University of Alberta

Movement behaviour and distribution of forest songbirds in an expanding urban landscape

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Ecology

Department of Biological Sciences

Fall 2010
Edmonton, Alberta

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DEDICATION

To the native songbirds of Calgary and other cities around the world. May they continue to grace our existence for centuries to come.

ABSTRACT

Urbanization is viewed as a major threat to global biodiversity because of its role in the loss and fragmentation of low-lying, productive habitats associated with coastal plains and river valleys. My study examines the effects of urbanization on the movements and distribution of songbirds in Calgary, Alberta, Canada. I conducted playback and translocation experiments to assess the permeability of small-scale (e.g. transportation corridors, rivers) and large-scale (e.g. multi-lane expressways, areas of urban development) features of the urban landscape, respectively. I then used these empirical data to parameterize spatially explicit models and determine functional landscape connectivity across the study area. Finally, using point surveys conducted at 183 sites across the urban matrix, I examined the role of land cover type, local vegetation characteristics, landscape-level forest cover, and isolation from natural features on the distribution of songbirds. In 563 playback trials involving the responses of 2241 birds, I found that the size of the gap in vegetation was the most important determinant of movement across linear features; the likelihood of movement sharply decreasing as the gap in vegetation exceeded 30 m. The results of 176 translocation trials provided further evidence of the barrier effect of gaps. Multiple gaps, in particular, constrained the movements of both yellow warblers (*Dendroica petechia*) and black-capped chickadees (*Poecile atricapillus*). The bird surveys revealed that natural forest stands played a critical role in sustaining regional avian diversity in the study area. Moreover, functional distance to the nearest forested natural area or water body often explained more variation in the probability of occurrence of focal species than straight-line distance, suggesting that barriers identified from the permeability experiments may have affected not only the movements of songbirds but their settlement patterns as well. Taken together, my results suggest that preserving a functionally connected network of natural areas is vital to conserving avian biodiversity in cities. My research describes novel methodologies for characterizing the composition and configuration of highly heterogeneous and fragmented landscapes. It also provides a unique examination of the link between the movement behaviour of individual birds and population-level distribution patterns within this context.

ACKNOWLEDGEMENTS

Studying birds in the field is hard work but the rewards are many. It was a real privilege to be able to spend so much time immersed in the world of avian behaviour and especially, to share my passion with such an outstanding crew of field assistants. Michelle Coombe, Sarah Crook, Dayna Goldsmith, Krystal Hennig, Kristin Jonasson, and Eileen Miranda deserve a huge word of thanks for making our field seasons as enjoyable and successful as they were. I especially appreciated their dedication to ensuring the highest quality of data and endless good cheer in spite of the early mornings, relentless mosquitoes, and other vagaries of field work. Michelle Coombe deserves special mention for enduring the winter season without complaint and assuming full responsibility of the playback experiments in the second year of the project, which allowed me to focus on the translocation work.

I am indebted to the volunteer birders from Nature Calgary who generously donated their exceptional birding skills toward the completion of over 400 bird surveys over the course of three summers. Beyond all expectation, most of these volunteers stayed with the project for its duration. Their dedication and persistence not only ensured continuity and consistency, but also awarded me much piece of mind during the busy field seasons. Thanks to Brenda Baker, Phil Cram, John Cartwright, Bernard and Thérèse Goulet, Carole Hachey, Aileen Pelzer, Nimali Sereviratne, Tony Timmons, Arthur and Donna Wieckowski, Rob Worona, and Gus Yaki for a truly invaluable contribution to the project.

This research would not have been possible without funding and in-kind contributions from a variety of sources. Project funding was provided by The Calgary Foundation (including contributions from Chris Dunkley Natural Environment Retention Fund, Community Fund, Calgary Beautification Fund, and Harvey Kowall Memorial Fund), Alberta Conservation Association Grants in Biodiversity, Bill Shostak Wildlife Award at the University of Alberta, Alberta Sport, Recreation, Parks and Wildlife Foundation, Mountain Equipment Coop, O2 Planning and Design Inc., and Lamont Development Inc. The City of Calgary generously donated digital data layers and provided valuable background information on the study area and assistance in identifying research priorities and test sites. The Orthoshop donated a high-resolution orthophoto of the study area, which proved invaluable for creating the many landscape variables used in my analyses. I was supported by scholarships from Alberta Ingenuity, the Natural Sciences and Engineering Research Council, and the Univeristy of Alberta.

I am grateful to the members of my supervisory committee, Erin Bayne, Susan Hannon, and Scott Nielsen, for the excellent advice and feedback they provided on many aspects of this project. Examiners Keith Tierney and Lenore Fahrig brought fresh perspectives, which led to substantial improvements to the thesis. My supervisor, Colleen Cassady St. Clair, went far and beyond the call of duty by offering me food and shelter during my many forays to Edmonton. Most importantly, though, she proved to be an exemplary mentor and tireless cheerleader at every stage of this journey. I benefited tremendously from her expert guidance as well as her thorough and insightful comments on earlier drafts

of this thesis. I also thank Charlene Nielsen, of the University of Alberta, and Paul Knaga, of Parks Canada, for helping to keep my analyses moving forward by providing invaluable and timely GIS advice.

Last but definitely not least, I would never have undertaken this degree without the enthusiastic support of my husband and best friend, Norm Vaughan. During the many absences and endless hours at the computer imposed by this project, Norm continually astounded me with his ability to keep our busy household running in spite of his own demanding career and the hectic schedules of our two sons. Eric and Alexandre showed great maturity and patience in making due with only 'half a mom' for so long. As this adventure comes to a close, I eagerly look forward to spending more quality time with my long-neglected family.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
AUC	Area Under the Receiving Operator Curve
GIS	Geographic Information System
MFR	Most Forested Route

CHAPTER 1

GENERAL INTRODUCTION

Worldwide, there is a trend toward increasing urbanization fuelled by a growing human population and a shift in settlement from rural regions to urban centres (Shochat *et al.* 2006). For the first time in history, there are as many people living in urban as in rural areas and by 2050, it is predicted that the number of urban residents will be equal to the total world population of 2004 (United Nations 2008). In North America, urban growth tends to be concentrated in suburban areas, causing many cities to expand much faster in area than in population (Zipperer *et al.* 2000, Marzluff *et al.* 2001). The result is rapid and permanent conversion of relatively natural land cover to a human-built environment, leading to the loss of many native species while encouraging the spread of abundant, non-native species (McKinney 2006, Olden *et al.* 2006, Clergeau *et al.* 2006, Holway and Suarez 2006). Moreover, urban areas are typically located within highly productive and biologically diverse ecosystems associated with low-lying coastal and riparian zones and therefore, contain a disproportionate amount of the world's biological diversity (Melles *et al.* 2003). For these reasons, urbanization is widely regarded as one of the leading causes of species extinction (Marzluff *et al.* 2001, Olden *et al.* 2006).

Although cities are generally viewed as places designed exclusively for humans, there are several reasons why they should also accommodate the needs of other species. First, species diversity is often used as a gauge of the health and stability of ecosystems and their ability to provide vital services, such as air and water purification, upon which we, as humans, depend for our health and very existence. Beyond such essential services, urban biodiversity provides a plethora of benefits to urban residents including visual aesthetics, noise buffering, increased property values, recreation, and psychological well-being (Savard *et al.* 2000, Tratalos *et al.* 2007). Finally, by offering opportunities for direct contact between humans and nature, biologically diverse urban natural areas may play a vital role in fostering support for the maintenance of biodiversity in more remote locations (Turner *et al.* 2004, Miller 2006). In urban areas, birds are generally viewed as important conservation targets because of their role as reliable bioindicators, their aesthetic value to humans, and their ability to provide vital ecosystem services like pollination and seed dispersal (Temple and Wiens 1989, Savard *et al.* 2000, Stutchbury 2007, Whelan *et al.* 2008).

In fragmented landscapes, biodiversity may be affected by habitat connectivity because without it, the exchange of genes and individuals is constrained and small, isolated populations become at greater of risk of extinction due to environmental and demographic stochasticity (Soule 1986). Most studies of habitat fragmentation have drawn on island biogeography and metapopulation theory and assumed that organisms perceive a binary landscape characterized by islands of suitable habitat embedded within a uniform, hostile matrix (e.g. Opdam *et al.* 1985, Bolger *et al.* 1991, Hinsley *et al.* 1995, Mazerolle and Villard 1999, Doherty and Grubb 2000, Fernandez-Juricic and Jokimaki 2001, Crooks *et al.* 2001). Within such a perspective, landscape metrics typically focus on the habitat component of the landscape with little attention paid to the nature of the intervening matrix (Bender and Fahrig 2005). Landscape composition is often measured in terms of percent habitat (usually forest cover) within a given radius whereas patch size, distance to nearest neighbouring patch, edge density, or variations thereof are typically used to describe landscape configuration. However, the reliability of such metrics for predicting ecological processes has been the subject of much debate (Schumaker 1996, Tischendorf and Fahrig 2000, Bender *et al.*2003, Neel *et al.* 2004). Patch-based metrics are not realistic in urban or other heterogeneous landscapes characterized by a complex mosaic of land cover types. The nature of the matrix and how an organism interacts with it can affect the importance of the spatial arrangement of habitat in determining population dynamics in fragmented systems (With *et al.* 1997, Norton *et al.* 2000, Ricketts 2001, Baum *et al.* 2004, Bender and Fahrig 2005, Castellon and Sieving 2006, Russell *et al.* 2007, Hansbauer *et al.* 2009).

While studies investigating the effects of habitat fragmentation on birds in forested or agricultural landscapes abound in the literature (e.g., Opdam *et al.* 1985, Machtans *et al.* 1996, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Villard *et al.* 1999, Doherty and Grubb 2000, Robichaud *et al.* 2002, Creegan and Osborne 2005), similar studies in urban landscapes are comparatively scarce. The few studies that have been conducted in an urban context have tended to focus on distributional patterns (e.g., Blair 1996, Mortberg 2001, Crooks *et al.* 2004, Melles *et al.* 2003. Bolger *et al.* 1997, Fernandez-Juricic. 2000a, Fernandez-Juricic 2000b, Clergeau *et al.* 2001, Lim and Sodhi 2004, Tablado-Almela 2006) rather than on mechanisms, such as individual behaviours or species interactions, which are likely to affect the persistence of species (Shochat *et al.* 2006).

Movement is a process of particular importance to the viability of populations in urban and other fragmented landscapes because it underlies dispersal, a process that allows for the immigration of individuals into small or declining populations and the colonization of vacant habitats (Bélisle and Desrochers 2002). In birds, dispersal typically involves exploratory movements during which individuals prospect for new territories, either during the post-fledging period or during the early breeding season (Morton 1992). Movement is also important throughout the year when birds must travel to access essential resources such as water, food, and shelter. More specifically, in winter, resident songbirds must travel extensively to find adequate forage at a time when food is scarce and yet energetic requirements are high due to low ambient temperatures (Dolby and Grubb 1999).

Urban landscapes contain a number of features that likely act as barriers to the movements of birds and other wildlife. For example, while transportation networks provide connectivity for humans, they generally have the opposite effect on natural systems, disrupting natural flows and processes including animal movements (Forman *et al.* 2003). This is particularly evident where transportation corridors intersect riparian corridors, which likely act as natural conduits of movement for a variety of taxa searching for food, mates, or new territories. Although the barrier effect of transportation corridors has been well documented in the literature (reviewed by Spellerberg 1998, Forman *et al.* 2003, Fahrig and Rytwinski 2009), researchers know surprisingly little about the specific attributes of these features (e.g., surface conditions, characteristics of adjacent vegetation, noise, or traffic) that actually inhibit wildlife movements (Jaeger *et al.* 2005). Because of the presence of a variety of roads of varying widths and traffic volumes, the urban landscape can be particularly advantageous for disentangling these effects. Finally, assuming that wildlife tend to preferentially move through habitats that are suitable for other functions such as feeding and resting (Chetkiewicz *et al.* 2006), it is plausible that urban development may also impede the movements of wildlife, particularly species that are generally associated with relatively natural environments.

Although birds are generally believed to be highly vagile, several studies have shown that the movements of forest birds are constrained when they travel in fragmented landscapes outside migratory periods (Villard *et al.* 1995, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Bélisle *et al.* 2001, Gobeil and Villard 2002, Robichaud *et al.* 2002). Various approaches have been taken to try to quantify the effects of landscape composition and configuration on bird movements (reviewed by Desrochers *et al.* 1999). One such approach has been to infer dispersal rates from patch occupancy patterns (Opdam *et al.* 1985, Betts *et al.* 2006). Typical conclusions from such studies are that smaller and more isolated patches tend to have lower colonization rates and contain fewer species. However, these studies have not effectively disentangled the precise mechanisms by which isolated patches may be unoccupied by a species. Such mechanisms may include psychological aversion to crossing openings, physical limitations on vagility, site tenacity, mortality during movement, low patch detectability, high within-patch extinction rates due to edge effects (Desrochers *et al.* 1999), or conspecific attraction (Stamps 1988, Bourque and Desrochers 2006).

A second approach has been to document the flows of birds through an area (e.g. Wegner and Merriam 1979, Machtans *et al.* 1996) or to passively document the trajectories of dispersing birds (e.g. Haas 1995). These studies have generally demonstrated higher movement rates among patches connected by forested corridors than more isolated patches. A major limitation of these studies is that they do not fully account for the motivation for movement. For example, the motivation of an individual to disperse from its natal patch will be highly influenced by natal philopatry of the species or by competitive pressure from within the natal patch (Desrochers *et al.* 1999).

In a third approach, researchers have developed experimental techniques that standardize the motivation of birds to cross different habitat elements such that their permeability can be quantified and compared. For example, taped playbacks of mobbing calls have been successfully used to lure birds across selected small-scale features such as roads or meadows (Sieving *et al.* 1996, Rail *et al.* 1997, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Bélisle and Desrochers. 2002, St. Clair. 2003, Awade and Metzger 2008). In larger-scale experiments, territorial birds have been translocated and their return time and success documented (e.g. Bélisle and St. Clair 2001, Bélisle *et al.* 2001, Gobeil and Villard 2002, Gillies and St. Clair 2008). Such experimental studies have greatly advanced our understanding of the decisions birds make when moving through a fragmented landscape. For example, playback experiments have revealed that some bird species are unwilling to cross gaps in forest cover wider than 50 m and will often use substantially longer forested detours to avoid traveling in the open (Desrochers and Hannon 1997, St. Clair *et al.* 1998). However, some ecologists view such studies with skepticism due to the lack of a link between fine-scale behavioural studies and broader patterns of species distributions, which are believed to be of greater importance to the persistence of species. This disconnect largely stems from differences in scale with behavioural ecologists focusing on the fine-scale movements of individuals and landscape ecologists looking at patterns of distribution through a much broader lens (Lima and Zolner 1996, Desrochers *et al.* 1999). Desrochers *et al.* (1999) asked whether it was possible to 'scale-up' from behaviour to explain occupancy patterns in the landscape but concluded, at the time, that it was still premature to answer this question. Bélisle and Desrochers (2002) later advocated using the results of fine-scale movement experiments to parameterize individual-based landscape connectivity models but offered little direction on how to accomplish this.

One modelling approach that lends itself particularly well to the integration of scales is 'least-cost path' modelling, which calculates the functional distance between patches based on the cost, or friction, experienced by individuals moving through a heterogeneous landscape (Adriaensen *et al.* 2003). Functional distances have in turn been successfully applied to graph theory to assess landscape connectivity for a variety of taxa including birds (e.g. Bunn *et al.* 2000, Awade and Metzger 2008) and large mammals (e.g. O'Brien *et al.* 2006). Functional connectivity has also been explored through simulation exercises (e.g.

With and Crist 1995, Schumaker 1996, With *et al.* 1999, Tischendorf *et al.* 2003). These modelling approaches have been hindered, however, by a paucity of empirical data accurately reflecting the movements costs associated with various land cover types or landscape features. As a result, cost surfaces are typically parameterized based on expert opinion (Beier *et al.* 2008), most often on the assumption that animals prefer to move through areas that are also most suitable for other functions such as breeding or foraging (Chetkiewicz *et al.* 2006). Consequently, establishing a clear link between fine-scale movement processes and broader scale distribution patterns has proven difficult.

My research attempts to bridge the gap between process and pattern by investigating the role of functional landscape connectivity in explaining the distribution of songbirds in the urban landscape of Calgary, Alberta. As one of the fastest growing metropolises on the continent, the city of Calgary represents a high priority for the study of the effects of urbanization on wildlife. Drawing on the complementary strengths of the approaches outlined above, I used a novel and integrated approach to first, experimentally determine the permeability of selected elements of the urban landscape and then, investigate whether functional landscape connectivity plays a role in explaining avian distributional patterns in a highly heterogeneous and fragmented landscape. Recognizing that responses to urban development are likely to vary among species, I took a multi-species approach in an effort to elucidate general principles that could be translated into practical management guidelines of benefit to multiple species.

In Chapter 2, I describe the results of 563 playback trials in which I used a taped recording of an avian mobbing call to lure birds across small-scale features of the landscape (e.g. roads, railways, rivers and bridges) and assess their willingness to cross these. This part of my research was unique in that it was replicated across three seasons (i.e. breeding, post-fledging, and winter). I felt it was important to examine movement behaviour across seasons because functional landscape connectivity is likely to vary as a result of differences in travel conditions, abundance of predators, food availability, or biological needs. In Chapter 3, I present the results of 176 translocation trials from which I tested the permeability of larger scale features such as major freeways and areas of urban development. These experiments focused on two species of forest songbirds with contrasting sensitivities to urban development and migratory behaviours: the black-capped chickadee (*Poecile atricapillus*, an urban-adapted year-round resident) and the yellow warbler (*Dendroica petechia*, an urban-sensitive Neotropical migrant). In Chapter 4, I describe how I used the results from my permeability experiments to parameterize spatially explicit cost-distance models within a geographic information system and determine the 'functional distance' between 183 survey sites and natural landscape features (e.g. forested natural areas, water) presumed to be important for birds either for key resources or as sources of dispersers. In the same chapter, I then examine the role of land cover type, local vegetation characteristics, and landscape composition and configuration (including functional connectivity) on the composition of avian communities and the occurrence of 25 focal species. A primary objective of my research was to identify management recommendations aimed at preserving avian diversity in Calgary and other urban landscapes. These are presented at the end of each chapter. I conclude this dissertation by discussing the most salient findings from my research and identifying directions for future research.

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CHAPTER 2

FACTORS AFFECTING THE PERMEABILITY OF TRANSPORTATION AND RIPARIAN CORRIDORS TO THE MOVEMENTS OF SONGBIRDS IN AN URBAN LANDSCAPE[1]

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[1] This chapter has been published as :
Tremblay, M.A. and C.C. St. Clair. 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. Journal of Applied Ecology 46: 1314-1322.

SUMMARY

1. Linear features associated with transportation and riparian corridors are known to inhibit the mobility of birds and other wildlife yet the factors contributing to their barrier effects are poorly understood. The diversity of roads in urban landscapes provides an opportunity for elucidating the relative importance of factors such as noise, traffic volume, gap width, and adjacent vegetation on animal movement.
2. Using an avian mobbing call as a lure, we tested the willingness of forest songbirds to cross four types of linear features in the urban landscape of Calgary, Alberta, Canada: (1) roads of varying widths and traffic volumes, (2) conventional railways and light transit lines, (3) transportation bridges across riparian corridors, and (4) rivers.
3. Using mixed effects logistic regression, we found that the size of the gap in vegetation was the most important determinant of movement ($P < 0.001$). As the gap in vegetation exceeded 30 m, the likelihood of movement decreased dramatically and by 45 m, birds were only half as likely to move across gaps as they were to move an equivalent distance in continuous tree cover. Traffic volume also had a significant dampening effect on movement (odds ratio = 0.952 per 1000 vehicle/day increase; $P < 0.001$) and generally explained more variation in the data than noise levels.
4. Railroads proved to be the most permeable of the features we tested, probably owing to their relatively narrow width, which never exceeded 30

m. Surprisingly, rivers were less permeable than the anthropogenic linear features we tested, with a significant barrier effect evident even at widths < 50 m.

5. The birds in our study showed a marked preference for flying over, rather than under, transportation bridges, particularly when adjacent vegetation was available.
6. *Synthesis and applications*. Our results suggest that linear features, both anthropogenic and natural, can significantly impede the movements of forest songbirds and that managing adjacent vegetation is a potentially effective way to mitigate these barrier effects in cities and other fragmented landscapes.

Key words: cities, fragmentation, landscape connectivity, linear features, mixed effects models, mobbing behaviour, roads, railways, rivers, seasons

INTRODUCTION

Many ecologists view urbanization as one of the most serious threats to global biodiversity (Marzluff *et al.* 2001). One reason for this concern is that cities are typically located in low-lying, biologically rich areas associated with coastal plains and riparian corridors, which contain a disproportionate amount of the world's biological diversity. Urban development causes the rapid and permanent alteration and fragmentation of these naturally productive areas, leading to the loss of many native species that are unable to adapt to such radical changes in their environment.

Movement is a behavioural mechanism of critical importance to the persistence of populations in fragmented landscapes because it supports the use of multiple small patches within home ranges, gene flow among populations, and the recolonization of patches that have become vacant. Although birds are often assumed to be highly vagile, studies have shown that urban development (Crooks *et al.* 2001), agricultural fields (St. Clair *et al.* 1998), and even features as subtle as low-traffic, narrow dirt roads (Develey & Stouffer 2001; Laurance *et al.* 2004) can impede the movements of some bird species, especially those reliant on forest or shrub cover. Moreover, because movement behaviour is influenced by an individual's state and motivation (Bélisle 2005), landscape permeability may vary seasonally due to differences in microclimate, abundance of predators, food availability, or biological needs (e.g. mate-finding, tending to offspring, and dispersal).

Urban landscapes contain a number of linear features that are likely to inhibit the mobility of birds and other wildlife. By far the most ubiquitous of such features are transportation corridors whose arterial networks pervade urban and natural landscapes worldwide (Forman *et al.* 2003; Clevenger & Wierzchowski 2006). Although the barrier effect of transportation corridors has been well documented in the literature, surprisingly little is understood about the factors (e.g. surface conditions, characteristics of adjacent vegetation, noise, or traffic) that actually inhibit movement and yet, such information is critical for developing effective mitigation strategies (Jaeger *et al.* 2005). The urban landscape represents an excellent testing ground for elucidating the relative effects of such factors due to the presence of a vast network of roads of varying widths and traffic volumes. Riparian corridors are another central component of many urban landscapes. In spite of their well-documented ecological importance, the integrity of urban riparian corridors is threatened by pressure to develop riverside properties. Transportation bridges, which create major interruptions in riparian corridors, constitute another potential threat. Although several studies have examined the effects of bridges on aquatic ecosystems (Forman *et al.* 2003), far less is known about their effects on avian and terrestrial fauna. Another element of riparian corridors that is generally misunderstood is the barrier effect of the rivers themselves on the movements of birds and other wildlife. Although it is often assumed that birds can move freely from one side of a waterway to another, this assumption remains largely untested.

The primary objectives of our study were to: (1) elucidate factors affecting the permeability of urban features associated with transportation or riparian corridors to the movements of forest songbirds, (2) compare the relative permeability of these features, and (3) identify practical strategies aimed at mitigating the barrier effects of linear features in urban and other fragmented landscapes. Using a digital recording of a black-capped chickadee *Poecile atricapillus* and red-breasted nuthatch *Sitta canadensis* mobbing call as a lure, we assessed the willingness of birds to cross four types of features: (1) roads of varying widths and traffic volumes, (2) conventional railways and light transit lines, (3) transportation bridges crossing over riparian corridors, and (4) rivers. This mobbing call is attractive to dozens of species (Hurd 1996; Turcotte & Desrochers 2002) and this procedure has been used by others (e.g. Desrochers & Hannon 1997; St. Clair *et al.* 1998; St. Clair 2003) to provide an unbiased (relative to gap configuration; Desrochers *et al.* 2002), standardized motivation for small scale movement. All treatments were evaluated in several seasons and in a variety of traffic and vegetation contexts.

METHODS

Study area

Our study took place within the city limits of Calgary, Alberta, Canada (51° 05’N, 114° 05’ W), a city of 1.2 million residents located 100 km east of the Rocky Mountains. The study area is characterized by a mosaic of green spaces and residential, commercial, and industrial areas, which supports a largely artificial ‘urban forest’ dominated by native and non-native varieties of spruce (*Picea* spp.), poplar (*Populus* spp.), birch (*Betula* spp.), and fruit (*Malus, Prunus spp*.) trees. This urban matrix is bisected by riparian corridors containing native balsam poplar *Populus balsamifera* forests, which are increasingly fragmented by urban development and a rapidly expanding transportation network comprising roads ranging from quiet residential streets to busy thoroughfares (< 1000-100,000 vehicles/day; City of Calgary 2006), a Canadian Pacific (CP) railway (20-25 trains/day; C. Brown, pers. comm.), and several light rapid transit (LRT) lines (~ 300 trains/day; City of Calgary 2008). The gap in vegetation associated with these features ranges from 14 to 103 m for roads and from 15 to 29 m for the railway and transit lines.

Data collection

Each permeability experiment was carried out by two investigators positioned on either side of a target linear feature and outfitted with a portable digital music (MP3) player connected to a 30-watt amplifier. Speakers were positioned on the ground, underneath trees or tall shrubs but away from dense low-lying vegetation that might inhibit sound projection. The volume was adjusted to ambient noise such that the recording could be readily heard to a distance of 100 to 200 m by the experimenters. In each trial, we broadcasted the mobbing call on one side of the feature (hereafter, the origin) until birds approached the speaker or 6 minutes had elapsed, whichever came first. To be included in the trial, birds had to approach the origin to within 10 m, demonstrate responsiveness to the mobbing call (i.e.

aggressive posturing and calling), and remain in the vicinity of the speaker for at least one minute. When these criteria had been met and we saw or heard no new birds approaching, the origin speaker was turned off and the speaker on the opposite side of the linear feature (i.e. the destination) was turned on. The destination speaker was played for a maximum of 6 minutes during which time we recorded whether each bird moved to within 10 m of the destination. We chose a 6-minute time limit to make our results comparable with St. Clair (2003) and to avoid loss of responsiveness due to habituation. For positive responses at bridge trials, we also recorded whether each bird moved over or under the bridge. Because laboratory studies have shown that the auditory range of birds is similar to that of humans (Dooling 2004), trials were excluded from analyses if the observer at the origin could not hear the destination recording and the birds showed no response to it. We also excluded from our analyses responses that we considered weak (i.e. lack of mobbing behaviour) or uncertain due to poor visibility. Deviant responses, such as a bird moving in the opposite direction as expected, were also excluded.

In addition to bird responses, we recorded a number of variables describing the physical features of each site including: gap width (gap in vegetation at least 1.5 m tall, based on estimated minimum cover requirements for birds), feature width, and trial distance (distance between the two speakers). For bridges, we also measured bridge clearance (vertical distance between ground and underside of deck), vegetation clearance (difference in height between adjacent vegetation and top of bridge), gap over (gap in vegetation over the bridge, from treetop to treetop), and gap under (gap in vegetation >1.5 m high, under the bridge). We measured distances to the nearest metre with a laser rangefinder and heights to the nearest 0.5 m with a clinometer. For all trials, we also measured ambient noise with a hand-held noise meter set to the A-weighted scale (precision = 0.1 dBA), which adjusts noise levels according to the perceptibility of sound frequencies to humans (Morris & Therivel 2001) and, presumably, birds (Dooling 2004). Because noise tended to fluctuate in our urban setting, we determined ambient noise from the mean of 24 recordings taken at 10-second intervals over a two-minute period. Mean daily traffic volumes for roads and bridges were obtained from a municipal traffic flow map (City of Calgary 2006). We conducted no trials under steady rain or high wind conditions.

