, unpublished data). Therefore we are not calculating a true GUD (i.e. diminishing returns) as other studies have done, rather we use food remaining as a proximate, patch-specific measure of foraging effort and use. Feeders were visited and observed daily to ensure sufficient contents, that the seed mix did not freeze into a single mass, and to identify species using the feeder. After 7 days, we collected the seeds from each feeder,

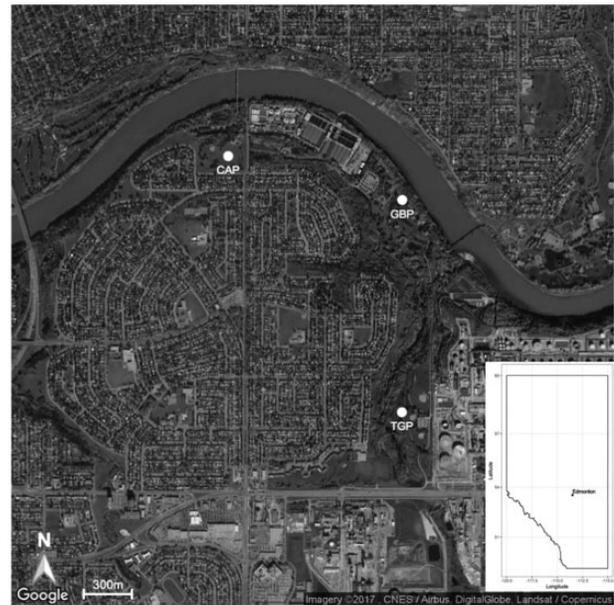


Figure 1: Map of the urban parks surveyed in Edmonton, Alberta, Canada. CAP is Capilano Park, GBP is Gold Bar Park, and TGP is Tiger Goldstick Park. All the parks are found along the North Saskatchewan River Valley park system (18 000 ha) that bisects the city of Edmonton and is the largest urban park system in Canada

air-dried the remaining seed for 3 days and weighed the remaining seeds (g). We assume that the remaining seed is a measure of foraging effort, and proportional to the perceived risk of the foraging location (Brown 1988). We noted the presence of four main granivorous songbirds while conducting the study: black-capped chickadees (*Poecile atricapillus*), dark-eyed juncos (*Junco hyemalis*), house sparrows (*Passer domesticus*) and red-breasted nuthatches (*Sitta canadensis*), but we cannot be certain these were the only species using the feeders. We excluded sites where we observed red squirrels (*Tamiasciurus hudsonicus*) or their sign from the analysis.

In addition to measuring the amount of food eaten (measured in grams) at each feeder, we also recorded the distance (m, log transformed) to the nearest cover comprised of vegetation taller than the feeding tray ( $>150$  cm), tree canopy cover (% arcsin transformed) estimated with four readings in the cardinal directions with a spherical densiometer, and distance (m, log transformed) to the natural treed source stand using a digital rangefinder (the contiguous river valley). We also recorded the average daytime high temperature for each week of the experiment when birds are active foraging (Bonter et al. 2013).

We used generalized linear mixed-effect models using the lme4 package implemented in R to model the amount of food eaten (Bates et al. 2015; R Core Team 2018). We incorporated feeding site as a random effect to account for the fact that some feeding sites were measured multiple times in a winter. We visually inspected the distribution of continuous variables included in the model to ensure they were independent of park location. We fit seven *a priori* candidate models representing the competing hypotheses that the amount of food eaten was best described by baseline variables (temperature and park location), local risk and the ability to evade predation (distance to cover and canopy cover), patch connectivity (distance to contiguous natural area and fragmentation cover type) or the combination of risk and connectivity. We used Akaike Information Criterion for small sample sizes ( $AIC_c$ ) to distinguish the most

parsimonious model from our candidate set of models as hypotheses for the explanation for the observed pattern of landscape use (Burnham and Anderson 2002), and inspected model residuals to confirm that errors were homogenous, approximated a normal distribution around zero and independent of model covariates. Finally, we as calculated the marginal and conditional  $r^2$  of the top ranked model from within the candidate set (Zuur et al. 2009; Nakagawa and Schielzeth 2013).