To provide a basis from which to assess the effect of gaps, each 'gap' trial conducted across a given feature was followed by an equivalent 'no-gap' trial in continuous forest cover (i.e. using the same distance and volume settings but located along, rather than across, the same or a similar feature; Fig. 2-1). To avoid potential biases related to either time of day or date, we tested our various feature types on a rotating basis and alternated between gap and no-gap trials. All trials were separated spatially by a minimum of 400 m or, when that was not possible (3 cases), temporally by at least 2 weeks to ensure independence among sites and avoid problems of habituation.

We conducted our experiments during three distinct periods: (1) breeding (4 May – 15 June 2005 and 1 May – 19 June 2006), (2) post-fledging (14 July – 26 August 2005 and 25 July – 31 August 2006), and (3) winter (12 January – 17

March 2006). We used the same experimental sites across each of these three seasons to isolate seasonal and site influences on movement and to avoid a possible bias caused by exhausting the 'best' sites in the earlier stages of the project although no site was used more than once during any given season. Trials were conducted between 0600 and 1400 during the breeding and post-fledging periods and between 0900 and 1600 in winter.

Statistical analyses

We used mixed effects logistic regression, performed using the 'xtmelogit' command in Stata 10 (StataCorp 2007) to analyze the responses of birds. Our models incorporated two random intercepts to account for the use of the same sites across seasons and the influence of conspecifics (e.g. mates or flock members) on individual responses (Crawley 2002; Rabe-Hesketh & Skrondal 2008). In all our analyses, we used Akaike Information Criterion (AIC) values to determine the most parsimonious model from a set of candidate models (Burnham & Anderson 2002). We also used AIC differences (Δ_i) and weights (w_i) to determine the relative likelihood of each candidate model being the best model of the set; lower differences and higher weights indicating a higher likelihood (*Ibid.*). To reduce problems of collinearity, we avoided entering in the same model variables with a Pearson coefficient > |0.6| (coefficients provided in Appendix 2-1). We assessed the fit of our top-performing models through the use of k-fold cross validation, using 5 folds (after Boyce *et al.* 2002 and Wiens *et al.* 2008). Model performance was determined by using a mean Spearman-rank correlation value describing the pattern of predicted values for the testing sets against those for the training sets; a stronger correlation indicating a better fit to the data.

In a first analysis, we aimed to identify factors affecting movement behaviour across all feature types combined. To limit the number of candidate models, we used a three-step process in which the top-performing model from one step served as the basis for a new set of candidate models for the subsequent step (after Wiens *et al.* 2008). In a first step, we focused on gap configuration and trial distance to assess the effect of gap while accounting for an expected waning of response with increasing distance between bird and stimulus. Secondly, we considered three site-related factors that might further affect movement behaviour: feature type, traffic volume, and ambient noise. In a third step, we considered possible seasonal or interspecific differences in movement behaviour through the addition of corresponding variables. We further examined seasonal influences on movement by repeating steps 1 and 2 separately for each season and comparing these outputs with those derived from the all-season data set. Small sample sizes for species other than the black-capped chickadee precluded the possibility of running single-species, mixed-effects models.

In a second analysis, we attempted to elucidate the primary determinants of movement across roads. We focused on roads because they constituted our largest sample and presented the most variation in factors that might be modified by landscape planners to benefit bird movement. Since we were more interested in characteristics of roads than the effect of gap presence/absence, we considered only gap trials in this analysis. Variables of primary interest included: gap width, feature width, traffic, and noise. Additionally, we included trial distance to accommodate sound attenuation, which might reduce bird responsiveness. We first compared univariable models and then compared the best-fitting one to derivatives containing one or more additional covariates.

In a third analysis, we examined the choice of travel route across bridges (i.e. over vs. under). Due to a small sample size, we restricted our analysis to a comparison of univariable models that included the following explanatory variables: noise, traffic, feature width, bridge clearance, vegetation clearance, darkness (bridge width/bridge clearance), and gap differential (i.e. gap over – gap under). We then graphically explored route selection as a function of the two most important variables identified from our models.

RESULTS

Of 925 trials initiated at 274 sites, 563 (60.9%) were successful in attracting at least one responsive bird to the origin speaker. From a total of 2740 birds at these successful trials, we eliminated those that exhibited weak or unclear responses (455 birds) or belonging to species that were not represented by a minimum of 15 independent conspecific groups (44 birds). Thus, we retained for our analyses the responses of 2241 individual birds, representing 697 conspecific groups distributed among 210 independent sites. Because the same sites were used across seasons, it is possible that some birds were used more than once though in different seasons. Our sample was heavily dominated by black-capped chickadees (n = 559 or 80.2% of conspecific groups) but also contained red-breasted nuthatches (89 groups), downy woodpeckers *Picoides pubescens* (30 groups), and white-breasted nuthatches *Sitta carolinensis* (19 groups). Retained trials were split roughly equally relative to gap configuration (290 gap and 273 no-gap) and season (163, 205, and 195 for breeding, post-fledging, and winter, respectively). However, we sampled roads and bridges more heavily (304 and 135 trials, respectively) than railways and rivers (33 and 89 trials, respectively) because the former offered greater variation in characteristics likely to affect movement behaviour and of relevance to urban planning and management (e.g. width, traffic volume, bridge height, etc.).

Factors affecting movement across all feature types

In step 1 of our model-selection process, the model containing terms for gap, distance, and their interaction provided a dramatically better fit than simpler models containing only one or two of these terms (Appendix 2-2). This result was consistent for the all-season model and the season-specific models. In step 2, the model containing traffic and feature type emerged as the best one. Step 2 produced similar results for the season-specific models with the exclusion of feature type in the post-fledging model and the addition of noise in the winter model. In step 3, adding terms for season, species, and a season-by-trial distance interaction substantially improved the fit of the all-season model. K-fold cross-validation of this best-fit model resulted in a mean Spearman-rank correlation of 0.9491 ($P < 0.0001$), suggesting an excellent fit to the data.

As expected, the likelihood of a bird moving to the destination speaker decreased significantly with increasing distance ($P < 0.001$; Table 2-1). Surprisingly, gap had no significant effect on movement; however, the gap-by-distance interaction was highly significant ($P < 0.001$). Whereas the likelihood of movement remained very high in no-gap trials up to a distance of approximately 100 m, in gap trials this likelihood decreased dramatically as trial distance exceeded 30 m (Fig. 2-2). By 45 m, birds were only half as likely to cross a feature as they were to travel a similar distance through continuous forest cover and by 75 m they were < 10% as likely to do so. The best-fit model also indicated that vehicular traffic had a significant dampening effect on movement (odds ratio = 0.952 for a 1000-vehicle/day increase in traffic; $P < 0.001$). The likelihood of movement was significantly lower in bridge and river trials compared to road trials. However, when only gap trials were considered in a separate analysis, bridges and roads had a very similar effect on movement whereas rivers were significantly less permeable than roads at trial distances < 50 m (Fig. 2-3; $P = 0.028$). Although the model showed no significant difference between road and railway trials across the full range of trial conditions, in reality the proportion of birds that crossed railways was always very high, probably due to the narrow width of these features (Fig. 2-3).

Our model revealed no significant differences among seasons when that factor was considered singly; however, we found a significant season-by-distance interaction indicating that birds were more likely to travel farther in winter relative to the breeding season. When we explored this interaction further by running separate models for no-gap and gap trials, we found a more pronounced effect in no-gap (*P* = 0.025) than in gap (*P* = 0.146) situations (Fig. 2-4). Finally, although black-capped chickadees were generally more likely to respond to our mobbing call than the other species, we found a striking consistency in bird responses relative to gaps with a sharp decline in movement evident for most species in gap trials > 50 m (Fig. 2-5).

Factors affecting movement across roads

Our analysis specific to roads revealed that gap width explained more variation in data than any of the other variables considered, including trial distance (Table 2-2). In step 2 of the model comparison, adding a variable for traffic improved the fit of the model. Gap width and traffic both had a negative effect on movement (*P* < 0.001 and *P* = 0.001, respectively; Appendix 2-3). K-fold cross-validation generated a mean Spearman rank correlation of 0.915 (*P* = 0.002), indicating good model fit.

Choice of travel routes across bridges

Our third analysis revealed that 2.2 times as many birds flew over, rather than under, bridges (66 and 30 birds, respectively) even though this was the less direct route between the speakers located at ground level. The two univariable models that explained the most variation in the data contained terms for gap differential and vegetation clearance (Table 2-3). Although these models were slightly shy of conventional significance (*P* = 0.115 and *P* = 0.073, respectively;

Appendix 2-4), graphical explorations revealed some striking trends. For example, we found a clear threshold for gap differential at 15 m (Fig. 2-6a) beyond which no birds crossed over a bridge. In addition, the proportion of birds crossing over a bridge clearly increased with increasing vegetation clearance above the bridge (Fig. 2-6b).

DISCUSSION

Factors affecting bird movements

Perhaps one of the most important findings of our study is the fundamental role of vegetation – particularly gap width – in influencing the movements of forest songbirds across urban features. We base this finding on several lines of evidence. First, our best-fit model across all feature types revealed a highly significant gap-by-distance interaction, with a striking 50% threshold at 45 m. Secondly, gap width was the most important determinant of movement across roads. Thirdly, gap differential was the primary factor determining the choice of travel route across a bridge.

Our finding of a 45-m threshold is highly consistent with that of similar mobbing-based studies conducted in more natural landscapes (Desrochers & Hannon 1997; St. Clair *et al.* 1998; Bélisle & Desrochers 2002). Reduced mobility across gaps by forest-dwelling birds has also been demonstrated in studies relying on methods other than mobbing experiments both in tropical (Develey & Stouffer 2001; Laurance *et al.* 2004; Awade & Metzger 2008) and temperate (Sieving *et al.* 1996; Rail *et al.* 1997) settings. The most plausible explanation why the birds in our study avoided crossing gaps > 45 m is the increased exposure to the risk of predation by locally common aerial predators such as merlins *Falco columbarius* and sharp-shinned hawks *Accipiter striatus*. Indeed, several studies have shown that songbirds, notably parids, adjust their use of open habitats to reduce predation risk (Rodriguez *et al.* 2001; Telleria *et al.* 2001; Desrochers *et al.* 2002).

Vegetation also appeared to play a key role in the choice of a travel path across bridges. The birds in our study displayed a strong preference for detouring above bridges rather than flying directly underneath them except when adjacent vegetation was clearly not conducive; for example, when the gap above was considerably wider than the gap below or when the bridge was higher than, or of relatively equal height to, the surrounding vegetation. This preference for movement over bridges may stem from a higher perceived predation risk or simply an aversion to the artificial conditions of light, vegetative cover, and substrate that typically exist underneath bridges and are known to inhibit movements of a number of taxa including large carnivores, ungulates, and amphibians (Forman *et al.* 2003).

A second, albeit secondary, factor that emerged as a significant determinant of movement was traffic. This is consistent with previous studies showing that high-traffic roads are less permeable to the movements of wildlife than low-traffic ones (Gibeau *et al.* 2002; Whittington *et al.* 2004; Alexander *et al.* 2005). We often observed birds attempting to cross a road but looping back to the roadside upon the approach of a vehicle, suggesting that birds may perceive moving traffic as a threat. Interestingly, other studies have shown that the movements of large mammals are primarily affected by traffic levels (Waller & Servheen 2005; Gagnon *et al.* 2007; Keller & Bender 2007) whereas smaller taxa including birds (Laurance *et al.* 2004) and small mammals (Swihart & Slade 1984, McGregor *et al.* 2008) appear to be most sensitive either to the gap in vegetation created by the road or the road surface itself. Our results, which showed that gap width had a greater effect on movement than traffic volume, are consistent with this general interpretation.

Compared to most other studies of movement behaviour, ours was unique in that it was replicated across three seasons. Although we expected that movements might be constrained in winter due to higher thermoenergetic costs, we instead found that birds generally moved greater distances in winter than in the snow-free seasons. This may be due to the tendency of many year-round resident birds to form winter flocks occupying joint territories that are typically much larger than single-pair breeding territories (Smith 1991). It does not appear that the greater propensity for movement in winter was a function of group size because bird groups were generally largest during the post-fledging period when movements were relatively constrained (mean group size = 1.92, 3.86, and 3.61 birds during the breeding, post-fledging, and winter periods, respectively). Interestingly, birds were only significantly more mobile in winter in the absence of a gap suggesting that gaps, especially wide ones, restricted movement in all seasons. In general, we found a high degree of consistency in the factors affecting movement across seasons, with terms for a gap-by-distance interaction and traffic being included in all three of our season-specific models.

Although our models indicated that noise was generally not a major determinant of movement behaviour across gaps, we found a significant negative correlation between noise and the probability of attracting birds to the origin speaker in our roadside trials (M. Tremblay, unpublished data). Other studies have also found a negative effect of noise load on bird densities in roadside habitats (Reijnen *et al.* 1995; Parris & Schneider 2008). In our study, poor habitat quality may also have been a contributing factor because vegetation along busy roads tended to consist of sparsely planted trees with poor understorey development. Whether caused by noise or poor habitat, the scarcity of birds along major roads suggests that fragmentation effects of roads may go beyond the strict barrier effects of these features and include effects on the quality and use of roadside habitats, an idea that warrants further investigation.

Relative permeability of tested features

The birds in our study responded similarly to bridges and roads, implying that the added vertical component of bridges (median height = 3.75 m; range = 1- 29 m) relative to roads did not significantly affect the willingness of birds to cross them. Railways were by far the most permeable feature type we tested, probably due their narrow width (< 30 m) and low traffic volumes compared to roads. Although the permeability of railways to wildlife movements is poorly documented in the literature, a few sources suggest that railways are relatively permeable to the movements of at least one other taxonomic group, large mammals (Page *et al.* 1996; Jalkotzy *et al.* 1997), although they can also constitute an important source of mortality for this group (Benn & Herrero 2002; Callaghan 2002).

Rivers were less permeable than the three anthropogenic features we studied. This somewhat counterintuitive finding is consistent with at least one other study in which rivers were found to have a greater barrier effect than either roads or meadows of equivalent widths (St. Clair 2003). St. Clair suggested that this result might have an evolutionary basis and speculated that birds may be genetically predisposed to perceive rivers as high risk areas due to the absence of cover and abundance of natural predators. In contrast, birds may be less attuned to the risks associated with more recent anthropogenic features despite the dangers they present such as raptors that selectively hunt along them (Meunier *et al.* 2000) or moving vehicles (Hell *et al.* 2005; Orlowski 2008). A second explanation is that rivers may serve as natural territorial boundaries, which birds may be reluctant to cross.

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Our results point to a number of practical measures that can improve the functional connectivity of urban and other fragmented landscapes for forest songbirds. First, bird movement will probably be increased by limiting gaps in vegetation to 45 m, particularly where transportation corridors bisect important habitat patches. This could be accomplished by the placement of trees on either side of a roadway or by the provision of treed medians, which could act as stepping stones for birds (see Gillies & St. Clair 2008; Boscolo *et al.* 2008), in essence reducing the gap by half. For both roadside and median plantings, tall overarching trees are preferable to shrubby material to ensure safe passage well above moving traffic. Secondly, because of their relatively narrow width and low traffic volumes, railways and light transit lines offer better landscape connectivity for forest birds than wide, high-volume roads. This adds a new argument to the already well-established case for trains as a cornerstone of sustainable transportation solutions, particularly in heavily populated areas. A final recommendation from our study is to limit bisection of riparian corridors, which provide natural conduits for movements amid typically high-quality habitats. As well, because birds showed a marked preference for flying over bridges rather than under them, bridges should be flanked with tall trees to enhance safe movement opportunities above these structures, wherever feasible. Alternatively, very high bridges that can accommodate continuous forest cover below them should be highly permeable to birds and most terrestrial and aquatic species. Because our study showed that birds were reluctant to cross rivers, even relatively narrow ones, it may be important to ensure that continuous habitat exists along at least one, and preferably both, sides of riparian corridors to allow for unfettered wildlife movements without the need to cross from one side to another.

In summary, although our study showed that linear features can impede the movements of forest songbirds, it also suggests that even simple, relatively inexpensive solutions, like the strategic placement of trees along transportation corridors, can enhance habitat connectivity for wildlife and thus, promote the integrity of natural systems within urban and other fragmented landscapes worldwide.

ACKNOWLEDGMENTS

This research was supported by a Discovery Grant from the Natural Science and Engineering Research Council (NSERC) to CCSC and NSERC and Alberta Ingenuity postgraduate scholarships to MAT. Further funding for the project was provided by the Alberta Conservation Association, University of Alberta Bill Shostak Wildlife Award, Alberta Sport, Recreation, Parks and Wildlife Foundation, ECO Canada, Nature Calgary, Mountain Equipment Coop, Lamont Development Inc., and O2 Planning and Design Ltd. In-kind support was provided by the University of Alberta, the City of Calgary, and The Orthoshop, Ltd. We are grateful to M. Coombe, K. Jonassen, and E. Miranda for their invaluable assistance in the field. We also thank E. Bayne and two anonymous reviewers for their insightful comments on previous drafts of the manuscript.

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Table 2-1. Variables affecting movement behaviour of forest songbirds relative to urban features according to best ‘all-season’ model from Appendix 2-2, derived from mixed effects logistic regression (Wald $X^2 = 140.58$, df = 17, $P < 0.0001$, LL = -789.43; N = 2241 individual birds in 691 conspecific groups at 210 sites).

Variable	**Odds ratio**[a]	**95%**	**C.I.**	***P***
Distance (m/10)	0.602	0.461	0.787	< 0.001
Gap	1.036	0.277	3.877	0.958
Gap x distance	0.533	0.415	0.686	< 0.001
Feature type (ref = roads)				
bridges	0.395	0.174	0.899	0.027
railways	1.544	0.306	7.776	0.599
rivers	0.222	0.067	0.735	0.014
Traffic (veh/day/1000)	0.952	0.930	0.974	< 0.001
Season (ref = breeding)				
post-fledging	1.361	0.312	5.939	0.682
winter	0.790	0.185	3.375	0.751
Season x distance (ref = breeding)				
post-fledging x dist	1.083	0.816	1.436	0.581
winter x dist	1.527	1.145	2.036	0.004
Species (ref = black-capped chickadee)				
downy woodpecker	0.209	0.043	1.007	0.051
red-breasted nuthatch	0.429	0.158	1.164	0.097
white-breasted nuthatch	0.490	0.051	4.747	0.538

[a] Odds ratios represent change in odds associated with 1-unit change in independent variable. < 1 = decreased odds (negative coef.); > 1 = increased odds (positive coef.).

Table 2-2. Comparison of candidate models explaining movement behaviour across roads (gap trials only; N = 667 individual birds in 193 conspecific groups at 56 sites).

Analysis / model	**LL**	**df**	**AIC**	**Δ_i**	**w_i**
Step 1: Univariable models					
1. Gap width	-272.96	4	553.9	0.0	0.753
2. Distance	-274.46	4	556.9	3.0	0.167
3. Feature width	-275.20	4	558.4	4.5	0.080
4. Traffic	-287.12	4	582.2	28.3	< 0.001
5. Noise	-299.19	4	606.4	52.5	< 0.001
6. Constant only	-303.83	3	613.7	59.8	< 0.001
Step 2: Variables added to model 1					
7. Traffic	-267.31	5	544.6	0.0	0.580
8. Noise	-267.64	5	545.3	0.7	0.415
9. No added variables	-272.96	4	553.9	9.3	0.006

Table 2-3. Comparison of univariable models explaining likelihood of birds flying over bridges (N = 212 individual birds in 79 conspecific groups at 26 sites).

Model	**LL**	**df**	**AIC**	Δ_i	w_i
1. Gap differential	-20.52	4	49.04	0.0	0.995
2. Vegetation clearance	-26.08	4	60.16	11.1	0.004
3. Bridge clearance	-28.33	4	64.65	15.6	< 0.001
4. Traffic	-29.15	4	66.30	17.3	< 0.001
5. Bridge width	-30.68	4	69.36	20.3	< 0.001
6. Noise	-30.97	4	69.94	20.9	< 0.001
7. Constant only	-32.40	3	70.79	21.8	< 0.001
8. Darkness	-31.70	4	71.40	22.4	< 0.001

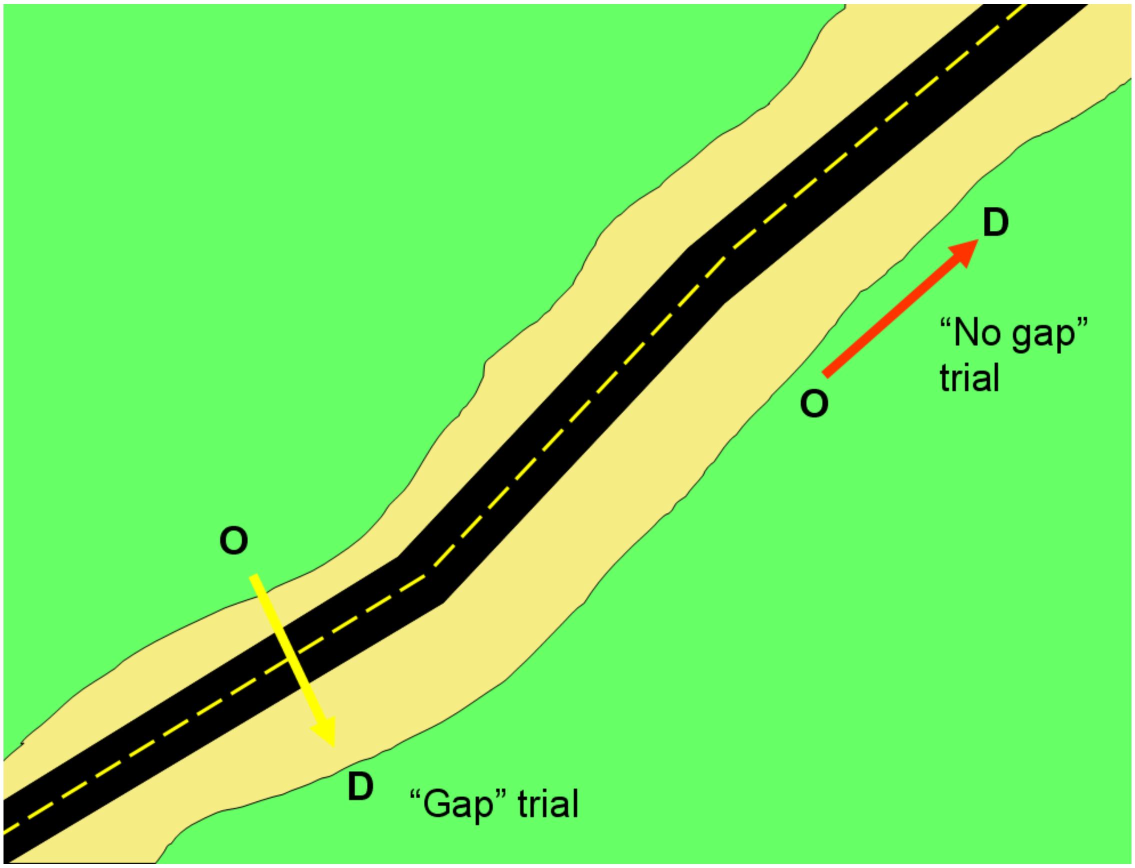


Figure 2-1. Paired sampling design used for playback trials. Each trial conducted across a feature was paired with an equivalent trial conducted under similar habitat and noise conditions but in continuous tree cover (O = origin speaker; D = destination speaker).

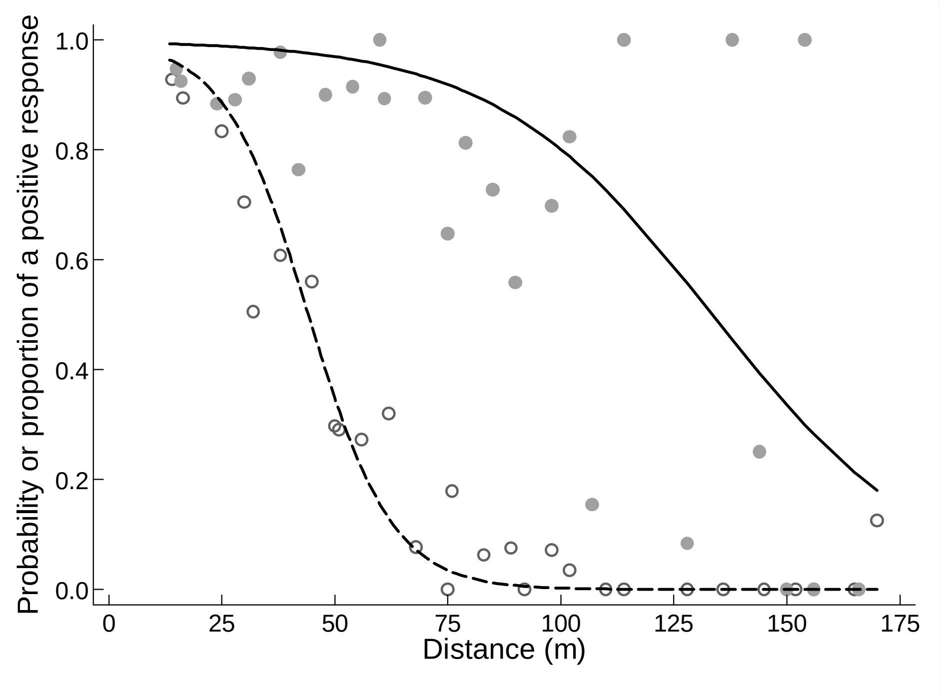


Figure 2-2. Probability of response as a function of trial distance in no-gap (solid line, full circles) and gap (dashed line; empty circles) trials. Lines represent the probability of a positive response predicted by mixed effects logistic regression. Points represent the proportion of positive responses within 5-m trial distance intervals.

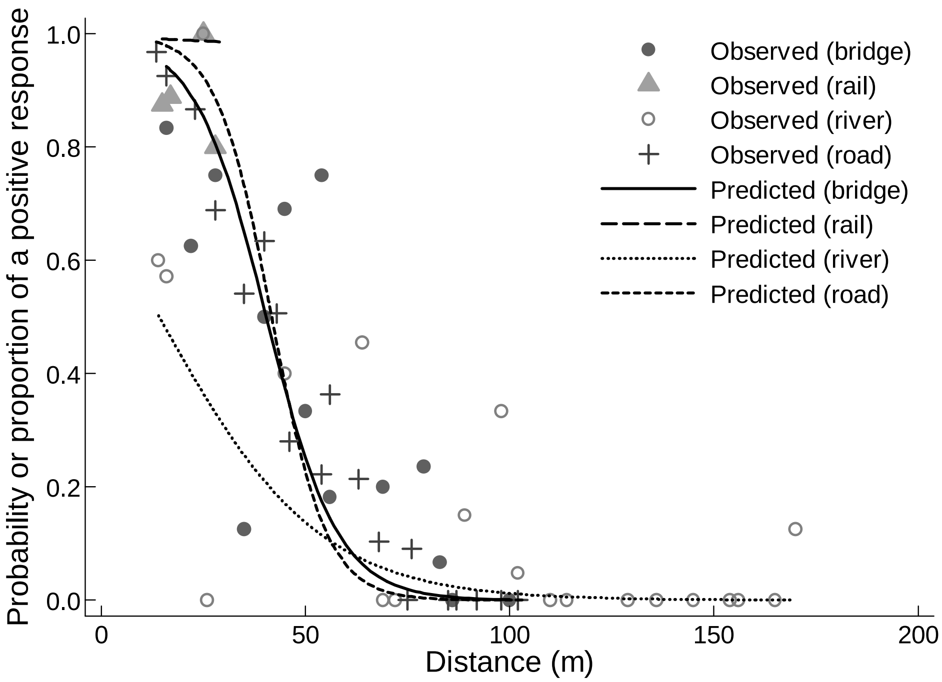
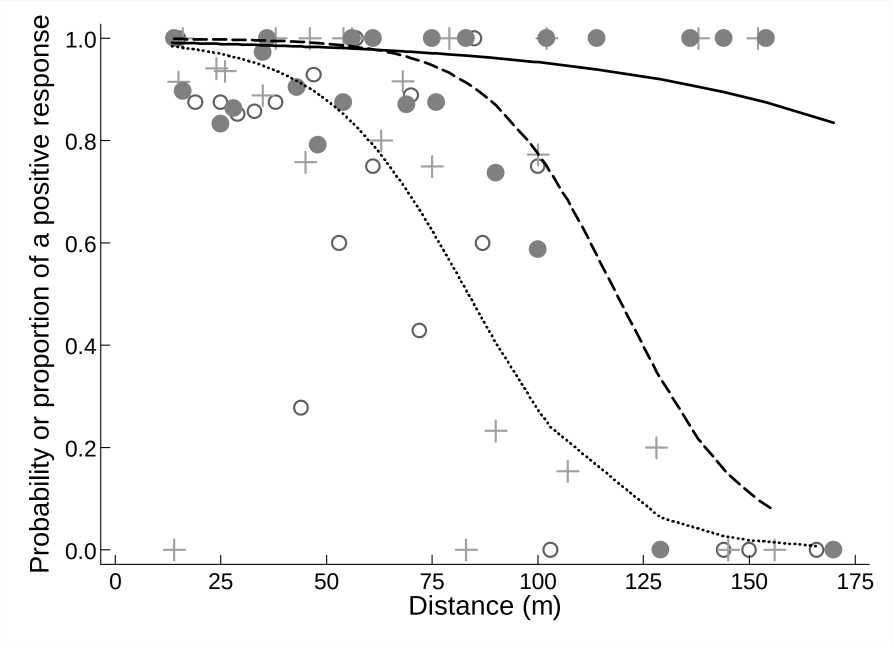


Figure 2-3. Crossing success as a function of trial distance and trial type in gap trials only. Lines and points as described in Fig. 2-2.

a)



b)

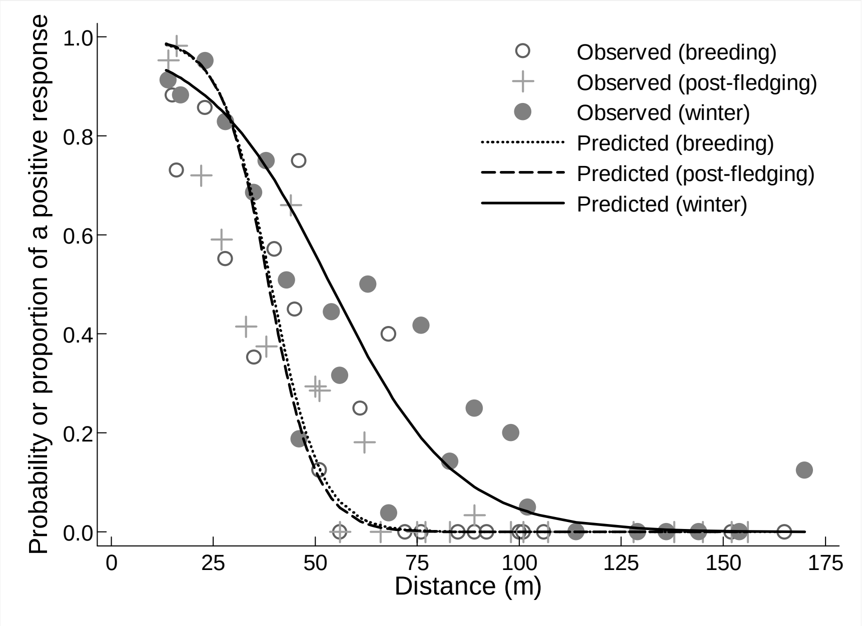


Figure 2-4. Seasonal variation in responses to playback experiments in a) no-gap and b) gap trials. Lines and points as described in Fig. 2-2.

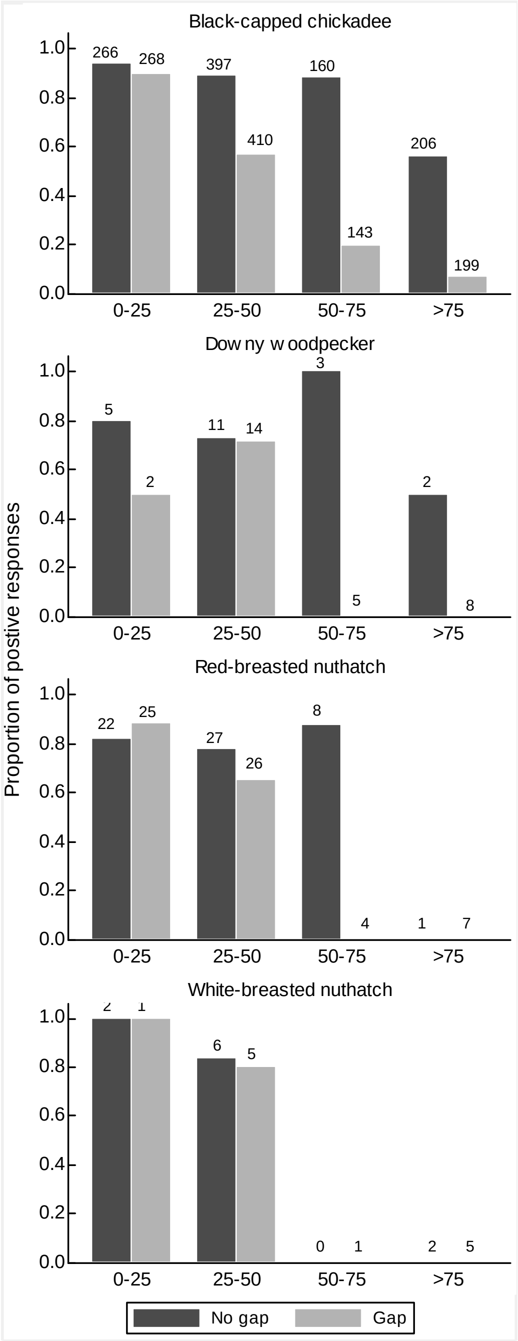
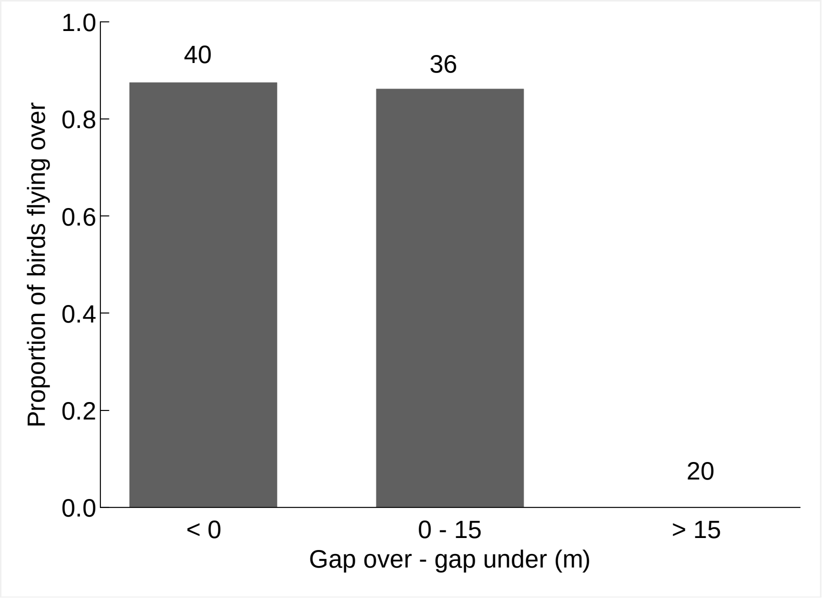


Figure 2-5. Proportion of positive responses, by species, in relation to trial distance (m) and gap configuration. Numbers above bars represent number of individual birds.

a)



b)

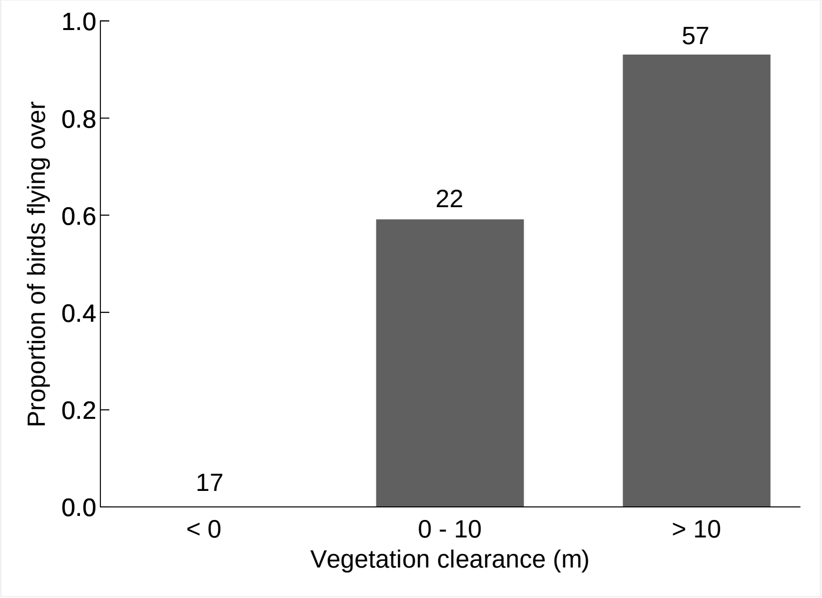


Figure 2-6. Proportion of birds flying over bridges as a function of a) difference in vegetation gap over and under the bridge and b) vegetation clearance above bridge. Numbers above bars represent number of individual birds.

Appendix 2-1. Correlations among independent variables (continuous variables only; numbers represent Pearson coefficients; correlations > |0.6| are in bold font)

a) Trials involving all feature types (gap and no gap trials)

	distance	traffic	noise
distance	1		
traffic	0.0932	1	
noise	-0.041	0.4965	1

N = 2241 individual birds in 691 conspecific groups at 210 sites.

b) Trials across roads (gap trials only)

	distance	traffic	noise	gap width	feature width
distance	1				
traffic	**0.6694**	1			
noise	0.3105	**0.6358**	1		
gap width	**0.9752**	**0.6526**	0.2831	1	
feature width	**0.8568**	**0.8157**	0.4101	**0.8454**	1

N = 667 individual birds in 193 conspecific groups at 56 sites.

c) Trials across bridges (gap trials only)

	noise	vegetation clearance	traffic	gap differential	bridge clearance	bridge width	darkness
noise	1						
veg clearance	0.1251	1					
traffic	0.4554	-0.292	1				
gap differential	-0.2256	-0.5587	0.1388	1			
bridge clearance	-0.1397	**-0.6615**	0.0590	**0.7183**	1		
bridge width	0.2655	-0.2891	**0.7719**	0.0695	-0.0299	1	
darkness	0.1345	0.1011	0.4777	-0.2999	-0.4673	**0.7838**	1

N = 212 individual birds in 79 conspecific groups at 26 sites.

Appendix 2-2**.** Comparison of candidate models explaining movement behaviour relative to urban features in Calgary, Alberta, Canada.

Model	**LL**	**df**	**AIC**	**Δ_i**	**w_i**
Step 1 comparison					
1. Gap + dist + gapXdist	-822.1	6	1656.2	0.0	1.000
2. Gap + distance	-833.9	5	1677.8	21.6	< 0.001
3. Distance	-877.5	4	1763.0	106.8	< 0.001
4. Gap	-884.7	4	1777.5	121.2	< 0.001
5. Constant only	-914.4	3	1834.9	178.6	< 0.001
Step 2 comparison (variables added to model 1)					
6. Type + traffic[1]	-809.7	10	1639.4	0.0	0.547
7. Type + traffic + noise[3]	-809.7	11	1641.4	2.0	0.202
8. Type + traffic + noise + noiseXgap	-809.4	12	1642.7	3.4	0.101
9. Traffic[2]	-814.5	7	1642.9	3.6	0.091
10. Traffic + noise	-814.0	8	1643.9	4.5	0.056
11. Type + traffic + typeXgap	-809.3	13	1644.5	5.1	< 0.001
12. Type + noise + noiseXgap	-814.2	11	1650.3	10.9	0.002
13. No variables added	-822.1	6	1656.2	16.9	< 0.001
14. Type + noise	-818.1	10	1656.3	16.9	< 0.001
15. Type	-819.5	9	1657.0	17.6	< 0.001
16. Noise	-821.7	7	1657.4	18.0	< 0.001
Step 3 comparison (variables added to model 6)					
17. Season + species + seasonXdist*	-789.4	17	1612.9	0.00	0.972
18. Season + species	-795.8	15	1621.5	8.67	0.013
19. Season	-799.2	12	1622.5	9.62	0.008
20. Season + species + seasonXgap	-794.3	17	1622.6	9.74	0.007
21. No variables added	-809.7	10	1639.4	26.50	< 0.001
22. Species	-806.7	13	1639.4	26.50	< 0.001

*Best all-season model; [1]Best breeding season model; [2]Best post-fledging season model; [3]Best winter season model.

Appendix 2-3. Best mixed effects logistic regression model explaining movement success across roads in Calgary, Alberta, Canada (Wald $X^2 = 48.60$, df = 5, $P < 0.0001$, LL = -267.307).

Analysis / variable	**Odds Ratio**	**95%**	**C.I.**	**P**
Gap width	0.326	0.221	0.481	< 0.001
Traffic	0.957	0.933	0.983	0.001

Appendix 2-4. Parameters of top-performing univariable models explaining the likelihood of a bird flying over a bridge, generated by mixed effects logistic regression.

Univariable Model	**Odds ratio**	**95%**	**C.I.**	***P***
Gap differential[a]	0.505	0.216	1.181	0.115
Vegetation clearance[b]	2.464	0.919	6.608	0.073

[a] Wald X^2 = 2.49, df = 4, P = 0.115, LL = -20.518

[b] Wald X^2 3.21, df = 4, P = 0.073, LL = -26.081

CHAPTER 3

PERMEABILITY OF AN URBAN LANDSCAPE TO THE MOVEMENTS OF FOREST SONGBIRDS

SUMMARY

1. Urbanization represents a major threat to biodiversity worldwide because it causes permanent degradation and fragmentation of biologically rich natural communities associated with coastal plains and river valleys where cities are typically located.

2. We conducted a series of translocation experiments within the urban landscape of Calgary, Alberta, Canada to assess the permeability of selected landscape elements for two species of forest songbirds with contrasting adaptabilities to urban development and migratory behaviours: the black-capped chickadee (*Poecile atricapillus*; an urban-adaptable year-round resident) and the yellow warbler (*Dendroica petechia*; an urban-sensitive Neotropical migrant).

3. Birds were caught in riparian habitats and translocated either within the riparian corridor of origin or across the urban matrix. Riparian translocations occurred in continuous forest, across one or several transportation bridges, or across a major river. In the urban matrix, birds were translocated across a single major road, well-treed developed areas, poorly-treed developed areas, or multiple gaps.

4. Using Cox regression we found the presence of gaps in forest cover explained more variation in return time than the amount of forest cover for both species. Multiple gaps, in particular, resulted in significantly longer return times compared to continuous forest. Chickadees exhibited longer return times when translocated across single linear gaps associated with bridges or roads. In contrast, yellow warbler movements appeared to be more constrained by urban development.

Synthesis and applications. To increase permeability for urban-sensitive species like the yellow warbler, conservation efforts should focus on preserving habitat connectivity along riparian corridors or other major swaths of natural vegetation where movements are likely to occur. For urban-adapted species like chickadees, enhancement of the urban matrix through the incorporation of elements designed to minimize gaps in vegetation, such as roadside trees and stepping stones, should be encouraged.

INTRODUCTION

Habitat loss and fragmentation caused by urban development have been associated with declines or local extinctions of many native taxa including mammals (Crooks 2002, Hansen *et al.* 2005), birds (Blair 1996, Crooks *et al.* 2004) and arthropods (Bolger *et al.* 2000, Holway & Suarez 2006). Most studies, however, have focussed on patterns in abundance and distribution of species with comparatively little experimental work done to understand the mechanisms underlying these patterns (Shochat *et al.* 2006). The concept of functional landscape connectivity, defined as 'the degree to which the landscape impedes or facilitates movement among resource patches' (Taylor *et al.* 1993), explicitly recognizes the behavioural link between process and pattern (Bélisle 2005; Chetkiewicz *et al.* 2006). Increasingly, empirical studies show that connectivity can play a role in explaining patterns of species occupancy (e.g. Betts *et al.* 2007; Awade & Metzger 2008; Martensen *et al.* 2008) and genetic diversity (Lindsay *et al.* 2008; Ortega *et al.* 2008) in fragmented landscapes. A major challenge in assessing connectivity is that movement is influenced by an individual's state and motivation. These in turn dictate the choice of destination and the amount of risk or energetic cost an individual is willing to incur (Bélisle 2005).

Experimental approaches have been developed to standardize both destination and motivation, allowing ecologists to quantify the permeability of specific landscape features. For example, researchers have used taped recordings of avian songs or calls to lure birds across small-scale landscape features to assess their willingness to cross these. Such experiments have revealed that the movements of forest birds are often constrained by the presence of gaps associated with anthropogenic features (Desrochers & Hannon 1997, Develey & Stouffer 2001, Bélisle & Desrochers 2002, Awade & Metzger 2008) or natural openings in forest cover (St. Clair 2003). At landscape scales, translocation experiments have been used to evaluate the effects of multiple gaps (Bélisle & St. Clair 2001) and variations in the amount and configuration of forest cover (Bélisle *et al.* 2001, Gobeil & Villard 2002, Gillies & St. Clair 2008) on bird movements. Landscape-scale factors clearly affect movement but these effects often vary among species, possibly due to differences in navigational and flying ability, habitat preference, or vulnerability to predation.

To date, experimental evaluations of functional landscape connectivity have been largely restricted to landscapes fragmented by agriculture or forestry, which are typically depicted as islands of suitable habitat within a matrix of non-habitat. The binary landscape model is unrealistic, however, in urban and other heterogeneous landscapes where different land cover types represent varying levels of suitability and permeability (Bender & Fahrig 2005, Chetkiewicz *et al.* 2006). Although there is a need to understand how human infrastructure and land use affect bird movements in urban settings, we know of no studies that have investigated the ability of birds to move within the urban context.

Here, we report on a set of experiments in which we used translocations to assess the permeability of broad-scale features of the urban landscape to the movements of two species of forest songbirds of similar size but with contrasting migratory behaviours and sensitivities to urban development: the black-capped chickadee (*Poecile atricapillus*), a nonmigratory omnivorous species commonly found within the urban matrix and a regular visitor to bird feeders, and the yellow warbler (*Dendroica petechia*), an insectivorous migratory species that is generally restricted to riparian habitats in the study area. We asked: (1) How do specific elements of the urban landscape affect the movements of translocated birds? (2) What characteristics of the landscape explain the most variation in return time? and (3) What strategies can be used to improve the permeability of the urban landscape for songbirds? We were particularly interested in the role of gaps and canopy cover as determinants of movement within a heterogeneous landscape. We predicted that gaps in forest cover would constrain movements, resulting in longer return times, and that multiple gaps would have a stronger barrier effect than single gaps. We also hypothesized that threshold levels in canopy cover would be more important than mean canopy cover conditions to moving birds.

METHODS

Study area

Our study took place within the city limits of Calgary, Alberta (51° 05'N, 114° 05' W) a city of 1.2 million residents located east of the Rocky Mountains in western Canada. The city is bisected by the Bow River and its main tributary, the Elbow River. Riparian corridors are dominated by native balsam poplar (*Populus balsamifera*) forests. The intervening urban matrix comprises a mix of residential, commercial, industrial, and recreational areas and managed parks. These areas support a forest dominated by a mix of native and non-native species of spruce (*Picea* spp.), poplar (*Populus* spp.), birch (*Betula* spp.) and fruit-bearing (e.g. *Prunus* and *Malus spp.*). Local canopy cover, measured at the scale of a 50-m radius circle, ranges from 2-36% in developed areas to 61-81% in forested natural areas (M. Tremblay, *unpublished data*). The landscape is heavily fragmented by a rapidly expanding transportation network.

Field experiments

From 5 May to 14 July 2006 and 8 May to 11 July 2007, we performed translocation experiments to assess the relative permeability of various features and land cover types of the urban landscape to the movements of black-capped chickadees (hereafter chickadees) and yellow warblers (hereafter warblers; Fig. 3-1). Both species generally produce a single brood annually and weigh approximately 10 g. Singing, and presumably territorial, males were lured to a mist net using a taped recording of a territorial song and decoys. Each bird was fitted with a US Fish and Wildlife Service metal leg band and two or three coloured celluloid bands to allow for individual identification from a distance. Once banded, birds were placed in cotton bags and transported by bicycle or automobile to the relocation point. During transport, bags were suspended by their drawstrings to ensure proper ventilation and reduce vibrations or impacts with hard surfaces. To further reduce stress, we ensured birds were not exposed to excessive noise or temperature extremes. Mean time in captivity was 53.7 min (+/- 19.6 s.d.).

Birds were typically caught in near-natural riparian habitats and moved across selected landscape features either within the riparian corridor of origin or across the urban matrix. Riparian treatments included: (1) continuous forest, (2) one or several transportation bridges, which have been shown to inhibit movements along riparian corridors (Tremblay & St. Clair 2009), and (3) the Bow River (Fig. 3-2). Urban matrix treatments included: (1) single road, (2) well-treed developed areas, (3) poorly treed developed areas, (4) multiple linear gaps (e.g. multiple roads or road + Bow River) and (5) multiple gaps, both linear and non-linear. Roads included in our study consisted of high-volume thoroughfares with at least 4 lanes and an unforested right-of-way averaging 184 m wide. The mean width of the Bow River was 123 m. We timed translocations to correspond to the nest building, egg incubation, nestling, and early fledging stages of the breeding season for each of our study species (early May to mid-June for chickadees; early June to mid-July for warblers). To avoid possible biases associated with the breeding phenology, we spread treatments out roughly evenly during the course of each field season. All birds were released in sites offering good tree cover to ensure they had access to shelter and forage before undertaking their return journey, regardless of treatment. Although we strove to maintain a consistent translocation distance of 1 km, mean distances varied somewhat among treatments due to the juxtaposition of unwanted features or the limited availability of suitable release sites (Appendix 3-1).

Birds were caught between sunrise and 12h00. We checked for the return of each bird to its territory according to the following schedule: 1.5 and 3.0 hours post-release, between 18h00 and 20h00 in the evening of the capture, and then once a day (approximately midday following morning translocations, for logistical reasons) for the five days following release. We chose to end our observation period after 5 days based on previous translocation studies in which most birds returned within this time period (Bélisle *et al.* 2001, Bélisle & St. Clair 2001, Gobeil & Villard 2002). During each check, one or two observers patrolled the area surrounding the capture site for 30 minutes, intermittently playing a taped territorial song while watching and listening for birds. We adjusted our search radius based on observed mean territory size for each species (100 m for chickadees; 50 m for warblers).

Landscape characterization

We used ArcGIS® 9 (ESRI 2007) combined with Hawth's Analysis Tools (SpatialEcology 2008) to create a suite of variables describing habitat conditions for each of our translocations. We used two approaches for describing the urban landscape based on how birds might perceive it. First, we described the habitat surrounding each translocation by applying a buffer around each translocation axis with a width equal to 0.25 times the length of this line (Fig. 3-3a). The result was an ellipsoid with a constant length to width ratio of 3, which we believed represented a reasonable search area for a bird seeking to return to its territory (see also Bélisle *et al.* 2001; Gillies & St. Clair 2008). Second, we described habitat conditions along a pathway representing the 'most forested route' (MFR) between capture and release points (Fig. 3-3a). Given that forest birds prefer to move through forested detours rather than open areas (Desrochers & Hannon 1997, St. Clair *et al.* 1998; Bélisle & Desrochers 2002, Hadley & Betts 2009), we felt that an MFR would represent a more realistic pathway between capture and release points than a straight line. MFRs, which are conceptually analogous to 'least-cost' paths used in cost-distance modelling (Adriaensen *et al.* 2003), were manually digitized from a high-resolution (0.5 m) orthorectified digital photo following 3 simple rules reflecting the assumptions that moving birds seek to minimize risk (i.e. exposure to gaps) and energetic costs (i.e. travel distance): (1) gaps were either circumvented or, in the case of continuous gaps, crossed using the shortest crossing route, (2) the entire route had to be contained within the ellipsoid, and (3) the pathway had to reflect continual movement toward the capture point (i.e., no backtracking). For each translocation, we then developed a series of variables describing conditions either within the ellipsoid or along the MFR (Table 3-1).

Forest cover variables

Using existing digital data sets from the City of Calgary, we created a polygon land cover layer in which developed areas were classified according to land use (e.g., residential, commercial, golf course, etc.) and natural areas were classified according to habitat type (e.g. spruce forest, low shrub, grassland, or water). Percent canopy cover was determined from densiometer readings taken during vegetation surveys conducted at 187 sites representing the full range of land cover types within the study area (M. Tremblay, *unpublished data*). For developed sites, we applied a correction factor to account for the presence of impervious surfaces like rooftops and roads from which densiometer readings were not taken.

We did this by generating 50 random points within a 50-m radius circle centred on each survey point and counting the number of points that coincided with an impervious surface. For each site, we then multiplied our initial canopy cover value by 1 – p, where p was the proportion of impervious points counted. We then summarized our corrected canopy cover values for each of our land cover types and, using these as a guide, visually estimated, from a high-resolution orthophoto (precision = 0.5 m), percent canopy cover for each land cover polygon within each of our translocation ellipsoids. Finally, we determined mean canopy cover for each ellipsoid by weighting the canopy cover value of each polygon contained within an ellipsoid by its area (*mean_cancov_ellip*; Fig. 3-3b). We used an analogous method to calculate mean canopy cover along each MFR (*mean_cancov_mfr*).

To test whether birds responded to threshold levels of canopy cover in their movements, we reclassified segments along each MFR as either 'forested' or 'nonforested' depending on whether canopy cover was above or below a given threshold value and then calculated the proportion of 'forested' segments along each MFR (Fig. 3-3c). We did this using a suite of threshold values ranging from 2 to 60 percent canopy cover, which resulted in 15 binary forest cover variables for each MFR (*bin_fcov_mfr_X*) and each ellipsoid (*bin_fcov_ellip_X*). To determine the most relevant threshold for each of our species, we compared the AIC values of univariable models and retained, for subsequent analyses, only those thresholds generating the lowest AIC.

Gap and barrier variables

We developed a number of variables describing the characteristics of gaps along each MFR (Table 3-1). Although most of these variables are self-explanatory, one exception is the sum of distance-weighted gaps (*sum_dist_gap_width*), which accounted for the possibility that the willingness of birds to take risks might decrease with increasing distance from their territories (Gillies 2008). Accordingly, we weighted the width of each gap by the distance, in km, between the far edge of the gap and the capture site. In a final set of variables, we accounted for the barrier effect of linear gaps by applying barrier ratings derived from previous gap-crossing experiments from the same study area (Tremblay & St. Clair 2009), which showed that the likelihood of birds crossing linear features did not vary linearly with gap width, but rather, dropped sharply as gap width exceeded 25-50 m (Appendix 3-2).