## Results

We found that the model that incorporated an interaction between connectivity effects and risk variables was overwhelmingly selected as the most parsimonious model from the *a priori* candidate set despite being the most complex model (Table 1). This model suggests that the amount of food eaten at a feeding site differed among parks and birds ate more food when temperature were warmer. Forage use depended on local conditions reflecting a bird's perception of risk, with more foraging occurring under increased canopy coverage and decreased distance to escape cover (Fig. 2). Connectivity measures influenced forage use with birds eating more when closer to natural contiguous cover (Table 2). Fragmentation type was retained in the most parsimonious model on its own and as an interaction with both distance to escape cover and natural contiguous cover (Table 2). The final model adequately fit the data with a marginal  $r^2$  of 0.69 and conditional  $r^2$  of 0.88.

The interaction of distance to natural area and fragmentation type suggests that individuals moving from the source natural area experienced a different rate of loss of connectivity in the open and diffuse fragmentation cover types relative to the continuous type (Table 2, Fig. 2). For example, while holding other variables constant, and at a distance to cover of 5 m, the open type promoted more feeding until declining by 30% at 35 m from the natural area. Over that same distance the seeds eaten at the feeders in diffuse type only declined by 15% and sustained more feeding past 35 m from the natural area relative to the open type. Similarly, the interaction between fragmentation cover type and distance to nearest cover suggests that perception of risk was context dependent and related to the proximity of suitable cover when available (Table 2, Fig. 2).

## Discussion

We found that the proximity and availability of cover influenced a bird's perception of risk. Birds ate more food (perceived less risk) when they were closer to the nearest cover, had more overhead canopy coverage and were closer to the contiguous natural area. This result is similar to previously studied bird systems (Lima 1985; Walther and Gosler 2001; Oyugi and Brown 2003; Lee et al. 2005). We found no evidence that high canopy cover increased perceived predation risk as in Carrascal and Alonso (2006), however, the semi-natural conditions in this urban setting did not present many inner forest like conditions. The amount of food eaten varied by fragmentation type reflecting a trade-off between the proximity of cover and the canopy coverage that the surrounding vegetation provides. As canopy coverage largely depends on leaf cover, this trade-off is likely seasonal (foliated vs. defoliated) and varies whether the predominant vegetation type is coniferous or deciduous (Jokimaki and Suhonen 1998). Indeed, these results represent the local context of the trade-off between foraging and perceived predation risk (van der Merwe and Brown 2008; Laundre et al. 2010; Bedoya-Perez et al. 2013).

The ability of an organism to move through fragmented habitats from potential source areas to foraging locations influenced local forage use. Evens et al. (2018) found that foraging effort in an insectivorous bird was related to the distance between breeding and foraging habitat. Thus, while accessibility has been investigated in terms of an energetic cost associated with foraging, as limited by individual morphology (Nolet et al. 2006), we show that the interaction between the distance to a natural source area and the type of fragmentation is important to bird forage use. While the configuration of patches in fragmented landscapes is known to influence movement and use by small mammals and birds, particularly in urban settings (Jokimaki and Suhonen 1998; St. Clair et al. 1998; Marzluff and Ewing 2001; Orrock and Danielson 2005; Tremblay and St. Clair 2009, 2011; Wilkinson et al. 2013), our study was not designed to distinguish between movement of individuals and changes in forager abundance. However, our results suggest that it is important to account for connectivity effects when ascribing risk effects foraging studies. As a consequence, experiments that do not account for connectivity (or other factors influencing landscape use, see Bedoya-Perez et al. 2013) may overestimate the importance of predation risk in distributing organisms, and their foraging, across the landscape.

Unlike Bonter et al. (2013), our results suggest that milder weather encourages more forage use. Their study noted that the predation-starvation tradeoff shifted to starvation avoidance when birds foraged to overcome the energetic cost associated with cold weather. We did not collect energetic data in our study. Thus, it may be that in our study birds conserved energy by remaining in natural areas (with wind protection). The increase in observed foraging during warmer weather is likely due to an overall increase in the levels of activities of birds.