Statistical analyses

We used Cox regression performed in STATA® 10 (StataCorp 2007) to identify factors affecting the return time of translocated birds. Cox regression (Cleves *et al.* 2004) is useful for analyzing 'time to event' data (here, return time to territory) and also takes into account whether the event occurs within the observation period (here, return success after 5 days). Candidate models were selected and evaluated using an information-theoretic approach based on Akaike's information criterion (AIC). We also calculated AIC differences (Δ_i) and weights (w_i) to assess support for each model (Burnham & Anderson 2002). To avoid problems of collinearity, we avoided including two variables with a Pearson correlation coefficient > |0.6| in any given model (Appendix 3-3), retaining only the one with the most explanatory power. Finally, we interpreted the 'best-fit' model from each analysis to provide some measure of the relationships between predictor and response variables.

In a first set of analyses, we compared differences in return time among treatments. We built separate species-specific models in addition to a combined model containing terms for species, treatment, and the interaction between treatment and species. In a second analysis, we strove to identify the role of landscape factors in explaining the return time of each of our study species. Given the exploratory nature of many of our variables and to reduce the number of candidate models, we divided our variables into 3 groups (forest cover, gap, and barrier) and retained only the variable from each group that produced the lowest AIC value based on a comparison of models containing a term for distance plus each landscape variable. We then built a series of candidate models representing different combinations of these retained variables. We included a term for distance in all our models to account for differences in mean translocation distances across treatments.

RESULTS

We performed 96 and 92 translocations on black-capped chickadees and yellow warblers, respectively. Of these, 8 chickadees and 4 warblers did not display clear territorial behaviour or were unusually difficult to locate upon their return to their presumed territories and were therefore eliminated from analyses, leaving 88 retained cases for each species. To avoid biasing results, exclusions were performed prior to analyses according to strict criteria that were independent of treatment or response.

Effect of treatment and species on return time and success

In general, chickadees took longer to return to their territories than warblers. By the end of the second visit (3-3.5 hours post-release), almost twice as many warblers (84%) had returned to their territories compared to chickadees (47%) and differences in return rate were evident across most treatment categories (Fig. 3-4a). By the end of the observation period, return rates remained lower for chickadees than for warblers in all but 3 treatment categories (Fig. 3-4b).

In translocations within riparian corridors, chickadees that were moved along continuous forest returned relatively quickly to their territories (median return time = 2.1 h; n = 12). By comparison, chickadees were significantly slower to return to their territories in the presence of bridges but, surprisingly, returned just as fast when crossing the Bow River (Table 3-2). In translocations across the urban matrix, return times were significantly longer in the presence of either a single road or multiple gaps of various types. In contrast, developed areas, when not combined with other features, did not affect the homing time of chickadees relative to continuous forest, regardless of tree cover.

Like chickadees, warblers translocated across continuous forest were quick to return to their territories (median return time < 1.5 h; n = 14) and took significantly longer to do so when translocated across multiple gaps (Table 3-2). In contrast, warbler movements within riparian corridors were not inhibited by bridges but were marginally constrained by the Bow River relative to forest. Whereas chickadee movements were unaffected by urban development, warblers exhibited longer return times in urban treatments and, surprisingly, this effect was stronger for well-treed than for poorly treed areas. Finally, warblers translocated across a single major road returned to their territory just as quickly as individuals translocated in continuous forest.

Our combined model showed that warblers were significantly more likely than chickadees to return to their territories at any given time across all treatments (haz. ratio = 3.33; $P = 0.003$; Appendix 3-4). The same model also revealed a significant species by treatment interaction in which warblers were more likely than chickadees to cross bridges (haz. ratio = 4.012; $P = 0.037$) but less likely to cross the Bow River (haz. ratio = 0.284, $P = 0.041$) and well-treed developed areas (haz. ratio = 0.336; $P = 0.081$).

Effect of landscape variables on the return of birds

In comparing the explanatory power of our binary forest cover variables in univariable models, we found that for chickadees, canopy cover thresholds of 2% and 4% generated the lowest AIC value within MFRs and ellipsoids, respectively (Fig. 3-5). In contrast, much higher threshold levels of 20% and 35% within MFRs and ellipsoids, respectively, offered the best fit for warblers. A second set of model comparisons showed that our best-fit binary forest cover variables generally explained more variation in return time than our variables representing mean canopy cover (Table 3-3). Based on the grouped variable comparisons in Table 3-3, we retained for our candidate models for chickadees terms representing binary forest cover along the MFR using a 2% threshold, total number of gaps, and distance-weighted barriers. For warblers, we retained terms for binary forest cover along the MFR using a 20% threshold, the proportion of gaps, and the sum of barriers.

Our best-fit model for chickadees included terms for distance-weighted barriers, distance, and binary forest cover using a 2% threshold and support for this model was more than twice as high as the next ranked model (Table 3-4). According to this model, the return time of chickadees was negatively affected by distance-weighted barriers and translocation distance whereas binary forest cover had a positive effect on movement (Table 3-5). For warblers, our best-fit model contained terms for distance and the sum width of gaps (Table 3-4). However, support for this model was low and only slightly higher than the other candidate models considered. This model showed that the return time of warblers increased in relation to both translocation distance and the sum of barriers, although the effect of the latter was slightly shy of conventional significance (Table 3-5).

DISCUSSION

Movement behaviour in relation to treatments

Multiple gaps, whether linear or otherwise, inhibited the movements of both our study species even though such features did not necessarily represent impediments to movements when occurring in isolation. Individual roads and rivers, for example, had little or no effect on warbler movements. However, in combination with other gaps return times of warblers were negatively affected. At least one other translocation study has shown that multiple barriers, even fairly narrow ones, can constrain the movements of some birds (Bélisle & St. Clair 2001). These findings underscore the importance of considering the cumulative effects of barriers when assessing functional landscape connectivity.

Other treatment effects observed were species-specific. The movements of chickadees were constrained by roads and bridges, which is similar to what we found using recorded bird calls to lure chickadees across linear gaps (Tremblay & St. Clair 2009). Yellow warbler movements were unaffected by such structures when tested individually. The warblers' greater ability to negotiate gaps is likely due in part to their presumably superior flying ability associated with their long-distance migratory behaviour. We also observed a marked difference in the ability of our study species to move through developed areas. This difference may stem from the propensity of animals to select for their movements habitats that are also suitable for other functions such as feeding or breeding (Chetkiewicz *et al.* 2006). This may help explain why areas of urban development were less permeable to yellow warblers, which are strongly associated with riparian habitats in western North America, compared to the more urban-adapted chickadees.

Effect of landscape variables on movement

Consistent with our initial hypothesis, binary forest cover variables generally explained more variation in return time than those describing mean canopy cover, suggesting forest birds may be more sensitive to the presence of a certain minimum level of canopy cover rather than to average canopy cover values encountered along a travel route. We found that threshold values of 2-4% canopy cover were the most relevant for chickadee movements, implying that even sparsely distributed trees may act as effective stepping stones for this species and perhaps explaining why chickadees had no difficulty travelling through developed areas with low canopy cover. Other studies have demonstrated the effectiveness of stepping stones in facilitating inter-patch movements by birds (Boscolo *et al.* 2008, Gillies & St. Clair 2008, Robertson & Radford 2009), frogs (Angelone & Holderegger 2009), and even insects (Baum *et al.* 2004, Dover & Settele 2009). In contrast to chickadees, warblers seemed most responsive to threshold levels of 20-40% canopy cover, suggesting that they require higher levels of forest cover for their movements. Interestingly, variables describing forest cover conditions along the MFR generally outperformed their ellipsoid-based counterparts, providing evidence that it may be more useful to focus on putative movement paths rather than landscapes or sub-landscapes (e.g. Gillies and St. Clair 2008, Bélisle *et al.* 2001, Gobeil & Villard 2002) when studying animal movements in fragmented landscapes. Taken together, these findings illustrate the importance of quantifying habitat conditions in ways that are reflective of how they are perceived by moving organisms, particularly in heterogeneous landscapes.

'Barrier' variables outperformed 'gap' variables in our best-fit models for chickadees, suggesting that, for this species, the barrier effect of gaps was not linear but increased sharply as a critical width was reached. There is broad support in the literature for threshold distances from the forest edge beyond which songbirds are reluctant to venture (e.g. Desrochers & Hannon 1997; St. Clair *et al.* 1998; Robertson & Radford 2009, Tremblay & St. Clair 2009), most likely because of perceived predation risk (Rodriguez *et al.* 2001). For warblers, barrier variables offered only marginally better fit than gap variables in our models. This weak result may be due to the fact that the permeability experiments from which we derived our barrier ratings did not include warblers, which may have led to poorly calibrated barrier variables for this species.

The willingness of some birds to cross a gap seems to be influenced by its location relative to a bird's territory, as evidenced by the negative effect of the sum of distance-weighted barriers (*sum_dist_barrier)* on chickadee movements. This indicates a more cautious response to gaps with increasing distance from the territory, which is consistent with one other study of avian movement behaviour (Gillies 2008). A distance effect may explain why chickadees translocated across the Bow River returned to their territories just as quickly as those translocated in continuous forest. This was unexpected given previous studies showing a strong barrier effect of rivers when trying to draw chickadees across them (St. Clair 2003; Tremblay & St. Clair 2009). An alternative explanation is that the river might have facilitated navigation by offering a clear direction of travel and an unobstructed view of a bird's territory across open water. In contrast, the Bow River had a marginally negative effect on warbler movements despite its proximity to capture sites, association with favourable habitat, and possible role as a navigational aid.

Finally, an obvious question that arises from our work is whether the barrier effects demonstrated by our homing experiments are applicable to dispersal movements, which are of primary importance to the persistence of populations in fragmented landscapes. The barrier effects observed in our study are probably conservative relative to the corresponding effects on dispersing individuals. Indeed, the movements of dispersing juveniles in search of a new breeding territory are undoubtedly more exploratory and less directional than that of translocated adults seeking to return to an established territory containing most, if not all, of their annual reproductive investment. Although we did not identify any absolute barriers to movement, our results, coupled with that of previous studies of bird (Desrochers & Fortin 2000) and butterfly (Haddad 1999) movements relative to edges, suggest that gaps in forest probably act as deflectors of movement. This may result in an anisotropic flow of dispersing individuals in heavily fragmented landscapes.

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Our results suggest two complementary approaches for increasing landscape permeability for urban birds. To benefit birds like yellow warblers, which are largely restricted to natural habitats in urban settings, conservation efforts should focus on preserving habitat connectivity along riparian corridors and other broad swaths of natural vegetation where movements are most likely to occur. Transportation bridges and other interruptions within riparian corridors caused by urban development should be kept to a minimum to allow for unfettered movement along such corridors. Where bridges are inevitable, their barrier effect can be mitigated by flanking such structures with tall trees to reduce gap width and provide safe passage for birds above moving traffic (see Tremblay & St. Clair 2009 for specifics).

A second approach, which targets urban-adaptable species like chickadees, consists of enhancing the permeability of the urban matrix itself through the incorporation of elements designed to minimize gaps in vegetation. For example, even sparsely distributed trees can facilitate bird movements through heavily developed areas. Particular attention should be paid to major transportation corridors because they create continuous gaps in forest cover that cannot be circumvented by moving birds. The barrier effect of such features can be at least partially mitigated through the placement of roadside trees and the incorporation of treed medians with an aim to reduce gap width (see Tremblay & St. Clair 2009). Similarly, the barrier effect of multiple gaps can potentially be reduced by the provision of treed areas between adjacent gaps, which can act as stepping stones. In all roadside plantings, tall trees should be favoured over shrubby vegetation to minimize the risk of collisions with vehicles. Finally, ‘green bridges' (i.e. structures featuring vegetative cover) may facilitate movement across major transportation corridors.

In summary, our study, which is the first to study the movements of songbirds in the urban context, showed that cities contain significant impediments to the movements of birds although responses to specific landscape elements vary among species due to differences in vagility or adaptability to urban conditions. Although our study focussed on songbirds, it yielded a number of novel insights of broad relevance to the study of animal movements in fragmented landscapes. In particular, it illustrated the importance of considering cumulative effect of multiple barriers, threshold levels in canopy cover and gap width, and distance to territory on movement behaviour. We also described innovative ways of quantifying landscape conditions in heterogeneous landscapes as they might be perceived by moving organisms.

ACKNOWLEDGMENTS

This research was supported by a Discovery Grant from the Natural Science and Engineering Research Council (NSERC) and a Canada Foundation for Innovation New Opportunities Grant to CCSC and NSERC and Alberta Ingenuity postgraduate scholarships to MAT. Further funding for the project was provided by The Calgary Foundation (with contributions from: Chris Dunkley Natural Environment Retention Fund, Community Fund, Calgary Beautification Fund, Harvey Kowall Memorial Fund), Alberta Conservation Association, University of Alberta Bill Shostak Wildlife Award, Alberta Sport, Recreation, Parks and Wildlife Foundation, ECO Canada, Nature Calgary, Mountain Equipment Coop, Lamont Development Inc., and O2 Planning and Design Ltd. In-kind support was provided by the University of Alberta, the City of Calgary, and The Orthoshop, Ltd. We are grateful to M. Coombe, S. Crook, K. Hennig, K. Jonassen, E. Miranda, and D. Goldsmith for their invaluable assistance in the field. We also thank E. Bayne, S. Neilsen and 3 anonymous reviewers for their insightful comments on previous drafts of the manuscript.

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Table 3-1. Definition of landscape variables.

Category	**Variable**	**Description**
Distance	distance	Straight-line distance between capture and release sites (m).
Forest Cover	mean_cancov_ellip	Mean percent canopy cover in ellipsoid[1].
	mean_cancov_mfr	Mean percent canopy cover along MFR[2].
	bin_fcov_ellip_X	Proportion of ellipsoid containing at least x% canopy cover.
	bin_fcov_mfr_X	Proportion of MFR containing at least x% canopy cover.
Gap[3]	sum_gap_width	Sum width of all gaps along MFR (m).
	sum_dist_gap_width	Sum of distance-weighted[4] widths of gaps along MFR (m).
	gap_proportion	Sum length of all gaps / total length of MFR (no units).
	max_gap_width	Width of widest gap along MFR (m).
	gap_no	Number of gaps along the MFR (no units).
Barrier	sum_barrier	Sum of all barrier values[5] along MFR (no units).
	sum_dist_barrier	Sum of all distance-weighted barrier values along MFR (no units).

[1] Area representing a buffer surrounding the translocation axis with a radius equal to 0.25 times the length of the translocation axis,

[2] MFR = Most forested route between the capture and the release point.

[3] Gaps defined as ‘open’ areas containing < 5 percent canopy cover, based on visual assessment of digital orthophoto.

[4] Weights proportional to distance from capture site.

[5] As determined from permeability experiments, reflecting a non-linear relationship between gap width and barrier effect.

Table 3-2. Effect of treatment on return time and success for individual species, as determined from Cox regression (N = 88 for each species).

Variable	**Hazard Ratio**[1]	**95% Confidence Interval**		***P***	**N**
Black-capped chickadees[2]					
Distance (m)	0.999	0.998	0.999	0.001	
Treatment (ref = forest)					12
Multiple gaps - linear	0.168	0.065	0.434	0.000	12
Bridge(s)	0.227	0.085	0.607	0.003	9
Multiple gaps - all types	0.236	0.086	0.650	0.005	7
Single road	0.371	0.147	0.935	0.035	8
Developed low	0.645	0.272	1.532	0.321	12
River	1.295	0.486	3.450	0.605	9
Developed high	0.811	0.351	1.872	0.623	19
Yellow warblers[3]					
Distance (m)	0.999	0.999	1.000	0.025	
Treatment (ref = forest)					14
Multiple gaps - linear	0.294	0.133	0.647	0.002	16
Developed high	0.225	0.081	0.627	0.004	8
Multiple gaps – all types	0.331	0.139	0.785	0.012	10
Developed low	0.522	0.229	1.190	0.122	13
River	0.491	0.196	1.232	0.130	10
Single road	0.745	0.314	1.766	0.504	9
Bridge(s)	0.915	0.377	2.220	0.845	8

[1] Refers to change in odds of return corresponding to a one-unit increase in the independent variable (> 1 indicates positive effect; < 1 negative effect).

[2] LR $X^2 = 40.30$, df = 8, $P < 0.0001$, LL = -277.1

[3] LR $X^2 = 24.14$, df = 8, $P = 0.0022$, LL = -306.8

Table 3-3. Grouped comparisons of preliminary[1] models for selection of candidate variables.

Univariable model	LL	df	AIC	Δ AIC	Weight
Black-capped chickadees					
Forest cover variables:					
dist + bin_fcov_mfr_2*	-289.51	2	583.015	0.000	0.449
dist + bin_fcov_ellip_4	-289.83	2	583.655	0.640	0.326
dist + mean_cancov_ellip	-290.52	2	585.036	2.022	0.164
dist + mean_cancov_mfr	-291.51	2	587.015	4.001	0.061
Gap variables:					
dist + gap_no*	-287.11	2	578.22	0.000	0.882
dist + gap_proportion	-289.69	2	583.38	5.159	0.067
dist + sum_gap_width	-290.34	2	584.68	6.460	0.035
dist + max_gap_width	-291.71	2	587.42	9.198	0.009
dist + sum_gap_width_dist	-291.93	2	587.87	9.645	0.007
Barrier variables:					
dist + sum_barrier_dist*	-284.07	2	572.13	0.000	0.680
dist + sum_barrier	-284.82	2	573.63	1.504	0.320
Yellow warblers					
Forest cover variables:					
dist + bin_fcov_mfr_20*	-314.15	2	632.30	0.000	0.389
dist + mean_cancov_mfr	-314.36	2	632.72	0.416	0.226
dist + bin_fcov_ellip_35	-314.76	2	633.51	1.212	0.217
dist + mean_cancov_ellip	-314.95	2	633.89	1.590	0.168
Gap variables:					
dist + gap_proportion*	-314.15	2	632.30	0.000	0.309
dist + sum_gap_width_dist	-314.36	2	632.72	0.416	0.251
dist + sum_gap_width	-314.76	2	633.51	1.212	0.168
dist + max_gap_width	-314.95	2	633.89	1.590	0.139
dist + gap_no	-314.99	2	633.99	1.689	0.133
Barrier variables:					
dist + sum_barrier*	-313.99	2	631.98	0.000	0.627
dist + sum_barrier_dist	-314.51	2	633.02	1.042	0.373

[1] All models contained a term for distance to control for differences in translocation distance among treatments

* Variables retained for candidate models.

Table 3-4. Comparison of Cox regression models explaining return time and success of black-capped chickadees and yellow warblers (N = 88 for each species).

Model	LL	df	AIC	ΔAIC	Weight
Black-capped chickadees					
dist_+ bin_fcov_mfr_2 + sum_dist_barrier	-282.10	3	570.21	0.000	0.493
dist + sum_barrier_dist	-284.07	2	572.13	1.923	0.189
dist + bin_fcov_mfr_2 + gap_no + sum_dist_barrier	-282.10	4	572.20	1.989	0.182
dist + gap_no + sum_dist_barrier	-283.53	3	573.06	2.851	0.119
dist + gap_no	-287.11	2	578.22	8.016	0.009
dist + bin_fcov_mfr_2 + gap_no	-286.29	3	578.59	8.379	0.007
dist + bin_fcov_mfr_2	-289.51	2	583.01	12.806	0.001
Yellow warblers					
dist + sum_barrier	-313.99	2	631.983	0.000	0.214
dist + gap_proportion	-314.15	2	632.301	0.318	0.183
dist + bin_fcov_mfr_20 + sum_barrier	-313.22	3	632.436	0.453	0.171
dist + bin_fcov_mfr_20	-314.31	2	632.613	0.631	0.156
dist + gap_proportion + sum_barrier	-313.59	3	633.178	1.195	0.118
dist + bin_fcov_mfr_20 + gap_proportion	-313.83	3	633.667	1.684	0.092
dist + gap_proportion + sum_barrier + bin_fcov_mfr_20	-313.17	4	634.347	2.364	0.066

Table 3-5. Variables affecting homing time and success of translocated birds, according to best-fit models derived from Cox regression. See Table 3-1 for variable definitions.

Variable	**Hazard Ratio**[1]	**95% Confidence Interval**		***P***
Black-capped chickadees[2]				
sum_dist_barrier (m)	0.442	0.277	0.705	0.001
distance (m/10)	0.990	0.984	0.996	0.001
fcov_mfr_bin2 (%)	2.204	0.981	4.951	0.056
Yellow warblers[3]				
distance (m/10)	0.992	0.987	0.997	0.003
sum_barrier (no units)	0.830	0.670	1.029	0.089

[1] As described in Table 3-2.

[2] LR $X^2 = 30.27$, df = 3, $P < 0.0001$, LL = -282.1

[3] LR $X^2 = 9.83$, df = 2, $P = 0.007$, LL = -314.0

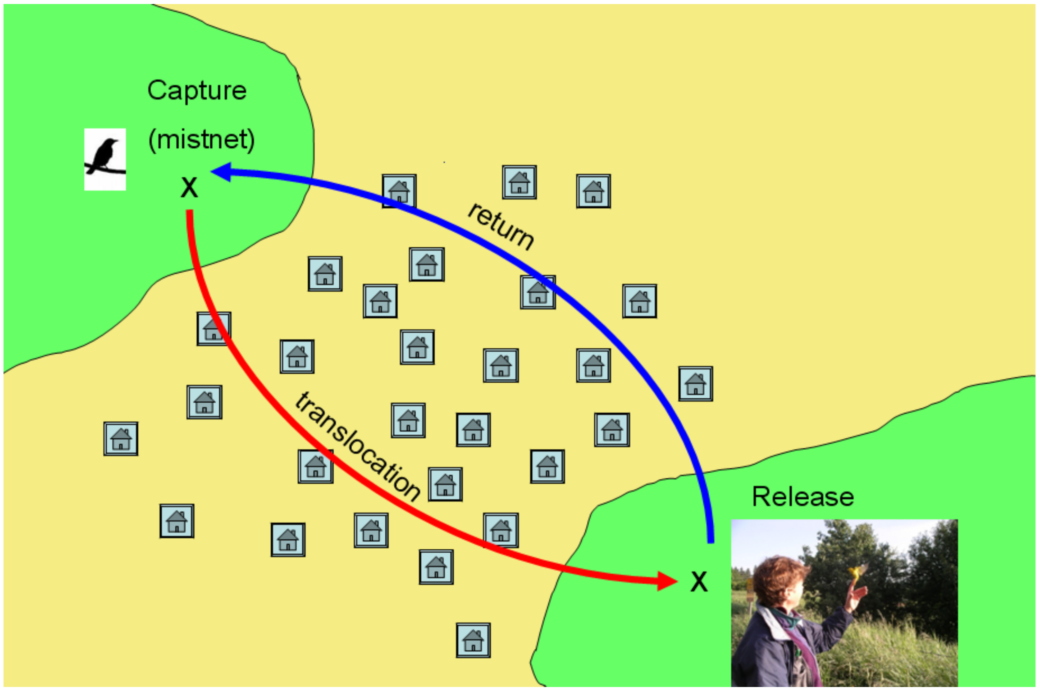


Figure 3-1. Schematic diagram of a translocation trial. Each trial consisted of capturing a bird in a mistnet, moving it across a selected feature of the urban landscape (here, developed area), releasing it, and documenting the time it took to return to its territory.

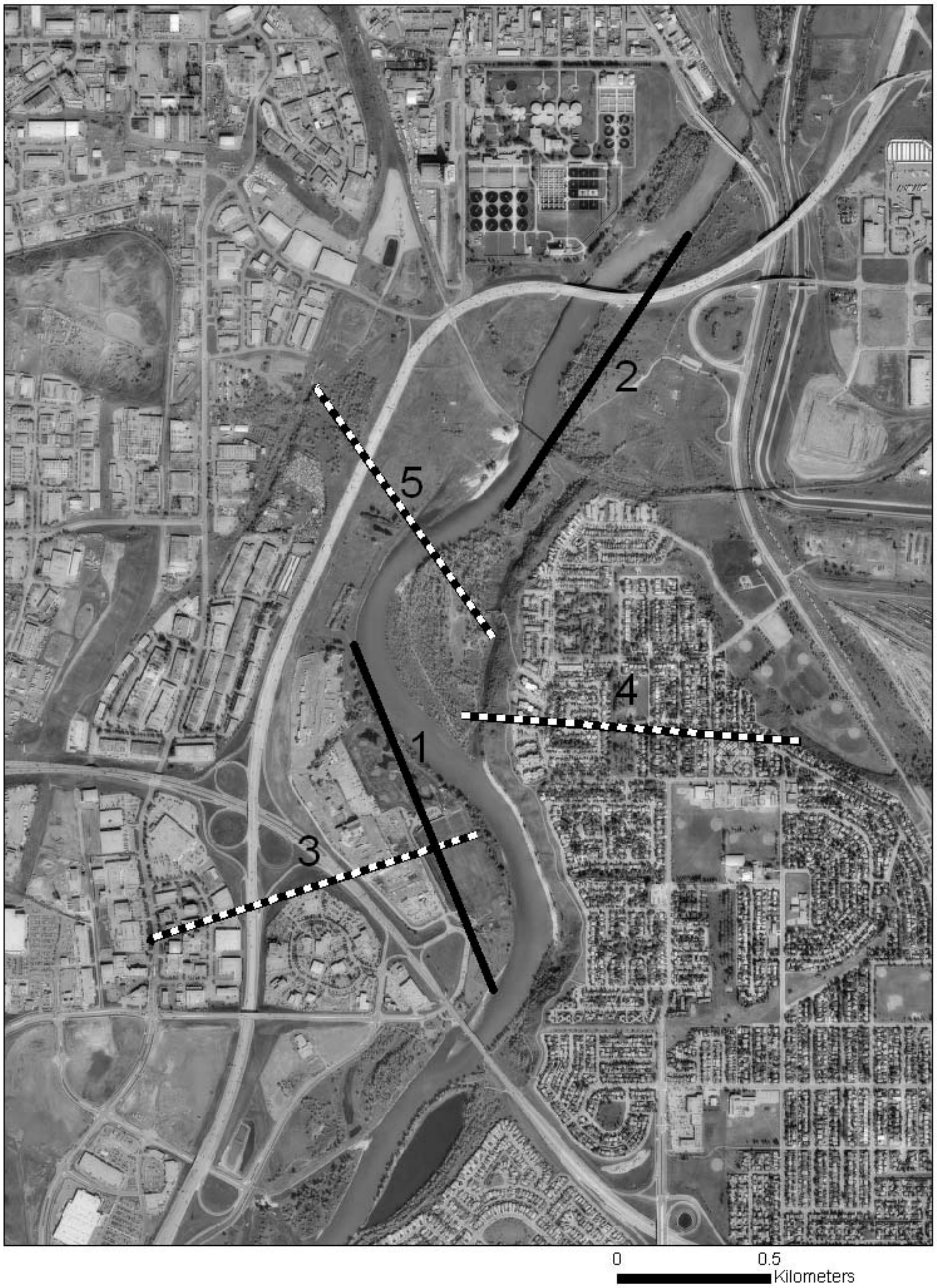
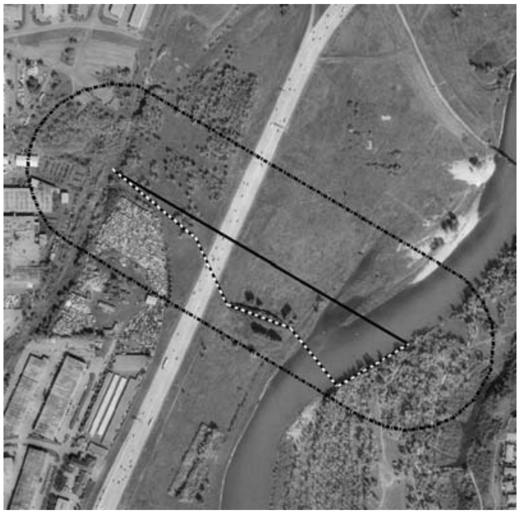
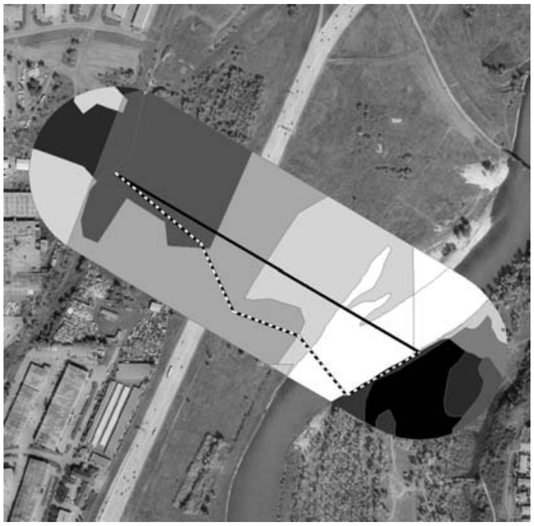


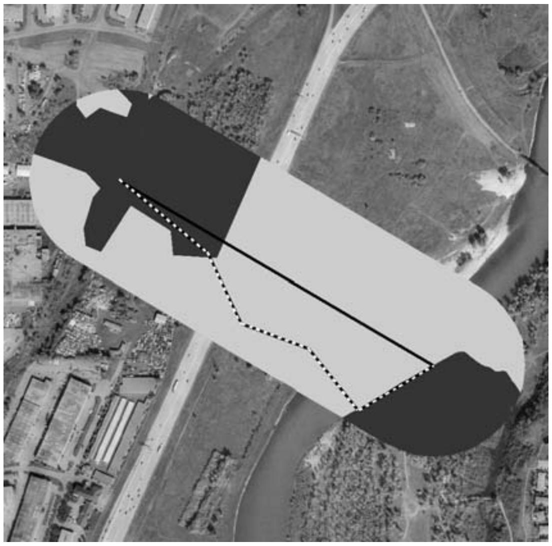
Figure 3-2. Examples of translocation trials conducted within riparian corridors (solid lines) and across the urban matrix (dashed lines). Specific treatments illustrated here include: 1) continuous forest, 2) transportation bridge, 3) multiple gaps – all types, 4) residential, and 5) multiple gaps – linear only (here, road + river).



a)



b)



c)

Figure 3-3. Determination of forest cover variables associated with a translocation across a road and river. a) Capture and release points were connected by the translocation axis (solid line) and the most forested route (MFR; dashed line). An ellipsoid was then created by drawing a buffer around the translocation axis (dotted line). b) A unique canopy cover value was assigned to each land cover polygon within the ellipsoid. These values were then used to determine 'mean' canopy cover, either within the ellipsoid or along the MFR. c) Land cover polygons were then reclassed into 'forested' (dark grey) or 'non-forested' (light grey) based on whether canopy cover level was above or below a given threshold value and these were used to determine 'binary' forest cover, either within the ellipsoid or along the MFR.

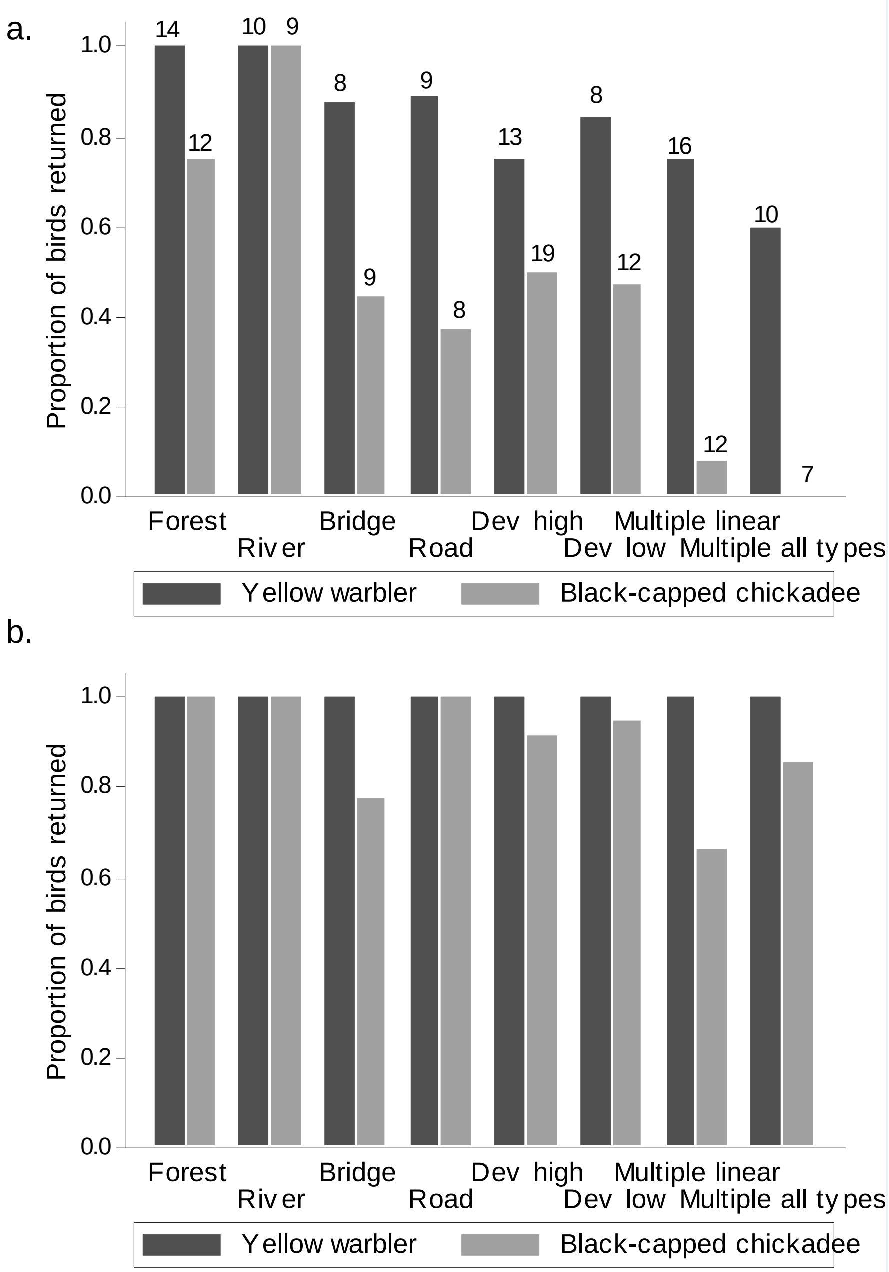


Figure 3-4. Proportion of birds returned to territory after the second (a; 3-3.5 hours post-release) and eighth (b; ~125 hours post release) visit, by treatment and species. Numbers above bars represent sample sizes and are the same for both graphs.

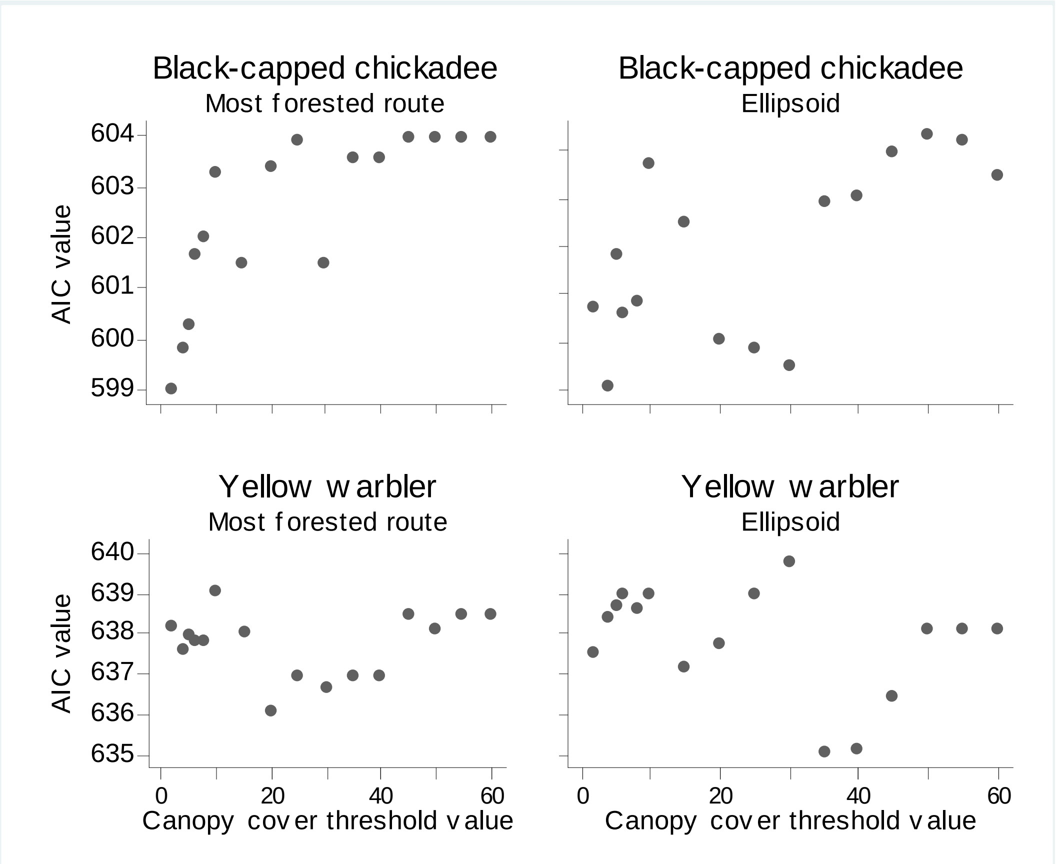


Figure 3-5. Comparison of the fit of univariable, Cox regression models describing the effect of different threshold values in canopy cover along most forested routes and within ellipsoids on the return time of translocated birds.

Appendix 3-1. Mean (and standard deviation) of landscape variables across treatment categories used in translocation experiments Calgary, Alberta, Canada. Numbers following treatment represent sample sizes for black-capped chickadees and yellow warblers combined. See Table 3-1 for variable definitions.

	Along riparian corridor			**Within urban matrix**				
Variable/Treatment	Forest(26)	River (19)	Bridge[1] (17)	Single road (17)	Multiple - linear[2] (28)	Multiple - all types[3] (17)	Developed high[4] (20)	Developed low[5] (32)
Distance (m)	1107 (307)	606 (432)	1067 (466)	826 (363)	1001(304)	1318 (348)	1356 (241)	1443 (234)
Forest cover (%)								
mean_cancov_mfr	46.7 (11.3)	27.2 (11.3)	31.3 (9.1)	17.0 (15.2)	21.8 (8.2)	9.2 (4.5)	28.9 (12.5)	9.3 (4.3)
bin_fcov_mfr_2	98.3 (3.4)	69.6 (20.0)	87.7 (7.4)	64.5 (25.8)	63.5 (13.3)	40.2 (19.9)	98.9 (2.0)	58.9 (37.8)
bin_fcov_mfr_20	92.9 (11.0)	52.3 (27.8)	71.7 (24.0)	28.7 (33.2)	41.3 (19.1)	14.0 (8.1)	58.8 (39.8)	9.0 (9.6)
mean_cancov_ellip	21.0 (8.8)	19.2 (5.7)	13.1 (3.1)	13.7 (8.0)	12.6 (4.0)	8.5 (2.9)	20.4 (6.9)	7.7 (3.0)
bin_fcov_ellip_4	68.5 (14.6)	60.9 (8.9)	52.8 (11.6)	61.6 (20.6)	48.3 (8.9)	28.5 (15.4)	86.3 (12.2)	42.7 (26.9)
bin_fcov_ellip_35	25.3 (21.2)	21.0 (15.0)	10.7 (9.0)	8.9 (15.0)	11.4 (7.4)	7.4 (4.3)	3.8 (4.4)	3.2 (4.3)
Gap (m)								
sum_gap_width (m)	23 (46)	125 (33)	130 (73)	303 (258)	383 (127)	959 (452)	17 (32)	714 (618)
sum_dist_gap_width	15 (34)	28 (15)	94 (102)	118 (141)	240 (123)	1052 (734)	10 (23)	1083 (1044)
gap_no	0.37 (0.56)	1.42 (0.51)	2.12 (1.32)	2.00 (1.06)	2.79 (0.99)	2.53 (1.01)	0.35 (0.59)	1.13 (0.91)
gap_proportion	0.02 (0.03)	0.30 (0.20)	0.12 (0.07)	0.37 (0.27)	0.37 (0.14)	0.65 (0.21)	0.01 (0.02)	0.44 (0.37)
max_gap_width	19 (37)	106 (25)	81 (43)	184 (109)	185 (68)	585 (338)	16 (27)	667 (627)
Barrier(no units)								
sum_barrier	0.04 (0.17)	1.20 (0.39)	1.25 (0.87)	0.95 (0.45)	2.36 (0.73)	2.25 (0.81)	0.19 (0.33)	0.22 (0.36)
sum_dist_barrier	0.04 (0.19)	0.25 (0.13)	0.87 (0.76)	0.41 (0.28)	1.44 (0.76)	1.27 (0.68)	0.10 (0.23)	0.17 (0.36)

[1] One or more bridges crossing over a riparian corridor.

[2] Two or more major roads or a major road + Bow River.

[3] Combinations of linear and non-linear gaps such as major road + industrial area or major road + river + industrial area.

[4] Developed areas with high tree cover (typically residential).

[5] Developed areas with low cover (industrial, commercial, downtown core, or poorly treed residential).

Appendix 3-2. Barrier rating associated with each linear barrier type (calculated as 1- probability of crossing from Fig. 2-3).

Width (m)	**Road**	**Bridge**	**Railway**	**River**
0-25	0.02	0.05	0.02	0.5
26-50	0.40	0.40	0.02	0.8
51-75	0.90	0.90	0.02	0.90
>75	0.95	0.95	0.02	0.95

Appendix 3-3. Correlations among independent variables (numbers represent Pearson coefficients; coefficients > |0.6| are in bold font)

a) Black-capped chickadee translocations (n = 88)

	distance	mean_cancov_mfr	bin_fcov_mfr_2	mean_cancov_ellip	bin_fcov_ellip4	sum_gap_width
distance	1					
mean_cancov_mfr	-0.313	**1**				
bin_fcov_mfr_2	-0.1037	0.5660	1			
mean_cancov_ellip	-0.3489	**0.6919**	0.4116	1		
bin_fcov_ellip4	-0.1881	0.4818	**0.6329**	**0.6569**	1	
sum_gap_width	0.4640	-0.5584	**-0.8622**	-0.4853	**-0.7005**	1
sum_dist_gap_width	0.5430	-0.4611	**-0.7430**	-0.3726	**-0.6037**	**0.9452**
gap_no	-0.0288	-0.2868	-0.3431	-0.3876	-0.4503	0.2817
gap_proportion	0.1136	-0.5845	**-0.9662**	-0.4436	**-0.6839**	**0.8915**
max_gapwidth	0.4759	-0.5151	**-0.8079**	-0.4253	**-0.6526**	**0.9628**
sum_barrier	-0.1002	-0.2349	-0.2190	-0.2607	-0.2776	0.1054
sum_dist_barrier	0.1444	-0.1923	-0.1413	-0.2784	-0.2335	0.1451

	sum_dist_gap_width	gap_no	gap_proportion	max_gap_width	sum_barrier	sum_dist_barrier
sum_dist_gap_width	1					
gap_no	0.1047	1				
gap_proportion	**0.7648**	0.3593	1			
max_gap_width	**0.9749**	0.1274	**0.8394**	1		
sum_barrier	-0.0596	**0.8273**	0.2161	-0.0631	1	
sum_dist_barrier	0.0443	**0.7265**	0.1299	-0.0033	**0.8776**	1

b) Yellow warbler translocations (n = 88)

	distance	mean_cancov_mfr	bin_fcov_mfr_20	mean_cancov_ellip	bin_fcov_ellip35	sum_gap_width
distance	**1**					
mean_cancov_mfr	-0.2148	1				
bin_fcov_mfr_20	-0.1845	**0.8776**	1			
mean_cancov_ellip	-0.4069	**0.6277**	**0.6157**	1		
bin_fcov_ellip_35	-0.4903	0.5881	0.4991	**0.7377**	1	
sum_gap_width	0.3709	**-0.6021**	-0.5431	-0.5330	**-0.3309**	1
sum_dist_gap_width	0.4835	-0.5145	-0.4747	-0.4695	**-0.3186**	**0.9407**
gap_no	-0.0334	-0.3432	-0.2912	-0.2728	-0.1407	0.4371
gap_proportion	-0.0675	**-0.6174**	-0.5516	-0.4020	-0.1839	**0.8558**
max_gap_width	0.3918	-0.5407	-0.4973	-0.4733	-0.3125	**0.9285**
sum_barrier	-0.1318	-0.2993	-0.2241	-0.1687	-0.0496	0.3471
sum_dist_barrier	0.1538	-0.2599	-0.1796	-0.2569	-0.1454	0.3297

	sum_dist_gap_width	gap_no	gap_proportion	max_gap_width	sum_barrier	sum_dist_barrier
sum_dist_gap_width	1					
gap_no	0.2152	1				
gap_proportion	**0.7221**	0.4988	1			
max_gap_width	**0.9737**	0.1908	**0.7679**	1		
sum_barrier	0.1262	**0.7671**	0.4655	0.1009	1	
sum_dist_barrier	0.1523	**0.7254**	0.3039	0.0876	**0.8622**	1

Appendix 3-4. Cox regression model showing the effect of treatment, species, and their interaction on the return times of black-capped chickadees and yellow warblers in translocation experiments conducted in Calgary, Alberta.

Variable	**Hazard ratio**	**95% confidence**	**interval**	***P***
Distance	0.990	0.985	0.995	0.000
Treatment (ref = forest)				
Bridge(s)	0.249	0.095	0.653	0.005
Developed high	0.601	0.260	1.388	0.233
Developed low	0.707	0.326	1.538	0.382
Multiple gaps - all types	0.247	0.091	0.670	0.006
Multiple gaps - linear	0.175	0.069	0.443	0.000
River	1.489	0.600	3.696	0.391
Single freeway	0.407	0.164	1.011	0.053
Species (ref = chickadees)	3.331	1.505	7.370	0.003
Treatment*species (ref as above)				
Bridge(s)	4.016	1.091	14.790	0.037
Developed high	0.336	0.099	1.142	0.081
Developed low	0.735	0.253	2.136	0.572
Multiple gaps - all types	1.304	0.359	4.735	0.687
Multiple gaps - linear	1.470	0.450	4.806	0.523
River	0.284	0.085	0.952	0.041
Single freeway	1.756	0.513	6.010	0.370

^{2}LR X^2 = 97.00, df = 16, -681.972, LL = -282.1

CHAPTER 4

EFFECTS OF LOCAL AND LANDSCAPE LEVEL FACTORS ON THE ABUNDANCE AND DISTRIBUTION OF BIRDS IN AN URBAN LANDSCAPE

ABSTRACT

Urbanization is viewed by many ecologists as one of the most serious threats to global biodiversity because urban development tends to overlap with some of the most biologically diverse areas on the planet, causing the loss of many native species while encouraging the spread of abundant, non-native species. We conducted point surveys at 183 sites spanning a broad gradient of urbanization from intensively developed sites to near-natural forest stands in the city of Calgary, Alberta, Canada. Using multiple linear and logistic regressions, we examined the role of land cover type, local vegetation characteristics, and landscape composition and configuration on the composition of avian communities and the occurrence of 25 focal species. We parameterized cost-distance models using the results of previous permeability experiments conducted in the same study area. We then determined the 'functional distance' between our survey sites and natural areas and water courses. Of the 55 species detected during our surveys, 39 (71%) were urban-sensitive species that were primarily associated with natural areas and among these, 21 (38%) were found exclusively in these areas. In developed areas, the density of trees and shrubs generally had a positive effect on the abundance and diversity of birds. The probability of occurrence of 15 of 17 urban-adaptable or urban-avoiding focal species was negatively correlated with isolation (i.e. distance or cost distance) from the nearest forested natural area or major water feature. For 11 of the 15 species, cost distance explained more variation in the probability of occurrence than straight-line distance, suggesting that rivers, roads, and urban development affected the

settlement patterns of birds, presumably by constraining dispersal or access to important resources. Taken together, our results suggest that protecting avian biodiversity in urban landscapes begins with the preservation and restoration of a network of high quality habitats that are functionally connected. In many urban areas, such habitats are provided by riparian corridors, which merit particular attention for retention and restoration. This study also demonstrates novel methodologies for characterizing the composition and configuration of heterogeneous landscapes and provides a unique examination of the link between fine-scale movement behaviour and species distributions within this context.

INTRODUCTION

Worldwide, there is a trend toward increasing urbanization fuelled by a growing human population and a shift in settlement from rural regions to urban centres (Shochat *et al.* 2006). Although the concentration of human populations in urban centres may be beneficial to biodiversity because it minimizes the human footprint on the global landscape, it is also problematic because urbanization causes the permanent loss and extreme fragmentation of habitats. These changes are especially damaging because cities typically occur in low-lying coastal plains and river valleys, which contain some of the most biologically diverse areas on the planet. This leads to the loss of many indigenous species that are unable to adapt to such radical degradation and fragmentation of their habitat. Consequently, diverse assemblages of native species are replaced with abundant, wide-ranging species, which thrive in human-dominated landscapes; a process known as biotic homogenization (McKinney 2006, Olden *et al.* 2006, Clergeau *et al.* 2006). For these reasons, urbanization is viewed by some ecologists as one of the most serious threats to global biodiversity (Marzluff *et al.* 2001). Birds are a group of particular conservation concern in urban areas because of their sensitivity to ecological perturbations, their ability to provide vital ecosystem services like pollination and seed dispersal, and their aesthetic value to humans (Savard *et al.* 2000, Stutchbury 2007, Whelan *et al.* 2008).

Several authors have studied bird distributions in urban landscapes using one or combinations of three broad approaches. A first approach has drawn on island biogeography (MacArthur and Wilson 1967) and metapopulation theory

(Hanski 1998) to explain species richness, immigration and extinction rates in remnant fragments of habitat surrounded by urban development (e.g. Soule *et al.* 1988, Fernandez-Juricic 2000, Bolger *et al.* 1991). This approach relies on a binary depiction of the landscape in which patches of suitable habitat are surrounded by a hostile matrix. In such studies, straight-line distance is often used to depict the degree of isolation among habitat patches and the matrix is assumed to be homogeneous; simplifications that are frequently unrealistic (Ricketts 2001, Bender and Fahrig 2005).

A second approach to studying bird assemblages explicitly recognizes the mosaic nature of urban landscapes by comparing patterns of avian distributions along a gradient of urbanization (e.g. Blair 1996, 2004, Crooks *et al.* 2004). Such studies have shown that avian richness and abundance tend to peak at intermediate levels of development but have offered few insights into possible determinants of this pattern. A third approach compares the relative importance of local versus landscape-level factors to explain species distributions in habitat fragments (e.g. Tilghman 1997, Mortberg 2001), within urban parks (Jokimaki 1999) or within the urban matrix (e.g. Melles *et al.* 2003, Tablado-Almela 2006). Such studies have typically shown that both local and landscape factors play a role in explaining avian assemblages. Another common finding is that species tend to vary considerably in their responses to these factors, which has inhibited the articulation of general principles and clear management guidelines that might benefit multiple species.

A core failing of all three approaches to understanding avian responses to urbanization is that they do not measure the permeability of urban features to the movement of birds. Nor do they accommodate the gradient of matrix types that influence occupancy in habitat patches. Fortunately, these limitations can be overcome. Accurate measures of isolation should assess functional landscape connectivity as it is perceived by an organism (Taylor *et al.* 1993) by reflecting travel costs associated with energy expenditure or predation risk (Bélisle and Desrochers 2002). This approach can be achieved with least-cost path modelling, which calculates the functional (or cost) distance between two points based on the 'friction' experienced by the study organism (Adriaensen *et al.* 2003). Although realistic cost-distance modeling has often been hindered by a lack of empirical data (Chetkiewicz *et al.* 2006, Beier *et al.* 2008), this problem is less apparent for forest-dwelling birds. For these species, several field-based experimental studies using audio playbacks have identified the relative and species-specific permeability of different landscape features such as clearings (Sieving *et al.* 1996, Rail *et al.* 1997, Desrochers and Hannon 1997, St. Clair *et al.* 1998, St. Clair. 2003, Bélisle and Desrochers 2002), rivers, and roads (St. Clair 2003, Tremblay and St. Clair 2009). Others have used both mensurative (e.g. Norton *et al.* 2000, Ricketts 2001) and manipulative (e.g. Castellon and Sieving 2006, Bender and Fahrig 2005) experiments to show how the matrix type can influence the presence of organisms in adjacent habitat patches and thus, provide more information about functional connectivity.

The purpose of our study was to examine, at multiple spatial scales, the patterns and determinants of bird distributions across a gradient of urbanization with an aim to identify strategies for preserving or enhancing avian biodiversity in urban landscapes. We were particularly interested in the role of functional landscape connectivity in explaining bird distributions in mosaic landscapes. Using results from previous permeability experiments conducted in the same study area (see chapters 2 and 3), we developed cost distance variables to describe the isolation of surveyed sites from natural features (e.g. forested natural areas or water bodies) believed to act as sources of key resources or dispersing birds. We also compared the performance of these cost distances to more conventional isolation variables that assume a homogeneous matrix. We asked four main questions: (1) How do different land cover types affect the composition of avian communities? (2) What factors affect the observed distribution patterns and at what scale do they operate? (3) Does functional landscape connectivity play a role in the distribution of species? (4) What management or planning strategies can be employed to retain avian biodiversity in cities?

METHODS

Study area

Our study was conducted in Calgary, Alberta, Canada (51° 05’N, 114° 05’ W), a city of approximately 1.2 million residents located in western Canada and straddling the ecotone between the Rocky Mountain foothills to the west and the Canadian prairies to the east. The city is bisected by naturally forested riparian corridors associated with the Bow River and its main tributary, the Elbow River. These riverine valleys are dominated by native balsam poplar (*Populus balsamifera*) forests although white spruce (*Picea glauca*) stands are also present in cooler, shaded sites. Aspen (*Populus tremuloides*) stands are also common in the western portion of the study area where they occur in ravines and scattered upland locations. These relatively natural areas are encased within an urban matrix characterized by a mosaic of residential, commercial, and industrial areas interspersed with a variety of green spaces and fragmented by a busy network of transportation corridors. The urban matrix supports an urban forest dominated by native and non-native varieties of spruce (*Picea* spp.), poplar (*Populus* spp.), birch (*Betula* spp.), and fruit (e.g. *Malus* spp., *Prunus* spp.) trees. The amount of tree cover varies considerably among land cover types with the highest median canopy cover values found in natural stands of balsam poplar (61%), aspen (63%) and spruce (82%; M. Tremblay, *unpublished data*). Within the matrix, canopy cover ranges from 2% in commercial and industrial areas to 35% in well-treed residential areas and manicured parks (*Ibid*.). The study area features a gentle topography with elevations ranging from 1060 m in river valleys to 1240 m on the surrounding hilltops (Foley 2006). Calgary's climate is considered semi-arid with annual precipitation averaging 445 mm per year (Environment Canada 2010).

Bird surveys

In 2005, we surveyed 29 sites within balsam poplar stands that were located within major riparian corridors using a stationary point count method with a 50-m radius (Bibby *et al.* 2000). Each site was surveyed three times between late May and early July. In this initial year of surveys, we varied survey times (10, 15, and 20 min.) to identify a species accumulation curve and determine the optimal survey time for subsequent years.