In increasingly fragmented urban areas, planners' ability to maintain connectivity among suitable habitat patches and provide refuges for individuals looking to avoid locally risky situations is crucial for conservation efforts (Jokimaki and Suhonen 1998; St. Clair et al. 1998; Marzluff and Ewing 2001; Tremblay and St. Clair 2009, 2011). In particular, care must be taken to avoid crossing critical connectivity thresholds that result in the isolation of larger patches, or the avoidance of smaller patches (With and Crist 1995). Isolation is problematic because resident foragers may not have access to foraging opportunities with low risk. As a result, residents may suffer increased predation rates or increased non-consumptive predation effects, potentially resulting in extirpation of individuals from the isolated patch (Lima and Dill 1990; Preisser and Blonick 2008). Our results suggest that planting trees or shrubs in large open areas may be enough to encourage bird use (Tremblay and St. Clair 2009, 2011; de Castro Pena et al. 2017).

Often connectivity and predation risk are studied separately by landscape and behavioural ecologist, respectively. In this study, we highlight the importance of considering landscape features that both increase risk factors and promote connectivity among patches. Predation risk differentially distributes organisms across the landscape; however, we must also consider the ability of individuals to move through fragmented landscapes, such as those frequently found in urban landscapes. Forage use, as measured by the amount of food eaten in experimental patches, is the result of individuals' ability to reach a feeding site (i.e. C in Brown 1988) and balancing risky foraging behaviours within the context of local conditions (P in Brown 1988; Bedoya-Perez et al. 2013). Clearly understanding the effect of predation risk and habitat connectivity on urban habitat use will require a behaviourally based landscape ecology approach (Belisle 2005).