In 2006 and 2007 we broadened the scope of the survey program to encompass a range of land cover types including residential, commercial, industrial areas, and managed parks. To the original 29 sites, we added 88 and 66 new sites in 2006 and 2007, respectively, for a total of 183 sites surveyed over one or more years (Fig. 4-1). Sites were chosen from a street map to provide variation in the amount of local tree cover, distance to nearest forested natural areas and water, and the presence of barriers between survey sites and such features. To standardize noise and human activity levels, all sites were located on relatively quiet streets and at least 100 m from the nearest major road or athletic field. Each survey lasted 15 minutes and consisted of two 5-minute segments of passive observation separated by a 5-minute segment of observation while broadcasting a taped recording of a black-capped chickadee (all scientific names are provided in Appendix 4-1) mobbing call. We used these recordings to increase bird detections (after Gunn *et al.* 2000) and broadcasted calls from a portable CD player using a standardized volume setting audible at 50 m. Each site was surveyed twice, once between late May and mid-June and once between mid-June and early July. This timing was selected to coincide with the breeding period of the greatest number of species (most migrants arrive by the third week of May).

In all years, trained observers were randomly assigned to sites and never surveyed the same site more than once. We used mean abundance rather than maximum abundance because repeated observations of a species at a site provide some indication of reproductive activity and are less prone to random errors related to the presence of non-breeding flocks or floaters or single-visit observer errors in number estimation or species recognition (Betts *et al.* 2005). Surveys were conducted between sunrise and 10h00, when birds are most vocal. For 2005 sites, we retained for analysis only 2 of 3 surveys to ensure equal sampling effort across all sites (i.e. 30 min. total survey time).

From these data, we derived 5 response variables: (1) presence/absence of each species that was detected at least once during one of the surveys, (2) mean abundance for each species (the total number of detections/number of surveys), (3) total bird abundance (the sum of all mean abundances), (4) total species richness (the total number of species detected at each site), and (5) Shannon-Weaver heterogeneity (hereafter, heterogeneity).

We surveyed 6 sites in both 2005 and 2006 and 6 sites in both 2006 and 2007 to detect interannual variations. Using paired t-tests we found no between-year differences in species richness. However, total bird abundances were significantly higher in 2005 than 2006 (mean abundance = 20.0 and 15.8, respectively; $P = 0.043$). Thus, for sites surveyed in both 2005 and 2006, we retained only the 2006 surveys for analysis. For sites surveyed only in 2005, we downwardly corrected abundance values by 20.83%. There was no significant difference in abundance between 2006 and 2007. Therefore, for sites surveyed in

2006 and 2007, we randomly selected surveys from one year or the other for retention in our analyses.

Vegetation characterization

To assess habitat conditions at each survey site, we conducted detailed vegetation surveys using a modified version of the BBIRD vegetation sampling protocol designed for assessing bird habitat in forest and shrub communities (Martin *et al.* 1997). We used a count-plot method in which the density of trees and shrubs was determined within systematically located plots, which varied in size according to tree or shrub density (Mueller-Dombois and Ellenberg 1974). This method was chosen over plotless sampling methods (e.g. nearest individual or point-centred quarter methods) because it was flexible enough to be carried out in both highly developed and natural sites, which we expected would differ considerably in both structure and composition.

For each site located in either a natural area or managed park, we sampled 3 square plots located 25 m and in directions of 60, 180 and 300 degrees from the centre point of the survey site. The tree plots measured either 100 m^2 or 400 m^2, depending on tree density with the choice of plot size aiming to ensure that a minimum of approximately 20 trees were surveyed. In each plot we measured the average canopy height using a handheld clinometer and calculating the mean of 3 measurements. We determined percent canopy cover with the aid of a densiometer, taking 16 readings at systematic locations and calculating the mean. Within each plot, we counted all trees according to species and size class (diameter at breast height): (1) 5-8 cm, (2) 8-23 cm, (3) 23-38 cm, and (4) > 38 cm. Snags were classified as either small (< 12 cm) or large (> 12 cm) and only snags > 1.4 m tall were counted. Shrubs and saplings were inventoried in plots laid out similarly to the tree plots but with smaller dimensions. Shrub plots measured either 25 m^2 or 100 m^2, the smaller plot size used for denser understoreys. We counted the number of stems > 1 m tall of each species for each of two size classes (< 2.5 cm or > 2.5 cm diameter at 10 cm above the ground). We considered shrubs to include all stems < 1.4 m high and all multi-stemmed plants, regardless of size. Saplings with a DBH < 5 cm were included in the shrub inventory.

In developed sites, we modified our plot design slightly to accommodate our restricted access to fenced private yards. We surveyed 3 rectangular-shaped plots 25 m in length and whose width corresponded to the distance between the sidewalk and the facade of buildings (typically 9-10 m, for an average plot size of 200-250 m^2). The 3 plots were systematically located on alternating sides of the street within 50 m of the survey site centre point. Trees and shrubs were inventoried in the same manner as in the case of the more natural sites with a few modifications to ensure that densiometer readings were not taken near buildings, which could obscure vision of the canopy layer.

From these field-based vegetation measurements, we generated a suite of local vegetation variables, which we divided into five groups describing the structure, composition, and structural heterogeneity of the canopy and shrub layers (Table 4-1).

Landscape characterization

We used ArcGIS version 9.2 (ESRI 2007) to generate landscape-level variables representing forest cover within 250, 500, and 1000 m of each site, corresponding to areas of 19.6, 78.5 and 314.2 ha, respectively (Table 4-2, Fig. 4-2a). These scales reflect those previously found to influence habitat use by forest passerines (Pearson 1993, Betts *et al.* 2006). Mean canopy cover was determined by visually assigning a canopy cover value to individual land cover polygons within a given radius and then calculating the mean of these values, weighted by the area of each polygon (see Fig. 4-2b). Canopy cover values were estimated from on-the-ground vegetation surveys conducted at 187 sites across the study area and assigned to polygons using a high-resolution (0.5 m) orthorectified aerial photograph (see Chapter 3 for details). We also calculated canopy cover corrected for the presence of movement barriers like freeways, major roads, and rivers, identified from previous permeability experiments (hereafter accessible canopy cover). For this variable, all polygons beyond the specified barriers were given a canopy cover value of 0 and the mean canopy cover recalculated as above (Fig. 4-2c).

We measured isolation as both straight-line and cost distance from natural features, namely the nearest forested natural area > 15 ha, the Bow River, and the nearest major water body. We hypothesized that relatively large natural areas might act as source populations for dispersing birds. The Bow River represents the main riparian corridor in our study area along which most native forest stands (many of which are < 15 ha) are located. Major water bodies included the Bow River, its main tributaries, and a large (388 ha) artificial lake.

Using ArcGIS, we calculated the cost distance separating each survey point to the natural features described above (Fig. 4-3). We used two separate cost surfaces derived from the results of previous permeability experiments showing that yellow warbler movements were primarily constrained by urban development whereas those of black-capped chickadees were mostly impeded by transportation corridors (hereafter warbler and chickadee cost surfaces; Table 4-3).

We also included straight-line distance to the city centre as a candidate variable to test for possible responses to building density or the presence of species typically found in city cores (e.g. house sparrows and rock pigeons). We did not use common patch-based metrics to describe our sites because most of our surveys were conducted within the urban matrix, which did not contain clearly defined patches.

Statistical analyses

In a first suite of analyses, we investigated the effect of local vegetation characteristics on bird distributions. We began by describing general patterns of bird distributions relative to land cover type. Second, we identified local determinants of total species richness, heterogeneity, and abundance. Third, we performed similar analyses using two different classification schemes: one based on a species' association with urban development using a nomenclature modified from Blair (1996; urban exploiters - primarily associated with built environments;

urban adapters - detected with roughly equal frequency in both built and more natural environments; and urban avoiders - almost exclusively associated with near-natural sites) and a second classification based on origin (i.e. native vs. non-native). In a fourth analysis, we identified correlates of the abundance and diversity of native birds specifically within developed sites (including residential, commercial, and industrial sites; N = 131). Fifth, we used logistic regression to identify factors explaining the presence or absence of individual focal species that were detected in at least 5% of the sites. Because we were interested in the relative importance of vegetation composition and structure on avian distributions, for each of our response variables, we built and compared a compositional and a structural vegetation model.

In a second suite of analyses, we broadened the spatial scope of investigation to include the effects of landscape variables on bird distributions. To do this, we repeated the last four analyses described above using both local- and landscape-scale predictors as candidate variables in our models. We compared the relative importance of straight-line vs. cost distance from natural features by letting these variables compete for inclusion in our models. To give each type of isolation variable an equal chance of being included, we considered only one cost distance variable for each type of natural feature (i.e. forested area, Bow River, or major water body) per model even though we had developed two cost surfaces. Hence, we used the chickadee cost surface for models involving urban exploiters, adapters, and non-native birds and the warbler cost surface for avoider and native bird models. We included local variables in these models because we wanted to assess the effects of landscape variables while controlling for differences in local vegetation conditions. Finally, we determined the relative importance of local vs. landscape-level variables in explaining avian distributions by comparing, for each of our response variables, the fit of models containing only local variables to ones containing both local and landscape variables.

All our analyses were performed using Stata 10 (StataCorp 2007). We used linear regression for our community-level and group-level analyses, with the exception of that of the avoider group, which displayed a heavily right-skewed distribution due to low numbers. To accommodate this, we reclassified the abundance of this group into three levels (low, moderate, and high) and analyzed this new categorical variable using generalized ordered outcome regression with a probit link (or probit ordered regression; Hardin and Hilbe 2007). Where necessary, variables were square-root or log transformed to meet the assumption of normality.

We used an information theoretic approach to model selection based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Burnham and Anderson suggested that only ecologically plausible models should be considered in the model selection process. However, in our study, building *a priori* models was difficult due to the large number of variables and limited available information on the factors affecting the distribution of our study species in an urban environment. Thus, we used a stepwise model building process designed to eliminate variables with weak explanatory power quickly and allow the strongest candidate variables to compete with one another for inclusion in subsequent models. In a first step, we grouped our predictor variables into categories representing broad local or landscape characteristics (as per Tables 4-1 and 4-2, respectively) and compared the AIC values of univariable models within each of these groups (Fig. 4-4). In a second step, we compared the best-fitting univariable model from the top models identified in step 1 to a suite of expanded models containing an additional term from the subset of best-fit variables from each category and identified a new best-fit model from this second suite of models. This process was repeated until the fit of the model could no longer be improved by the addition of new variables. We chose this method over more traditional stepwise model-building procedures because it avoids the use of an arbitrary inclusion threshold based on *P*-values. Another advantage is that the outcome is not influenced by the order in which variables are considered.

To avoid problems of collinearity, we avoided including two variables with a Pearson correlation coefficient > |0.6| in any given model, retaining only the one with the most explanatory power, as measured with AIC (coefficients provided in Appendix 4-2). We measured the fit of our linear models using adjusted R^2 and that of our logistic models using the Area under the Receiver Operator Characteristic Curve (AUC). The AUC describes the relationship between sensitivity (probability of correctly classifying positive cases) and 1-specificity (probability of correctly classifying negative cases) for an entire range of possible cutpoints (Hosmer and Lemeshow 2000). The AUC returns an index between 0.5 and 1.0, with 0.5, 0.7, 0.8 representing no, acceptable, and excellent discrimination, respectively (*Ibid.*).

RESULTS

Composition of the avian community

A total of 55 species were detected during the bird surveys that were retained for analyses. Of these, 9 species were classified as urban exploiters, 7 as adapters, and 39 as avoiders (Table 4-4). All species were native to the study area except for three European introductions (rock pigeon, house sparrow, and European starling) and one highly anthropophilic Northern American species first found in the study area less than 10 years ago (house finch). Of the 55 species, most rely primarily on forested or shrubby habitats for nesting and foraging with the exception of the rock pigeon, house sparrow, house finch, and barn swallow (associated with human-made structures), the red-winged black-bird (associated with marshes), and a few species that typically nest in trees but may forage in open areas (e.g. common grackle, American robin, black-billed magpie, American crow, common raven, northern flicker, chipping sparrow). Remarkably, over half of all species (28) were strongly associated with natural areas (i.e. over 70% of detections) and 21 species were found exclusively in natural areas, even though these areas represented only 22% of our survey sites. Eleven species were found exclusively in balsam poplar stands: grey catbird, belted kingfisher, hairy woodpecker, eastern kingbird, northern rough-winged swallow, white-breasted nuthatch, savannah sparrow, Lincoln's sparrow, white-crowned sparrow, Baltimore oriole, and the common nighthawk. One species, the rose-breasted grosbeak, was found only in an aspen stand whereas three species - the golden-crowned kinglet, western tanager, and dark-eyed junco - were restricted to spruce stands.

Diets varied considerably both within and among groups although exploiters tended to be omnivorous or have seed-dominated diets whereas adapters and avoiders were largely insectivorous with seeds, invertebrates, and fruit often complementing the diet (Appendix 4-1). Nest locations and types also varied within groups with the exception of the adapter group in which 4 of 5 species were cavity nesters. Non-native species were concentrated in the exploiter group (rock pigeons, house finches, and house sparrows) with the exception of the European starling, which was classified as an urban adapter.

Avian distributions relative to land cover type

Total species richness was highest in balsam poplar stands, which contained an average of 11.4 species per site. This was over 50% higher than aspen, spruce, managed parks, well- and moderately treed residential sites, which contained, on average, between 6.9 and 7.5 species (Fig. 4-5a). Poorly treed residential sites contained significantly fewer species (mean = 5.2) and, predictably, species richness was lowest in commercial and industrial sites, which averaged 4.0 species per site. Species heterogeneity followed much the same pattern as species richness relative to land cover type (Fig. 4-5b). In contrast, mean abundance showed a bi-modal distribution, peaking in both balsam poplar (14.6 birds/site) and well- and moderately treed residential sites (14.8 and 13.1 birds/site, respectively; Fig. 4-6d). Aspen, spruce, manicured park, and poorly treed residential sites contained intermediate levels of birds, ranging from 8.4 to 9.9 birds/site. Expectedly, industrial and commercial sites contained the fewest number of birds (6.6 birds/site).

When separated by groups, the abundance of urban exploiters was highest in developed areas, peaking in well-treed residential sites (mean = 8.2 birds/site) and decreasing steadily with decreasing tree cover to a low of 4.4 birds/site in commercial and industrial areas (Fig. 4-6a). At 3.2 birds/site, managed parks contained slightly fewer exploiters than commercial and industrial sites although this difference was not statistically significant. Exploiters were significantly scarcer in natural areas than in all other sites with mean numbers < 2.1 birds/site. The abundance of urban adapters was relatively constant across natural areas, managed parks, and well- and moderately treed residential sites, varying between 5.1 and 6.1 birds/site (Fig. 4-6b). In contrast, their numbers were significantly lower in poorly treed residential sites (3.3 birds/site) and lower still in commercial or industrial sites (1.8 birds/site). Urban avoiders were most abundant in balsam poplar stands (6.6 birds/site) with aspen and spruce sites containing only 41% as many birds from this group (~2.7 birds/site; Fig. 4-6c). All other land cover types contained only marginal numbers of avoiders with mean abundances generally < 1 bird/site. The pattern of distribution of native and non-native species closely resembled that of the adapter and exploiter groups, respectively (Fig. 4-6e and 4-6f).

Our detailed vegetation surveys revealed sharp contrasts in the density of trees and shrubs between sites located in natural areas compared to those within the urban matrix. Natural areas contained on average 5 to 10 times more trees and shrubs than the other land cover types in our study area (Fig. 4-7). As well, natural forest stands and managed parks tended to contain a higher proportion of native trees and shrubs than developed sites.

Influence of local vegetation factors on bird distributions

At the community level, our structural models explained more variation in species diversity (richness and heterogeneity) and bird abundance than our compositional models (Table 4-5). According to these structural models, richness and heterogeneity were positively influenced by percent canopy cover within 50 m. In contrast, total bird abundance showed a positive relationship with the density of shrubs and mean canopy height.

At the group level, structural models outperformed compositional models in explaining the abundance of native, non-native, and urban adaptable birds (Table 4-5). The number of native and urban adaptable birds was positively correlated to canopy cover within 50 m whereas non-native birds showed a negative association with the density of small trees. The abundance of both urban exploiters and avoiders was best explained by compositional factors, though these two groups showed contrasting relationships to native vegetation. Whereas exploiters were negatively associated with the density of native trees, avoiders were positively associated with native shrubs.

Structural models explained more variation in both the richness and abundance of native birds in developed sites than compositional models.

Richness was positively associated with the density of shrubs and large trees as well as with structural heterogeneity whereas abundance showed a positive association with canopy cover within 50 m. Surprisingly, our compositional models showed that both the richness and abundance of native birds in developed sites were positively associated with the density of non-native shrubs and trees.

We found considerable consistency in the types of variables that were included in the models within each of our groups based on urban sensitivity. Within the exploiter group, compositional models explained more variation in the occurrence of 7 out of 8 species than structural models (Table 4-6). The fit of the best-fit models within this group ranged from poor (AUC = 0.60 for rock pigeons) to excellent (AUC = 0.85 for house sparrows) with a mean AUC value of 0.68. This group displayed mixed responses to the presence of shrubs with 3 species (American crow, black-billed magpie, and chipping sparrow) showing a negative association with native shrubs while blue jays and house finches were positively correlated to small and large shrubs, respectively. Responses to tree variables were generally negative with the except for American crows, chipping sparrows, and common grackles, which were positively associated with non-native trees, tree species heterogeneity, and fruit trees respectively.

Of the 5 species within our adapter group, two species (American robin and black-capped chickadee) responded more strongly to structural variables whereas for European starlings, house wrens, and red-breasted nuthatches our compositional models offered the best fit (Table 4-6). AUC values for best-fit models within this group were slightly higher than for exploiters with values ranging from 0.67 (European starling) to 0.86 (black-capped chickadee) with a mean value of 0.74. All species within this group showed a positive association with shrub variables. Responses to tree variables were also generally positive except for European starlings, which showed a positive association with large trees but a negative association with tree species heterogeneity.

Within the avoider group, the occurrence of 7 of 12 species was best explained by compositional models (Table 4-6). Model fit was higher than the two previous groups with AUC values ranging from 0.77 for brown-headed blackbirds and 0.95 for grey catbirds (mean AUC = 0.87). Like adapters, all avoider species showed a positive association with shrub variables. Likewise, our avoider models contained a majority of positive associations with tree variables although 3 species (northern flicker, song sparrow, and tree swallow) were negatively associated with tree species heterogeneity and red-winged blackbirds showed a negative association with coniferous trees.

Multi-scale determinants of bird distributions

According to our models combining local and landscape-level variables, both our measures of community-level diversity (richness and heterogeneity) showed a significant positive relationship to percent canopy cover within 50 m and a negative relationship to distance to the Bow River (Table 4-7). Total bird abundance was positively and significantly correlated to shrub density and mean canopy height and, like our measures of diversity, negatively correlated to distance to the Bow River. Somewhat surprisingly, total abundance was also negatively correlated to the density of deciduous trees.

The abundance of native birds increased with the density of fruit-bearing shrubs, mean canopy cover within 250 m, and distance to downtown while decreasing with increasing distance from the Bow River and the nearest major water body. Our models for the abundance of non-native species and exploiters were quite similar, which was not surprising given the considerable overlap between these two groups. Both groups were negatively associated with the density of native or small trees and isolation (i.e. straight-line or cost distance) from the Bow River yet tended to increased with increasing density of small shrubs, structural heterogeneity and distance from a forested natural area. In addition, non-native species showed a marginal negative association with mean canopy cover within 500 m. The abundance of urban adapters was positively influenced by mean canopy cover within 250 m and, to a lesser degree, by distance to the downtown core. In contrast, this group showed a decreasing relationship with increasing distance from a forested natural area. The abundance of urban avoiders was strongly and positively correlated to total shrub density. Avoiders also showed a strong negative association with cost distance to a major water body.

Both the richness and abundance of native birds in developed sites tended to increase with the density of non-native shrubs, structural heterogeneity, canopy cover within 250 m corrected for accessibility, and distance to downtown while showing a negative association with distance to a forested natural area. Richness was also positively influenced by the density of large trees.

As previously, we discuss the results of our species-specific models within the context of our three groups reflecting sensitivity to urban development. Shrub variables were generally absent from our exploiter models with only one model (American crow) containing a term for native shrubs and this relationship was strongly negative (Table 4-8). Local tree characteristics were important for 4 of 8 species within this group but the direction of these relationships was mixed (2 positive, 3 negative). Five models in this group included variables representing landscape-level canopy cover and all of these associations, except for one (house sparrow), were positive. In one model (house finch), accessible canopy cover explained more variation in occurrence than mean canopy, lowering the AIC value by 6.44. With the exception of the chipping sparrow and blue jay models, all models within this group contained a term representing isolation from natural features (forested natural area or water) and the majority of these relationships were positive (Fig. 4-8). Of the 7 isolation variables included in this group of models, cost distance explained more variation than straight-line distance in 3 cases (Fig. 4-8), lowering the AIC value from between 0.68 and 1.07 (Table 4-8). Finally, 3 exploiter species showed a significant relationship to distance from downtown. This relationship was negative in two cases (black-billed magpie and house sparrow) and positive in the other (blue jay).

Two of 5 models within the adapter group (European starling and house wren) contained shrub variables and both these relationships were positive (Table

4-8). Local tree variables were included in the European starling and red-breasted nuthatch models. The former was positively associated with maximum canopy height but negatively associated with tree species heterogeneity whereas the latter was showed a marginally positive relationship with coniferous trees. At the landscape level, all adapter species except for the house wren showed a positive association with mean canopy cover within either 250 or 500 m. Moreover, all models within the adapter group contained a term representing isolation from natural features. Four out of 6 these relationships were negative and in the same proportion of cases, cost distance explained more variation than straight-line distance (Fig. 4-8), lowering the AIC value by 0.47 to 3.83 (Table 4-8).

In the avoider group, 4 of 12 models included local shrub variables and all of these relationships were positive (Table 4-8). Only 2 models in this group contained local tree variables. Northern flickers showed a positive association with canopy cover within 50 m and tree swallows were negatively correlated with tree species heterogeneity. Landscape-level canopy cover was also poorly represented in this group of models; it was included in only 3 instances. Ruby-crowned kinglets were positively associated with accessible canopy cover within 500 m whereas brown-headed cowbirds and tree swallows showed a negative association with canopy cover within 250 m and accessible canopy cover within 1000 m, respectively. Isolation from natural features was represented in 10 models within this group and all of these relationships were negative. In 9 of 14 relationships with isolation from natural features, cost distance explained more variation in occurrence probability than straight-line distance (Fig. 4-8). The inclusion of cost distance variables resulted in a substantial improvement in model fit (ΔAIC > 2) for 3 species (downy woodpecker, least flycatcher, and yellow warbler) while for the other 4 species (northern flicker, song sparrow, tree swallow, and warbling vireo) the AIC value was lowered by less than 2.

Interestingly, our models containing both landscape and local variables outperformed our local-only models for virtually all our community-, group- and individual-level response variables (Tables 4-9 and 4-10). One exception was the occurrence of cedar waxwings, which was influenced solely by the local density of small shrubs (Table 4-8). The inclusion of landscape variables generally resulted in a substantial lowering of AIC values ranging from 8.17 to 33.81 (mean = 21.11) for our group-level models and 0 to 43.31 (mean = 13.08) for our species-specific models.

DISCUSSION

Our bird surveys carried out over 183 sites clearly showed that the composition of avian communities and the occurrence of individual focal species varied dramatically across the urban landscapes as a function of land cover type, local vegetation characteristics, landscape-level forest cover and isolation from various features.

Influence of land cover and local vegetation characteristics on bird distributions

A remarkable 71% of species found in our study area were associated primarily with natural areas (i.e. urban avoiders) while 38% of species were detected exclusively in these sites. The role of natural areas as biodiversity hotspots in urban landscapes has been observed in other study areas as well. For example, natural forest fragments in Ohio and California contained many woodland species that tended to drop out of the system as land use became more urban (Blair 1996, 2004). Similarly, species richness in Vancouver, Canada was highest in the most natural sites and decreased monotonically with increasing urbanization Melles *et al.* (2003). In our study area, riparian balsam poplar stands supported particularly diverse avian communities, containing on average over 50% more species than spruce or aspen stands. Balsam poplar stands also contained 11 species that were unique to this forest type. The importance of riparian ecosystems to birds for foraging, breeding, movement, and as migration stopovers has been well documented in the literature, particularly in arid or semi-arid climates and in landscapes that are heavily impacted by agriculture (Knopf and Samson 1994, Skagen *et al.* 1998, Rottenborn 1999, Akresh *et al.* 2009). Although spruce and aspen stands supported less abundant and diverse avian communities than their balsam poplar counterparts, they were nonetheless the unique contributors of at least 4 species (golden-crowned kinglet, yellow-rumped warbler, dark-eyed junco, rose-breasted grosbeak), suggesting they too played an important, albeit lesser, role in maintaining regional avian diversity.

The relative importance of natural areas to the native bird community can best be explained by their radically higher tree and shrub densities compared to managed parks and developed sites. Studies in Ohio and California also found that natural preserves contained many more trees and shrubs than open spaces, golf courses or developed areas (Blair 1996, 2004). Similarly, the density of shrubs was an important determinant avian diversity in urban woodlands in Massachussetts (Tilghman 1987). In our study, the high density of trees and shrubs in natural areas likely benefited native bird communities by harbouring more insects (the main food source of avoiders), providing security cover from predators (Jokimaki and Huhta 2000, Doherty and Grubb 2000), and offering a variety of nesting materials and substrates. Riparian balsam poplar stands likely contained particularly high amounts of insects due to the proximity to water, possibly explaining why they supported more abundant and diverse bird communities.

In residential areas, bird abundance, species richness, and species heterogeneity were lower than in balsam poplar stands though roughly equivalent to that of aspen and spruce stands. Moreover, these values tended to increase with increasing canopy cover or tree density. Similarly, the abundance and diversity of birds in the nearby city of Edmonton, Alberta tended to increase with increasing tree cover in residential neighbourhoods (Edgar and Kershaw 1994). Interestingly, residential areas in our study were always strongly dominated by exploiters and adapters (53-60% and 38-42%, respectively) while avoiders were largely absent (4-7%) and this composition remained remarkably constant regardless of tree cover. The abundance of exploiters can best be explained by the availability of anthropogenic nesting sites (e.g. nest boxes, eaves) and food sources (e.g. garbage, feeders), which are readily utilized by this group (Erhlich *et al.* 1988). Other studies have found that even modest levels of development in urban and exurban areas caused an increase in the incidence of habitat generalists but a decrease in the incidence of specialists (Fraterrigo and Wiens 2005, Blair 1996).

Like residential areas, managed parks contained a similar number and diversity of birds as spruce and aspen stands. The composition of the avian community, however, was unique in that, unlike natural areas, it contained almost no urban avoiders and unlike residential areas, contained very few exploiters. A paucity of avoiders in managed parks was also documented in Ohio and California where golf courses, though rich in species, supported only 50% of the woodland species that presumably comprised the native bird community prior to their construction (Blair 1996, 2004). Similarly, although species richness did not differ between managed and unmanaged parks in a small city in Finland, differences in community composition were apparent with some species present more often in unmanaged parks (Jokimaki 1999). The most plausible explanation for the relative paucity of avoiders in managed parks is the relative scarcity of trees and shrubs (and associated nesting sites and food sources) compared to natural areas. The nesting success of birds in managed parks, particularly those nesting close the ground, could also be negatively affected by disturbance caused by humans and their pets (Jokimaki *et al.* 2005). The low numbers of exploiters was likely due to the relative absence of buildings. The sharp contrast in avian composition between natural areas and managed parks provides evidence that the conservation value of urban parks can vary radically depending on their management regime.

Not surprisingly, commercial and industrial sites were the most depauperate in our study area. Commercial areas do not offer many opportunities for incorporating native stands of vegetation that are likely to be used by urban-avoiding birds, presumably because of their high human densities and intensive use of space. In addition, the availability of human refuse at these sites is attractive to scavengers and nest predators (e.g. gulls, corvids) which, coupled with a lack of security cover, creates unfavourable breeding conditions for native birds (Jokimaki *et al.* 2005). Industrial areas, although equally devoid of birds, showed more promise for restoration efforts due to a less intensive land use, which allowed for the persistence of small pockets of native vegetation. For example, red-winged blackbirds and yellow-headed blackbirds were observed in a small wetland in the midst of an industrial park. Although industrial areas will probably never serve as important refugia for native birds, the provision of roadside trees (Fernandez-Juricic 1999) and scattered pockets of native vegetation, acting as stepping stones, can facilitate bird movements through these areas and this may be especially important where they intersect important bird habitats (see Chapter 3).

Influence of landscape-level canopy cover

Several authors have recognized that birds respond to environmental factors operating at multiple scales (e.g. Pearson 1993, Hinsley *et al.* 1995, Grand *et al.* 2004) and our study provides additional support for this idea. We found that in addition to local factors, landscape composition and configuration were important determinants of avian distributions in our study, as demonstrated by the fact that our multi-scale factors generally offered much greater explanatory power than our local models.

Landscape-level canopy cover was included in many of our models but the spatial scale of this variable varied among groups and species. At the group level, canopy cover within 250 m had a positive effect on the abundance of native and urban adaptable birds as well as the richness and abundance of native birds in developed sites. In contrast, non-native species were negatively associated with canopy cover at the 500-m scale. At the species level, birds responded to canopy cover at a variety of scales and most of these relationships were positive. The importance of landscape-level forest cover to the distribution of birds has been documented in both urban (e.g. Mortberg 2001, Melles *et al.* 2003) and more natural settings (e.g. Pearson 1993, Trzcinski *et al.* 1999, Villard *et al.* 1999, Lee *et al.* 2002).

The relationships among bird distributions, habitat variables, and landscape characteristics can be described as ecological neighbourhoods (Addicott *et al.* 1987), which relate a particular ecological process (e.g. foraging, dispersal) to the temporal and spatial scales appropriate to the process (Turner *et* *al.* 2001). For example, the inclusion of large-scale canopy cover in two of our corvid models (American crow and blue jay) can be explained by the tendency of these species to forage over large areas (Cornell and AOU 2010). Conversely, landscape-scale canopy cover did not affect the occurrence of highly territorial species like least flycatchers and yellow warblers, which typically occupy very small territories (< 0.5 ha; Cornell and AOU 2010). There were, however, a number of exceptions to this general relationship. For example, the chipping sparrow, red-breasted nuthatch and ruby-crowned kinglet (all small birds with relatively small territories, generally < 5 ha; Cornell and AOU 2010) responded to landscape canopy cover within 500 or 1000 m. For these species and perhaps others, it is possible that social factors such as conspecific attraction (Stamps 1988) may have influenced distributional patterns. Conspecifics may attract dispersing individuals as cues of suitable habitat or as potential contributors to subsequent territory defense, predator detection, and mating opportunities (Muller *et al.* 1997). In a study of boreal forest songbirds in Quebec, over half of the species studied were spatially aggregated relative to their conspecifics (Bourque and Desrochers 2006). The authors suggested that conspecific aggregation increases the area sensitivity of birds because it requires that forest patches be large enough to accommodate several territories; a phenomenon that may also apply to some birds in our study.

Overall, accessible canopy cover (i.e., canopy cover corrected for the presence of barriers to movement) played only a modest role in explaining avian distributions in our study; it was included in only 2 of 5 group-levels models and

3 of 12 species-specific models containing a term for landscape-scale canopy cover. House finches and ruby-crowned kinglets were both positively associated with this variable. Given the relatively small territory size of these species (< 5 ha; Cornell and AOU 2010), the presence of barriers likely may have disrupted dispersal patterns rather than daily foraging movements. In contrast, tree swallows showed a negative association with accessible canopy cover. Given this species' reliance on open areas for foraging (Cornell and AOU 2010), a negative association with landscape-level tree cover is not surprising. More puzzling, however, is why accessible canopy cover had more explanatory power than mean canopy cover. This may be due to a statistical artifact since accounting for accessibility generally leads to lower canopy cover values and this may have resulted in a stronger negative relationship and thus, better model fit, compared to mean canopy cover.

We know of only one other study that has examined the role of habitat accessibility in explaining species occurrences in fragmented landscapes. Eigenbrod *et al.* (2008) found that accessible habitat within 1000 m was a much better predictor of amphibian species richness in ponds than total habitat within the same radius. In contrast, our results relative to accessible canopy cover were more equivocal. The apparent discrepancy between these findings may be explained by the much greater vagility of birds (and presumably lower sensitivity to barriers) compared to that of amphibians.

Isolation from natural features

Terms for isolation from natural features (water, Bow River, or natural area) were included in all our community- and group-level models and 21 out of 25 of our species-specific models, suggesting that landscape configuration strongly influenced avian distribution patterns in our study area. Moreover, for urban avoiders and adapters, cost distance explained more variation in the probability of occurrence almost twice as often as did straight-line distance, accounting for 13 out of 20 species-isolation relationships. This suggests that the presence of barriers may have affected not only the movements of individual birds but their settlement patterns as well, presumably by constraining dispersal. However, the improvement in model fit caused by the inclusion of cost distance instead of straight-line distance was often modest, lowering the AIC value by > 2 in only 4 of 13 cases. This is most likely attributable to the high degree of correlation between our cost distance and straight-line distance variables (Pearson correlations > 0.95; Appendix 4-2), which left little room for substantial gains in model fit. In our study area, the high degree of correlation between cost and straight-line distance variables may have been caused by the parallel alignment of natural areas (many of which are located along the Bow River) and movement barriers like the Bow River itself and the Deerfoot Trail, the expressway most often included in our translocation treatments. Accounting for functional connectivity might lead to larger gains in model fit in more complex landscapes featuring a lower degree of correlation between cost and straight-line distances.

The idea that functional connectivity should affect the distribution of organisms in heterogeneous landscapes has long been recognized in theory (e.g. Taylor *et al.* 1993) and predicted by simulation-based studies (e.g. With and Crist 1995, Schumaker 1996, With *et al.* 1999, Bender *et al.* 2003, Tischendorf *et al.* 2003). Our results provide novel empirical evidence of a possible link between the behavioural process of movement at the scale of individual birds and population-level patterns of species distributions within a highly heterogeneous and fragmented landscape. We know of only two other studies where functional connectivity was assessed empirically and used to explain or predict the distribution of birds. In one study, researchers used playback experiments to assess the gap-crossing abilities of two Atlantic rainforest birds (Awade and Metzger 2008) and then used this information to develop a measure of functional landscape connectivity based on graph theory (Urban and Keitt 2001). They found that models that included gap-crossing capacity better explained the abundance of their study species compared to structural models based only on patch area and straight-line distances although, surprisingly, the relationships between functional connectivity and species occurrence were positive. Another study combined step selection functions with cost distance modelling to assess functional landscape connectivity for dispersing juvenile robins (*Petroica longipes*) fitted with radio-transmitters (Richard and Armstrong 2010). This study showed that dispersing robins preferred moving through native forest, followed by plantations, shrublands, and pasture, in decreasing order of preference. Recent studies in genetics are providing additional, albeit indirect, evidence that barriers to movement can disrupt the flow of individuals (and therefore genes), leading to the genetic isolation populations of grizzly bears (Proctor *et al.* 2005) and birds (Lindsay *et al.* 2008, Ortega *et al.* 2008). More specific to the urban landscape, a recent study showed that genetic diversity was lower in an urban population of tree sparrows than in a suburban one in China (Zhang 2009). The authors of this study concluded that the urban environment was limiting dispersal and gene flow among urban tree sparrows compared to their suburban counterparts.

Interestingly, our models showed that the occurrence of avoiders and adapters tended to be negatively correlated to isolation (straight-line or cost distance) from natural features whereas the occurrence of exploiters often increased with increasing isolation from such features when other local and landscape variables were held constant. We propose two possible mechanisms to explain the generally negative relationship between adapters and avoiders and isolation from natural features. A first explanation is that riparian and other forested areas contain resources, like nest sites or food items, which these birds require for their survival. Under this hypothesis, individuals would settle close enough to such areas so as to be able to access the resources contained within them on a daily basis. This is indeed what we found for some urban avoiders, such as least flycatchers or song sparrows, which were never found more than 160 m from a major water body. However, this explanation does not work well for native urban-adapted species such as black-capped chickadees or house wrens, which showed a significant negative correlation with isolation from the nearest forested natural area >15 ha or water, respectively, but whose mean distance to such areas was 1554 and 718 m, respectively. These distances far exceed expected daily travel distances of birds whose territories generally do not extend beyond a 125-m radius (i.e. territory size < 5 ha; Cornell and AOU 2010). However, such distances are within the realm of typical dispersal distances for such birds, suggesting the existence of a possible source-sink dynamic (Pulliam 1988) in which natural areas and riparian corridors may support source populations for dispersing birds, with dispersal success decreasing as a function of isolation from such sources. Indeed, the detection of urban-adaptable birds within the matrix during point counts is not necessarily a good indication of reproductive success (Betts *et al.* 2005). A source-sink dynamic has important implications for the conservation of birds in urban landscapes as it suggests that urban natural areas may play a critical role in supporting not only populations of urban avoiders within them but also populations of native urban adapters within the matrix. A better understanding of recruitment processes in urban areas represents a worthy direction for future research.

The oft-positive association between exploiters and isolation from natural features is equally intriguing. For example, sites where house sparrows and house finches were present were significantly farther from water (mean = 1628 and 2042 m, respectively) than sites where these species were absent (mean = 390 m and 1030, respectively; t-test $P < 0.001$ in both cases). American crows showed a similar pattern relative to natural areas (2624 vs 1591 m for sites with and without crows, respectively; t-test $P < 0.001$). A possible explanation for this is that proximity to developed areas, buildings, and garbage may have increased with increasing distance from natural features. This seems unlikely, however, because transitions between natural and developed areas in the urban landscape tend to be very abrupt, leading to the close juxtaposition between developed and natural areas. An alternative explanation is the possibility of spatial partitioning between exploiters and adapters within the urban matrix whereby exploiters may be occupying areas that are less desirable for adapters. Further evidence of spatial partitioning is provided by differences in distributional patterns among bird groups relative to the city centre. Whereas at the group level, native birds, urban adapters, and native birds within developed sites all increased with increasing distance to city centre, urban exploiters and non-native birds showed no such relationship.

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

Our research showed that protecting avian biodiversity in urban landscapes begins with the preservation and restoration of a network of natural areas that are, ideally, functionally connected. Natural forests contained a greater diversity of species and many species that were almost completely absent from the urban matrix. Thus, natural areas play an essential role in maintaining avian biodiversity in urban landscapes, one that cannot be filled by managed parks or residential areas, even when these have high values of canopy cover. Because of their disproportionately large contribution to the regional diversity pool, riparian forest stands represent biodiversity hotspots deserving of the highest level of protection, particularly in arid or semi-arid climates. Although they may contain fewer species, other natural vegetation communities may also make unique contributions to regional diversity and therefore may constitute additional conservation targets. Because urban development adjacent to natural forest fragments can affect bird communities within them (Rottenborn 1999, Friesen *et al.* 1995), natural areas should be buffered from built areas. Our results suggest that natural areas are important not only for harbouring urban-avoiding birds but also for sustaining urban-adaptable species within the urban matrix. The importance of proximity to natural areas for urban adaptable species suggests a possible reliance on these areas for resources or as a source of dispersers.

Managed parks can be made more attractive to native birds through the provision of vegetation resembling more closely that of natural areas (i.e. higher densities of native trees and shrubs and less mowed grass). The relative absence of exploiters, which may inhibit the reproductive success of urban sensitive species through either competition for resources or nest predation, may make managed parks better targets than developed areas for increasing the numbers of urban avoiders through vegetation management. Our models showed that increasing trees and shrubs in residential areas also leads to greater bird abundance and diversity. However, residential areas contained no species that were unique to this land cover type, suggesting that while planting trees may be important for supporting the presence of native birds within the urban matrix, this management action will do little to enhance regional avian diversity. Finally, our results showed that isolation from natural areas and water negatively affected many species, particularly avoiders and adapters. Thus, reducing the number of barriers to movement, especially near natural areas and water course, should be a priority. The permeability of roads and bridges, for example, can be effectively increased through the strategic management of adjacent vegetation (see Tremblay and St. Clair 2009 for details).

In closing, it is clear from our study that both local and landscape level factors affect the distribution of birds in urban landscapes. In particular, our results underscore the importance of considering the location of habitat relative to possible barriers to movement. Although species respond to urban development in unique ways, we found that these responses could be classified into three broad categories (i.e. exploiters, adapters, and avoiders), which provided a useful framework for describing the effects of development on birds, one that is also easily graspable by urban managers and planners and other non-scientific groups involved in urban planning. Our research also showed that the effects of urbanization on birds cannot be adequately described using only broad measures like total abundance or richness but rather, requires careful consideration of the composition of avian communities as well.

ACKNOWLEDGMENTS

This research was supported by a Discovery Grant from the Natural Science and Engineering Research Council (NSERC) and a Canada Foundation for Innovation New Opportunities Grant to CCSC and NSERC and Alberta Ingenuity postgraduate scholarships to MAT. Further funding for the project was provided by The Calgary Foundation (with contributions from: Chris Dunkley Natural Environment Retention Fund, Community Fund, Calgary Beautification Fund, Harvey Kowall Memorial Fund), Alberta Conservation Association, University of Alberta Bill Shostak Wildlife Award, Alberta Sport, Recreation, Parks and Wildlife Foundation, ECO Canada, Nature Calgary, Mountain Equipment Coop, Lamont Development Inc., and O2 Planning and Design Ltd. In-kind support was provided by the University of Alberta, the City of Calgary, and The Orthoshop, Ltd. We are especially grateful to volunteers from Nature Calgary who conducted the bird surveys: Brenda Baker, John Cartwright, Phil Cram, Bernard Goulet, Thérèse Goulet, Carole Hachey, Aileen Pelzer, Nimali Sereviratne, Tony Timmons, Rob Worona, Arthur Wieckowski, and Gus Yaki.

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Table 4-1. Definition of local vegetation variables used as candidate predictors in analyses.

Category	Variable	Description
Structural variables		
Shrub structure	shrub_small	Density of small shrubs - < 2.5 cm measured 10 cm above ground (stems/100 m^2)
	shrub_large	Density of large shrubs - > 2.5 cm measured 10 cm above ground (stems/100 m^2)
	shrub_total	Total density of shrubs (stems/100 m^2)
Tree structure	mean_canopy_hgt	Mean height of forest canopy (m)
	max_canopy_hgt	Maximum height of forest canopy (m)
	cancov_50	Mean forest cover within plots (%)
	tree_small	Density of trees < 23 cm dbh[a] (stems/100 m^2)
	tree_large	Density of trees > 23 cm dbh (stems/100 m^2)
	tree_total	Total density of trees – all sizes (stems/100 m^2)
Combined structure	veg_struct_hetero	Shannon-Weaver index of heterogeneity of shrub and tree class sizes
Compositional variables		
Shrub composition	shrub_native	Density of native shrubs (stems/100 m^2)
	shrub_nonnative	Density of nonnative shrubs (stems/100 m^2)
	shrub_conifer	Density of coniferous shrubs (stems/100 m^2)
	shrub_decid	Density of deciduous shrubs – non fruit-bearing (stems/100 m^2)
	shrub_fruit	Density of deciduous shrubs – fruit-bearing (stems/100 m^2)
Tree composition	tree_native	Density of native trees (stems/100 m^2)
	tree_nonnative	Density of nonnative trees (stems/100 m^2)
	tree_conifer	Density of coniferous trees (stems/100 m^2)
	tree_decid	Density of deciduous trees (stems/100 m^2)
	tree_fruit	Density of fruit-bearing trees (stems/100 m^2)
	tree_hetero	Shannon-Weaver index of heterogeneity of tree species
	snag_small	Density of snags (<12 cm dbh; stems/100m^2)
	snag_large	Density of snags (>12 cm dbh; stems/100m^2)
	snag_total	Density of snags (all sizes; stems/100m^2)

[a] Diameter at breast height

Table 4-2. Definition of landscape-level forest cover and isolation variables used as candidate predictors in analyses.

Category	Variable	Description
Canopy cover	cancov_250 cancov_500 cancov_1000	Mean canopy cover within 250, 500, or 1000 m
	access_cancov_250_sm access_cancov_500_sm access_cancov_500_lg access_cancov_1000_lg	Mean canopy cover within 250, 500, or 1000 m, without having to cross any small[a] or large[b] barriers.
Distance to forested natural area > 15 ha.	dist_nat	Straight distance to the nearest forested natural area > 15 ha.
	costdist_nat_bcch	Cost distance to nearest forested natural area > 15 ha using cost layer derived from translocation and playback experiments on black-capped chickadees. Use as a candidate variable in urban exploiter, adapter and non-native bird models.
	costdist_nat_ywar	Cost distance to nearest forested natural area > 15 ha using cost layer derived from translocation experiments on yellow warblers. Use as a candidate variable in urban avoider and native bird models.
Distance to Bow River	dist_bow	Straight distance to the Bow River.
	costdist_bow_bcch costdist_bow_ywar	Cost distance to the Bow River, using cost layers as described above.
Distance to major water course	dist_water	Straight-line distance to a major water body.
	costdist_water_bcch costdist_water_ywar	Cost distance to the nearest major water body, using cost layers as described above.
Distance to downtown	dist_dtown	Straight-line distance to central point in downtown core.

[a] Small barriers included: Major roads including freeways and major thoroughfares with a minimum of 4 lanes and all major water bodies.

[b] Large barriers included: Freeways and the Bow River only.

Table 4-3. Empirically derived resistance values used in the development of cost surfaces.

Feature	**Warbler**[1]	**Chickadee**[2]
Residential low	1.9	1.6
Residential high	4.4	1.2
Commercial or industrial	3.4	1.9
River	20.4	30.0
Roads	13.4	30.0
Forested natural areas	1.0	1.0
Shrubby natural areas	1.5	1.5
Recreational parks	3.4	1.9
Golf courses	2.0	1.2
Open areas	3.0	4.2

[1] Calculated as 1/hazard ratio of Cox regression models comparing the return time to territory of individual yellow warblers translocated across an urban feature compared to that of individuals translocated across continuous forest cover (see Table 3-2). For linear features (i.e. rivers and roads), values were multiplied by 10 to reflect a higher resistance per area than other land cover types.

[2] Same as above but based on black-capped chickadee translocations with the exception that river and road friction values were derived from playback experiments showing a strong barrier effect of these features (see Appendix 3-2).

Table 4-4. Proportion of sites within land cover types containing individual species in Calgary, Alberta, Canada[1]. All species are native to the study area except where otherwise noted.

Species	**N**[2]	**Balsam poplar**	**Aspen**	**Spruce**	**Managed park**	**Res high**	**Res med**	**Res low**	**Intensive development**	**Group**	**% in nat areas**	**Exclusive land cover**[3]
N		27	7	6	12	19	40	55	17			
Focal species (detected at > 5% of sites)												
American crow	79	0.19	0.43	0.17	0.67	0.63	0.58	0.31	0.59	exploit	0.01	
Black-billed magpie	107	0.52	0.29	0.33	0.67	0.68	0.68	0.55	0.65	exploit	0.05	
Blue jay	15	0.04	0.00	0.00	0.00	0.05	0.23	0.07	0.00	exploit	0.00	
Chipping sparrow	77	0.11	0.00	0.33	0.58	0.68	0.60	0.45	0.18	exploit	0.03	
Common grackle	16	0.04	0.14	0.00	0.17	0.16	0.08	0.11	0.00	exploit	0.01	
House finch*	53	0.00	0.00	0.00	0.08	0.63	0.50	0.36	0.00	exploit	0.00	
House sparrow*	138	0.30	0.00	0.00	0.50	1.00	0.98	0.93	0.88	exploit	0.00	
Rock pigeon*	27	0.04	0.00	0.00	0.08	0.11	0.15	0.22	0.29	exploit	0.00	
American robin	164	0.93	1.00	0.83	0.83	0.95	1.00	0.91	0.53	adapt	0.03	
Black-capped chickadee	124	0.89	1.00	1.00	0.92	0.89	0.88	0.42	0.06	adapt	0.05	
European starling*	60	0.74	0.14	0.00	0.50	0.26	0.13	0.27	0.47	adapt	0.01	
House wren	39	0.56	0.43	0.17	0.25	0.26	0.13	0.13	0.00	adapt	0.01	
Red-breasted nuthatch	56	0.26	0.43	0.83	0.42	0.58	0.48	0.11	0.00	adapt	0.09	
Brown-headed cowbird	25	0.48	0.14	0.33	0.08	0.00	0.08	0.09	0.00	avoid	0.11	
Cedar waxwing	14	0.30	0.14	0.00	0.00	0.05	0.05	0.04	0.00	avoid	0.05	
Downy woodpecker	15	0.33	0.29	0.00	0.17	0.05	0.03	0.00	0.00	avoid	0.05	
Grey catbird	10	0.37	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	0.10	b. poplar
Least flycatcher	16	0.48	0.29	0.17	0.00	0.00	0.00	0.00	0.00	avoid	0.13	

Northern flicker	26	0.48	0.14	0.00	0.25	0.16	0.13	0.02	0.00	avoid	0.02	
Ruby-crowned kinglet	12	0.00	0.00	0.50	0.08	0.16	0.13	0.00	0.00	avoid	0.27	
Red-winged blackbird	11	0.33	0.00	0.00	0.08	0.00	0.00	0.00	0.06	avoid	0.07	
Song sparrow	11	0.37	0.00	0.17	0.00	0.00	0.00	0.00	0.00	avoid	0.18	
Tree swallow	13	0.37	0.00	0.00	0.00	0.00	0.00	0.05	0.00	avoid	0.06	
Warbling vireo	15	0.33	0.29	0.00	0.17	0.00	0.00	0.04	0.00	avoid	0.05	
Yellow warbler	37	0.93	0.57	0.17	0.17	0.00	0.05	0.05	0.00	avoid	0.05	
Non-focal species (detected at < 5% of sites)												
Barn swallow	1	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	exploit	0.00	
Mourning dove	3	0.04	0.00	0.00	0.00	0.00	0.00	0.02	0.06	adapt	0.11	
Pine siskin	1	0.00	0.00	0.00	0.00	0.05	0.00	0.00	0.00	adapt	0.00	
Common raven	6	0.11	0.14	0.00	0.00	0.05	0.00	0.00	0.06	avoid	0.11	
Common nighthawk	1	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	1.00	b. poplar
Belted kingfisher	3	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	0.33	b. poplar
Hairy woodpecker	1	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	1.00	b. poplar
Western wood-peewee	9	0.30	0.00	0.00	0.08	0.00	0.00	0.00	0.00	avoid	0.10	
Eastern kingbird	4	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	0.25	b. poplar
Red-eyed vireo	7	0.07	0.43	0.33	0.00	0.00	0.00	0.00	0.00	avoid	0.43	
Northern rough-winged swallow	1	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	1.00	b. poplar
White-breasted nuthatch	2	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	0.50	b. poplar
Golden-crowned kinglet	4	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	avoid	1.25	spruce
Swainson's thrush	4	0.00	0.14	0.00	0.00	0.00	0.00	0.04	0.06	avoid	0.06	

Hermit thrush	2	0.04	0.00	0.17	0.00	0.00	0.00	0.00	0.00	avoid	1.00	
Tennessee warbler	3	0.04	0.14	0.00	0.00	0.05	0.00	0.00	0.00	avoid	0.22	
Orange-crowned warbler	2	0.00	0.14	0.00	0.00	0.05	0.00	0.00	0.00	avoid	0.25	
Yellow-rumped warbler	3	0.00	0.00	0.33	0.00	0.00	0.00	0.02	0.00	avoid	0.89	
Western tanager	1	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	avoid	2.00	spruce
Clay-coloured sparrow	8	0.22	0.14	0.17	0.00	0.00	0.00	0.00	0.00	avoid	0.25	
Savannah sparrow	1	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	1.00	b. poplar
Lincoln's sparrow	2	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	0.50	b. poplar
White-crowned sparrow	1	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	1.00	b. poplar
White-throated sparrow	6	0.11	0.29	0.17	0.00	0.00	0.00	0.00	0.00	avoid	0.33	
Dark-eyed junco	1	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	avoid	2.00	spruce
Rose-breasted grosbeak	1	0.00	0.14	0.00	0.00	0.00	0.00	0.00	0.00	avoid	1.00	aspen
Yellow-headed blackbird	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	avoid	0.00	
Brewer's blackbird	7	0.15	0.00	0.00	0.00	0.00	0.03	0.02	0.06	avoid	0.08	
Baltimore oriole	9	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	avoid	0.11	b. poplar
American goldfinch	4	0.07	0.14	0.00	0.00	0.00	0.03	0.00	0.00	avoid	0.19	

[1] Shading represents frequency categories as follows:

80-100% 60-80% 40-60% 20-40% 0-20%

[2] Number of sites where detected.

[3] Land cover type where species was exclusively found.

* Non-native species.

Table 4-5. Best models describing structural and compositional local vegetation factors explaining avian communities in Calgary, Alberta. All models were derived from linear regression except for the urban avoider model, which was derived using ordered probit regression for a categorical response variable. Model in bold represents the best-fitting model for each response variable. Only variables significant at $P < 0.1$ are shown here. See Appendix 4-3 for model details.

Response variable	Model type	Shrub variables	Tree variables	LL	AIC	ΔAIC	w_i	Adjusted R^2
Community Level (N = 183 sites)								
Richness^{ln}	**Structural**		**+ cancov_50^{sqrt}** ***	**-49.12**	**102.24**	**0.00**	**0.999**	**0.36**
	Compositional	+ shrub_fruit^{ln} ***		-55.26	116.53	14.29	0.001	0.31
Heterogeneity^{a}	**Structural**		**+ cancov_50^{sqrt}** ***	**-83.98**	**173.95**	**0.00**	**0.999**	**0.33**
	Compositional	+ shrub_fruit^{ln} ***	+ tree_decid^{sqrt} **	-91.37	188.74	14.79	0.001	0.27
Abundance	**Structural**	**+ shrub_total^{ln}** ***	**+ mean_can_hgt** ***	**-523.93**	**1053.85**	**0.00**	**0.999**	**0.21**
	Compositional	+ shrub_fruit^{ln} ***		-531.72	1067.43	13.58	0.001	0.15
Group Level Abundances (N = 183 sites)								
Native species^{sqrt}	**Structural**		**+ cancov_50^{sqrt}** ***	**-175.23**	**354.47**	**0.00**	**1.000**	**0.40**
	Compositional	+ shrub_fruit^{ln} ***	+ tree_decid^{sqrt} **	-190.66	387.32	32.85	0.000	0.28
Non-native species^{sqrt}	**Structural**		**- tree_small^{ln}** ***	**-224.05**	**452.10**	**0.00**	**0.608**	**0.25**
	Compositional		- tree_native^{sqrt} ***	-224.49	452.98	0.88	0.392	0.25
Urban exploiters^{sqrt}	Structural	+ shrub_small^{ln} **	- tree_small^{ln} ***	-223.13	452.26	6.42	0.039	0.28
	Compositional		**- tree_native^{sqrt}** ***	**-220.92**	**445.84**	**0.00**	**0.961**	**0.30**
Urban adapters^{sqrt}	**Structural**		**+ cancov_50^{sqrt}** ***	**-180.01**	**364.03**	**0.00**	**0.999**	**0.20**
	Compositional	+ shrub_fruit^{ln} ***		-186.89	377.78	13.75	0.001	0.14
Urban avoiders	Structural		+ tree_total^{ln} ***	-154.55	315.10	8.42	0.015	0.17^{b}
	Compositional	**+ shrub_native^{ln}** ***		**-150.34**	**306.68**	**0.00**	**0.985**	**0.20^{b}**

Native Species in Developed Sites Only (N = 131 sites)								
Richness^{sqrt}	**Structural**	**+ shrub_total^{ln} *****	**+ tree_large^{ln} ***** **+ veg_struct_hetero^{sqrt} ****	**-67.63**	**143.26**	**0.00**	**0.999**	**0.37**
	Compositional	+ shrub_nonnative^{ln} ***	+ tree_nonnative^{sqrt} ***	-75.80	157.61	14.35	0.001	0.29
Abundance^{sqrt}	**Structural**		**+ cancov_50^{sqrt} *****	**-123.75**	**251.49**	**0.00**	**0.999**	**0.36**
	Compositional	+shrub_nonnative^{ln} ***	+ tree_nonnative^{sqrt} ***	-130.00	266.00	14.51	0.001	0.29

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$

^{ln} Natural log transformed

^{sqrt} Square-root transformed

[a] Calculated using Shannon-Weaver index.