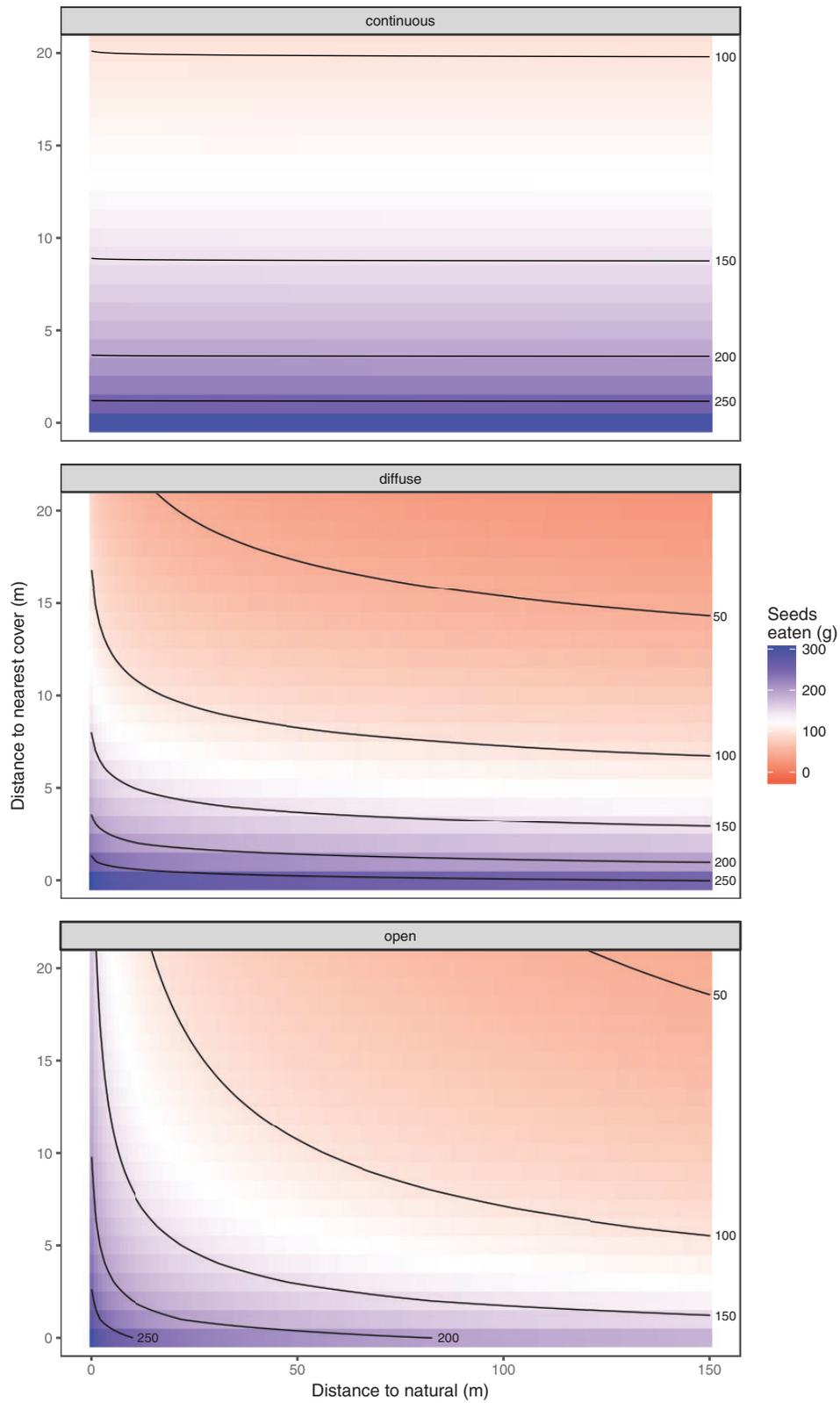


Figure 2: Model predictions for the amount of seeds eaten in grams as a function of distance to natural area (m; x-axis) and distance to nearest cover (m; y-axis) for each fragmentation type in Gold Bar Park (GBP). Isolines (or contours) of grams of food eaten are given to aid interpretation, where the value for a particular isoline is recoded at the right most position of each line. Additional model variables (temperature and canopy cover) are held at their mean values

**Table 1:** Model selection results for candidate models representing hypotheses about the influence on foraging of predation risk and landscape connectivity on bird foraging, where K is the number of estimated parameters, LL the log-likelihood, AIC<sub>c</sub> the Akaike Information Criterion calculated for small sample sizes, ΔAIC<sub>c</sub>, the difference in AIC<sub>c</sub> values from the top ranked models, and w<sub>i</sub>, the Akaike weights for each model

Model	K	LL	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	w <sub>i</sub>
Base + risk * connect (dnat * frag + dcov * frag)	15	-509.3	1054.2	0	0.995
Base + risk * connect (dcov * frag)	13	-517.6	1065.3	11.1	0.003
Base + risk * connect (dnat * frag)	13	-518.5	1067.1	13.0	0.001
Base + risk + connect	11	-526.1	1077.1	22.9	<0.001
Base + risk	8	-540.7	1099.0	44.8	<0.001
Base + connect	9	-544.5	1108.9	54.8	<0.001
Base	6	-576.9	1166.7	112.5	<0.001

The models consist of variables contained within components; **base** contains the average daytime temperature for each experiential week (temp) and the named park location (park), **risk** contains the transformed canopy cover (canopy) and distance to nearest cover (dcov) and **connect** contains the fragmentation context of the feeding site (frag) and the transformed distance to natural area (dnat). The asterisk (\*) denotes an interaction effect between **risk** and **connect** variables which are specified in parentheses. All models included feeding site as a random effect.

**Table 2:** Model coefficients and standard errors for the top ranked model estimating the amount of food eaten (g) by birds over a 7-day period in winter (n = 101, groups = 62)

Model component	Variable	Estimate	SE
Base	Intercept	301.47	117.06
	Temp	3.82	1.14
	Park = GBP	24.34	18.69
	Park = TGP	79.66	21.18
Risk	dcov	-65.96	36.56
	Canopy	-12.86	46.68
Connect	dnat	-0.19	23.09
	Type = open	7.24	98.44
	Type = diffuse	10.29	93.87
Risk * connect	dcov * open	20.36	33.13
	dcov * diffuse	-7.48	39.70
	dnat * open	-24.29	25.45
	dnat * diffuse	-12.01	25.22
Random effect (SD)	Feeding site	Intercept = 52.68	Residual = 42.16

The top ranked model included the following components; **base** containing the average daytime temperature for each experiential week (temp) and the named park location (park), **risk** containing the transformed canopy cover (canopy) and distance to nearest cover (dcov), and **connect** containing the site fragmentation (frag) and the transformed distance to natural area (dnat). The asterisk (\*) denotes an interaction effect between **risk** and **connect** variables as specified in the table. The reference category for **frag** and **park** were “continuous” and CAP, respectively.

### Acknowledgements

This work was completed, in part, as undergraduate research projects by A.U. and M.G. Feeders, seeds, and field assistance was provided by the Department of Biology and students of the King’s University, respectively. The data used in this analysis are freely available by request from the authors. The article was improved by the comments of two anonymous reviewers.

**Conflict of interest statement.** None declared.

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