[b] Pseudo-R^2

Table 4-6. Best models, derived from logistic regression, describing structural and compositional local vegetation factors explaining the occurrence of focal species in Calgary, Alberta. Bold font indicates best-fitting model for each species. Only variables significant at $P < 0.1$ are shown here. See Appendix 4-4 for model details.

Focal species	**Model type**	**Shrub variables**	**Tree variables**	**LL**	**AIC**	**ΔAIC**	**w_i**	**AUC[a]**
Urban Exploiters								
American crow	Structural		- tree_small^{ln} **	-122.75	251.50	5.98	0.048	0.61
	Compositional	**- shrub_native^{ln} ***	**+ tree_nonnative^{sqrt} ****	**-119.76**	**245.52**	**0.00**	**0.952**	**0.62**
Black-billed magpie	Structural		- tree_total^{ln} ** + veg_struct_hetero^{sqrt} *	-120.55	247.10	2.55	0.218	0.60
	Compositional	**- shrub_native^{ln} *****		**-120.27**	**244.55**	**0.00**	**0.782**	**0.63**
Blue jay	**Structural**	**+ shrub_small^{ln} ***	**- tree_small^{ln} ***	**-49.20**	**104.40**	**0.00**	**0.540**	**0.67**
	Compositional[b]		(+ tree_hetero^{sqrt})	-50.36	104.72	0.32	0.460	0.64
Chipping sparrow	Structural		- tree_small^{ln} ***	-124.54	239.61	8.75	0.012	0.61
	Compositional	**- shrub_native^{ln} ***	**+ tree_hetero^{sqrt} *****	**-124.54**	**230.86**	**0.00**	**0.988**	**0.68**
Common grackle	Structural[b]		(- tree_small^{ln})	-53.69	111.37	6.72	0.034	0.48
	Compositional		**+ tree_fruit_sqrt** ***	**-50.33**	**104.65**	**0.00**	**0.966**	**0.71**
House finch	Structural	+ shrub_large^{ln} **	- tree_small^{ln} ***	-94.09	196.19	0.89	0.391	0.74
	Compositional		**- tree_native^{sqrt} *****	**-95.65**	**195.30**	**0.00**	**0.609**	**0.68**
House sparrow	Structural		- tree_total^{ln} ***	-75.18	154.35	9.66	0.008	0.79
	Compositional		**- tree_native^{sqrt} *****	**-70.35**	**144.69**	**0.00**	**0.992**	**0.85**
Rock pigeon	Structural		- cancov_50^{sqrt} ***	-72.72	149.44	0.45	0.444	0.66
	Compositional		**- tree_snag_total^{sqrt} ***	**-72.50**	**148.99**	**0.00**	**0.556**	**0.60**

Urban Adapters								
American robin	**Structural**	**+ shrub_total^{ln} *** + veg_struct_hetero^{sqrt} ***		**-55.47**	**116.93**	**0.00**	**0.697**	**0.70**
	Compositional	+ shrub_conif^{ln} **		-57.30	118.60	1.67	0.303	0.66
Black-capped chickadee	**Structural**	**+ cancov_50^{sqrt} *** - veg_struct_hetero^{sqrt} ****		**-79.62**	**165.23**	**0.00**	**1.000**	**0.86**
	Compositional	+ shrub_fruit^{ln} ***		-95.70	197.39	32.16	0.000	0.77
European starling	Structural		+ tree_large^{ln} **	-113.72	231.43	12.25	0.002	0.58
	Compositional		**- tree_hetero^{sqrt} *****	**-107.59**	**219.18**	**0.00**	**0.998**	**0.67**
House wren	Structural	+ shrub_small^{ln} *** + veg_struct_hetero^{sqrt} *		-85.43	176.85	4.42	0.099	0.71
	Compositional	**+ shrub_fruit^{ln} ****	**+ tree_snag_large^{sqrt} ***	**-83.21**	**172.43**	**0.00**	**0.901**	**0.73**
Red-breasted nuthatch	Structural		+ max_can_hgt^{sqrt} ***	-100.82	207.64	5.91	0.050	0.72
	Compositional	**+ shrub_nonnative^{ln} *****	**+ tree_conif^{sqrt} *****	**-97.87**	**201.73**	**0.00**	**0.950**	**0.73**
Urban Avoiders								
Brown-headed cowbird	Structural		+ tree_total^{ln} ***	-66.06	136.12	10.89	0.004	0.71
	Compositional	**+ shrub_native^{ln} *****		**-60.61**	**125.23**	**0.00**	**0.996**	**0.77**
Cedar waxwing	**Structural**	**+ shrub_small^{ln} *****		**-40.58**	**85.16**	**0.00**	**0.746**	**0.81**
	Compositional	+ shrub_native^{ln} ***		-41.65	87.31	2.15	0.254	0.79
Downy woodpecker	**Structural**	**+ cancov_50^{sqrt} *** - veg_struct_hetero^{sqrt} ****		**-35.52**	**77.05**	**0.00**	**0.994**	**0.90**
	Compositional		+ tree_snag_large^{sqrt} ***	-41.65	87.31	10.26	0.006	0.79
Grey catbird	Structural	+ shrub_small^{ln} ***		-24.55	53.10	7.12	0.028	0.92
	Compositional	**+ shrub_native^{ln} *****		**-20.99**	**45.98**	**0.00**	**0.972**	**0.95**

Least flycatcher	**Structural**	**+ cancov_50^{sqrt} ***** **- veg_struct_hetero^{sqrt} ****		**-27.27**	**61.86**	**0.00**	**0.747**	**0.95**
	Compositional	+ shrub_native^{ln} ***		-30.01	64.03	2.17	0.253	0.94
Northern flicker	**Structural**		**+ cancov_50^{sqrt} *****	**-63.88**	**131.77**	**0.00**	**0.840**	**0.78**
	Compositional	+ shrub_fruit^{ln} **	- tree_hetero^{sqrt} ***	-64.55	135.09	3.32	0.160	0.75
Red-winged blackbird	Structural		+ cancov_50^{sqrt} ***	-33.12	72.23	8.02	0.018	0.84
	Compositional	**+ shrub_native^{ln} ****	**- tree_conif^{sqrt} ****	**-29.10**	**64.21**	**0.00**	**0.982**	**0.88**
Ruby-crowned kinglet	Structural		+ max_can_hgt^{sqrt} **	-40.76	85.52	11.68	0.003	0.73
	Compositional	**+ shrub_conif^{ln} *****		**-34.92**	**73.84**	**0.00**	**0.997**	**0.81**
Song sparrow	Structural		+ cancov_50^{sqrt} ***	-29.60	65.19	4.85	0.081	0.88
	Compositional	**+ shrub_native^{ln} *****	**- tree_hetero^{sqrt} ***	**-27.17**	**60.34**	**0.00**	**0.919**	**0.92**
Tree swallow	Structural		+ tree_large^{ln} ***	-43.70	91.39	18.07	0.000	0.68
	Compositional	**+ shrub_native^{ln} ***	**- tree_hetero^{sqrt} *****	**-33.66**	**73.32**	**0.00**	**1.000**	**0.85**
Warbling vireo	**Structural**		**+ cancov_50^{sqrt} *****	**-41.02**	**86.05**	**0.00**	**0.866**	**0.82**
	Compositional	+ shrub_native^{ln} ***		-42.89	89.79	3.74	0.134	0.80
Yellow warbler	Structural		+ cancov_50^{sqrt} ***	-61.46	126.93	38.93	0.000	0.87
	Compositional	**+ shrub_native^{ln} *****		**-42.00**	**88.00**	**0.00**	**1.000**	**0.94**

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$

[a] Area under the Receiving Operator Curve

[b] No significant variables in best-fit model; non-significant variables appear in brackets.

^{ln} Natural log transformed

^{sqrt} Square-root transformed

Table 4-7. Best models explaining local and landscape factors affecting avian communities in Calgary, Alberta, Canada. All models were derived from linear regression, except for the urban avoider model, which was derived using ordered probit regression for a categorical response variable. Variables incorporating a measure of connectivity are in bold font. Only variables significant at the *P* < 0.1 are presented here. See Appendix 4-5 for model details.

Response variable	**Local shrub**	**Local tree**	**Landscape-level Forest cover**	**Isolation from features**	**Adjusted R^2**	**ΔAIC^a**
<u>Community level</u>						
Richness^{ln}		+ cancov_50^{sqrt} ***		- dist_bow^{sqrt} ***	0.40	
Heterogeneity^b		+ cancov_50^{sqrt} ***		- dist_bow^{sqrt} ***	0.37	
Abundance	+ tot_shrub^{sqrt} ***	+ mean_can_hgt^{sqrt} *** - tree_decid^{sqrt} **		- dist_bow^{sqrt} ***	0.26	
<u>Group level abundances</u>						
Native species^{sqrt}	+ shrub_fruit^{ln} ***		+ cancov_250^{sqrt} ***	- dist_bow^{sqrt} ** + dist_dtown ** - dist_water^{sqrt} **	0.50	
Non-native species^{sqrt}	+ veg_struct_hetero^{sqrt} ** + shrub_small^{ln} ***	- tree_small^{ln} ***	- cancov_500^{sqrt} *	+ dist_nat^{sqrt} *** **- costdist_bow_bcch^{sqrt} ****	0.39	0.14
Urban exploiters^{sqrt}	+ shrub_small^{ln} *** + veg_struct_hetero^{sqrt} **	- tree_native^{sqrt} ***		+ dist_nat^{sqrt} *** - dist_bow^{sqrt} **	0.41	

Urban adapters^{sqrt}		+ cancov_250$^{0.5}$ ***	- dist_water^{ln} *** + dist_dtown *	0.28	
Urban avoiders	+ tot_shrub^{ln} ***		**- costdist_water_ywar^{sqrt}** ***	0.25^{c}	- 3.21
Developed sites (native species only)					
Richness^{sqrt}	+ shrub_nonnative^{ln} *** + tot_tree_large^{ln} * + veg_struct_hetero^{sqrt} **	**+ access_cancov_250^{sqrt}** ***	- dist_nat^{sqrt} *** + dist_dtown **	0.48	- 2.76
Abundance$^{0.5}$	+ shrub_nonnative^{ln} *** + veg_struct_hetero^{sqrt} *	**+ access_cancov_250^{sqrt}** ***	- dist_nat^{sqrt} *** + dist_dtown ***	0.52	- 8.23

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$.

^{sqrt} Square-root transformed variables.

^{ln} Natural log transformed variables.

[a] Difference in AIC value resulting from inclusion of permeability-based variables in best-fit model compared to same model in which permeability term has been replaced by conventional term (e.g. cost distance replaced by straight-line distance).

[b] Calculated using Shannon-Weaver index.

[c] Pseudo-R^2.

Table 4-8. Best models, derived from logistic regression, explaining local and landscape factors affecting the presence or absence of individual focal species in Calgary, Alberta, Canada. Variables incorporating a measure of permeability are in bold font. Only variables significant at the *P* < 0.1 are presented here. See Appendix 4-6 for model details.

Focal species	**Local shrub**	**Local tree**	**Landscape-level Forest cover**	**Isolation from features**	**Area under ROC curve**	**ΔAIC^{a}**
Urban Exploiters						
American crow			+ cancov_1000^{sqrt} ***	**+ costdist_nat_bcch^{sqrt}** ***	0.74	-0.94
Black-billed magpie	- shrub_native^{ln} *** + veg_struct_hetero^{sqrt} *			**- costdist_bow_bcch_sqrt** *** - dist_dtown **	0.74	-0.68
Blue jay	- veg_struct_hetero*		+ cancov_1000^{sqrt} ***	+ dist_dtown^{sqrt} ***	0.82	
Chipping sparrow		+ tree_hetero^{sqrt} *** - tree_small^{ln}***	+ cancov_1000^{sqrt} ***		0.74	
Common grackle		+ tree_fruit^{sqrt} ***		**- costdist_bow_bcch^{sqrt}** **	0.79	-1.08
House finch		- tree_small^{ln} **	**+ access_cancov_500_sm^{sqrt}** ***	+ dist_water^{ln} ***	0.88	-6.44
House sparrow			- cancov_250$^{0.5}$ **	+ dist_water^{ln} *** - dist_dtown *	0.88	
Rock pigeon		- snag_tree^{sqrt} **		- dist_bow_sqrt *** + dist_nat_sqrt ***	0.75	

Urban Adapters						
American robin			+ cancov_250$^{\text{sqrt}}$ *	+ dist_dtown$^{\text{sqrt}}$ *** **- costdist_nat_bcch$^{\text{sqrt}}$** *	0.84	-1.03
Black-capped chickadee		- veg_struct_hetero$^{0.5}$ *	+ cancov_250$^{\text{sqrt}}$ ***	**- costdist_nat_bcch**$^{\text{sqrt}}$ ***	0.91	-3.83
European starling	+ shrub_native$^{\text{ln}}$ **	- tree_hetero$^{0.5}$ *** + max_can_hgt$^{\text{sqrt}}$ **	+ cancov_500$^{\text{sqrt}}$ ***	**+ costdist_nat_bcch$^{\text{sqrt}}$** ** - dist_bow$^{\text{sqrt}}$ *	0.78	-0.47
House wren	+ shrub_fruit$^{\text{ln}}$ ***			- dist_water$^{\text{ln}}$ *** + dist_dtown *	0.77	
Red-breasted nuthatch		+ tree_conif$^{\text{sqrt}}$ *	+ cancov_500$^{\text{sqrt}}$ ***	**+ costdist_water_bcch$^{\text{ln}}$** **	0.86	-1.90
Urban Avoiders						
Brown-headed cowbird	+ shrub_native$^{\text{ln}}$ ***		- cancov_250$^{\text{sqrt}}$ **	- dist_nat$^{\text{sqrt}}$ ***	0.84	
Cedar waxwing	+ shrub_sm$^{\text{ln}}$***				0.81	
Downy woodpecker				**- costdist_water_ywar$^{\text{ln}}$** *** (1) **- costdist_bow_ywar$^{\text{ln}}$** ** (2)	0.92	-2.61 (1) -0.30 (2)
Grey catbird				- dist_water_ln *	0.97	

Least flycatcher				**- costdist_water_ywar**^{ln}***	0.96	-7.06
Northern flicker		+ cancov_50^{sqrt} **		**- costdist_bow_ywar**^{sqrt} * - dist_dtown *	0.82	0.21
Ruby-crowned kinglet	+ shrub_conif^{ln} *** - veg_struct_hetero^{sqrt} *		**+ access_cancov_500_lg**^{sqrt} **		0.93	0.37
Red-winged blackbird				- dist_nat^{sqrt} ** - dist_bow^{sqrt}**	0.92	
Song sparrow				- dist_water^{ln} *** **- costdist_bow_ywar**^{sqrt} *	0.97	-0.25
Tree swallow		- tree_hetero^{sqrt}**	**- access_cancov_1000**^{sqrt} ** (1)	**- costdist_nat_ywar**^{sqrt} *** (2)	0.94	-1.40 (1) -0.86 (2)
Warbling vireo				**- costdist_water_ywar**^{ln} ***	0.82	-1.70
Yellow warbler	+ total_shrub^{ln} **			**- costdist_water_ywar**^{ln} *** (1) **- costdist_bow_ywar**^{sqrt} ** (2)	0.97	-4.37 (1) -0.54 (2)

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$

^{sqrt}Square-root transformed

^{ln} Natural log transformed

[a] Difference in AIC value resulting from inclusion of permeability-based variables in best-fit model compared to same model in which permeability term has been replaced by conventional term (e.g. cost distance replaced by straight-line distance).

Table 4-9. Comparison of best local and multi-scale models explaining the distribution and composition of avian communities in Calgary, Alberta, Canada.

Response variable	**Model**	**AIC**	**ΔAIC**	**w_i**
Community level				
Richness	Local only	102.24	10.91	0.004
	Local + landscape	**91.33**	**0.00**	**0.996**
Heterogeneity	Local only	173.95	10.07	0.006
	Local + landscape	**163.88**	**0.00**	**0.994**
Abundance	Local	1053.85	8.17	0.017
	Local + landscape	**1045.68**	**0.00**	**0.983**
Group level abundances				
Native species	Local	354.47	29.13	0.000
	Local + landscape	**325.34**	**0.00**	**1.000**
Non native species	Local	452.10	33.72	0.000
	Local + landscape	**418.38**	**0.00**	**1.000**
Exploiters	Local	445.84	29.62	0.000
	Local + landscape	**416.22**	**0.00**	**1.000**
Adapters	Local	364.03	15.57	0.000
	Local + landscape	**348.46**	**0.00**	**1.000**
Avoiders	Local	306.68	17.73	0.000
	Local + landscape	**288.95**	**0.00**	**1.000**
Native species in developed sites only				
Richness	Local	143.3	22.32	0.000
	Local + landscape	**120.9**	**0.00**	**1.000**
Abundance	Local	251.5	33.81	0.000
	Local + landscape	**217.7**	**0.00**	**1.000**

Table 4-10. Comparison of best local and multi-scale models explaining the occurrence of individual focal species in Calgary, Alberta, Canada.

Response variable	**Model**	**AIC**	**ΔAIC**	w_i
Urban exploiters				
American crow	Local only	245.52	16.78	0.000
	Local + landscape	**228.74**	**0.00**	**1.000**
Black-billed magpie	Local only	244.55	20.42	0.000
	Local + landscape	**224.13**	**0.00**	**1.000**
Blue jay	Local only	104.40	7.46	0.023
	Local + landscape	**96.94**	**0.00**	**0.977**
Chipping sparrow	Local only	230.86	6.54	0.037
	Local + landscape	**224.32**	**0.00**	**0.963**
Common grackle	Local only	104.65	2.69	0.207
	Local + landscape	**101.96**	**0.00**	**0.793**
House finch	Local only	195.30	43.31	0.000
	Local + landscape	**151.99**	**0.00**	**1.000**
House sparrow	Local only	144.69	11.66	0.003
	Local + landscape	**133.03**	**0.00**	**0.997**
Rock pigeon	Local only	148.99	12.52	0.002
	Local + landscape	**136.47**	**0.00**	**0.998**
Urban adapters				
American robin	Local only	116.93	11.25	0.004
	Local + landscape	**105.68**	**0.00**	**0.996**
Black-capped chickadee	Local	165.23	30.78	0.000
	Local + landscape	**134.45**	**0.00**	**1.000**
European starling	Local only	219.18	17.18	0.000
	Local + landscape	**202.00**	**0.00**	**1.000**
House wren	Local only	172.43	6.19	0.043
	Local + landscape	**166.24**	**0.00**	**0.957**
Red-breasted nuthatch	Local only	201.73	38.11	0.000
	Local + landscape	**163.62**	**0.00**	**1.000**
Urban avoiders				
Brown-headed cowbird	Local only	125.23	6.07	0.046
	Local + landscape	**119.16**	**0.00**	**0.954**
Cedar waxwing	Local only	85.16	0.00	0.500
	Local + landscape	**85.16**	**0.00**	**0.500**
Downy woodpecker	Local only	77.05	3.18	0.170
	Local + landscape	**73.87**	**0.00**	**0.830**

Grey catbird	Local only	45.98	3.90	0.125
	Local + landscape	**42.08**	**0.00**	**0.875**
Least flycatcher	Local only	61.86	8.76	0.012
	Local + landscape	**53.10**	**0.00**	**0.988**
Northern flicker	Local only	131.77	7.35	0.025
	Local + landscape	**124.42**	**0.00**	**0.975**
Red-winged blackbird	Local only	64.21	12.39	0.002
	Local + landscape	**51.82**	**0.00**	**0.998**
Ruby-crowned kinglet	Local only	73.84	8.68	0.013
	Local + landscape	**65.16**	**0.00**	**0.987**
Song sparrow	Local only	60.34	18.95	0.000
	Local + landscape	**41.39**	**0.00**	**1.000**
Tree swallow	Local only	73.32	15.90	0.000
	Local + landscape	**57.42**	**0.00**	**1.000**
Warbling vireo	Local only	86.05	2.45	0.227
	Local + landscape	**83.60**	**0.00**	**0.773**
Yellow warbler	Local only	88.00	14.39	0.001
	Local + landscape	**73.61**	**0.00**	**0.999**

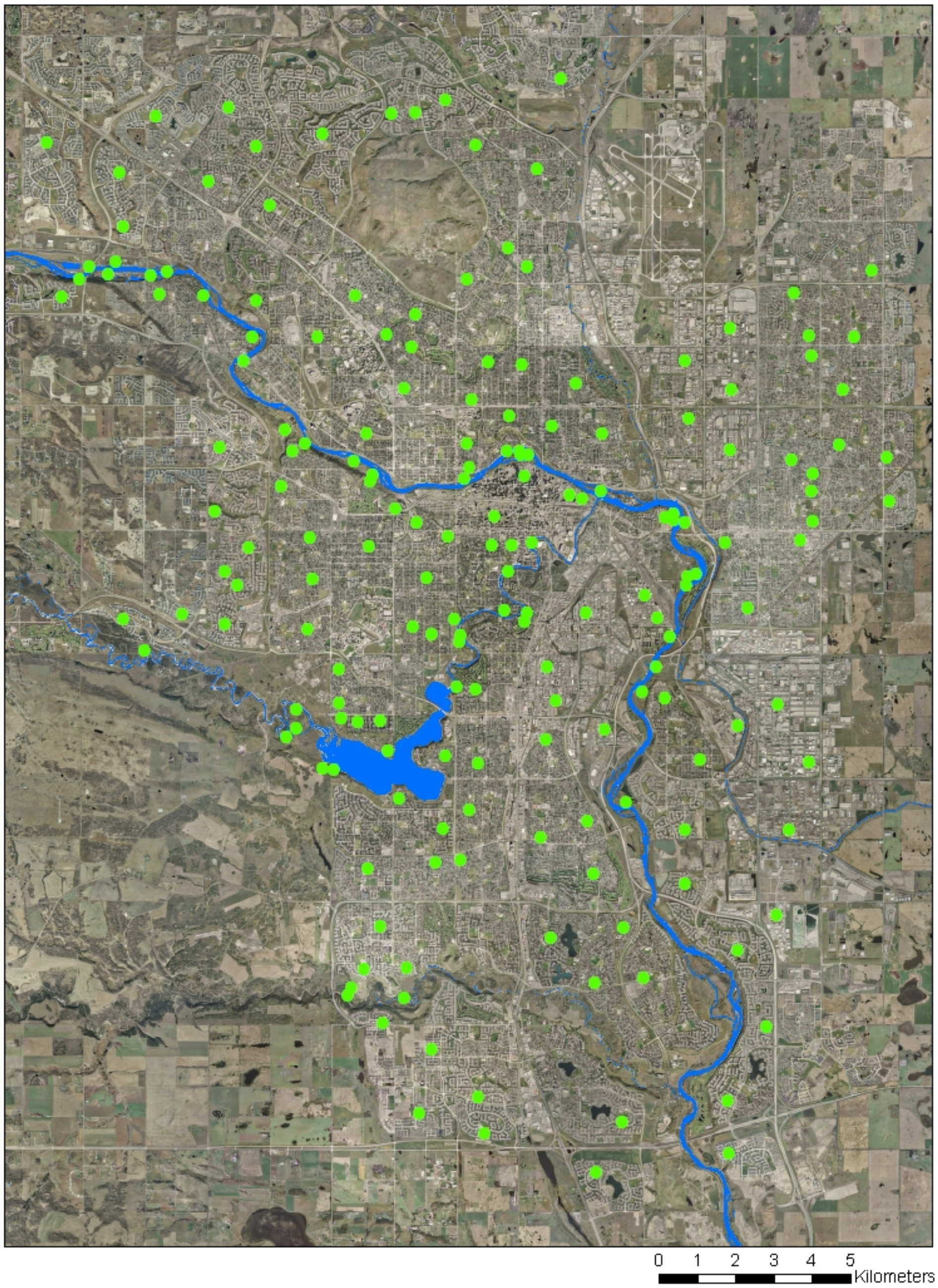
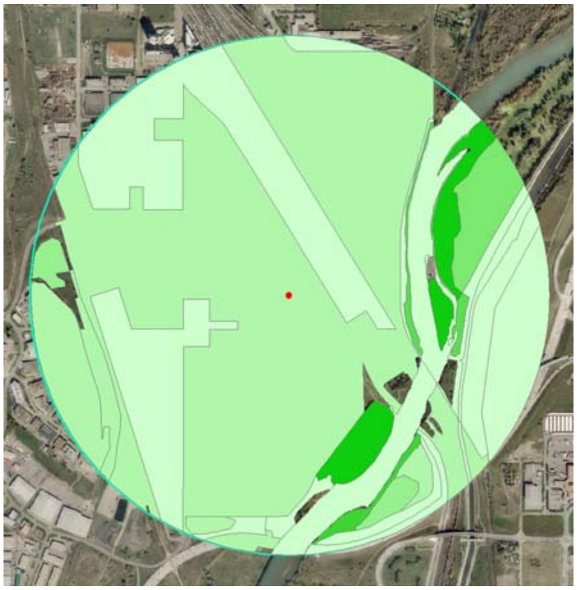


Figure 4-1. Distribution of 183 bird survey sites used in Calgary, Alberta, Canada, 2005-2007.

a)



b)

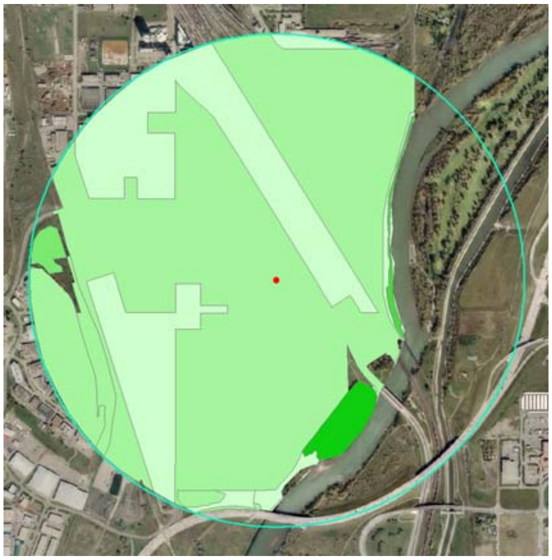
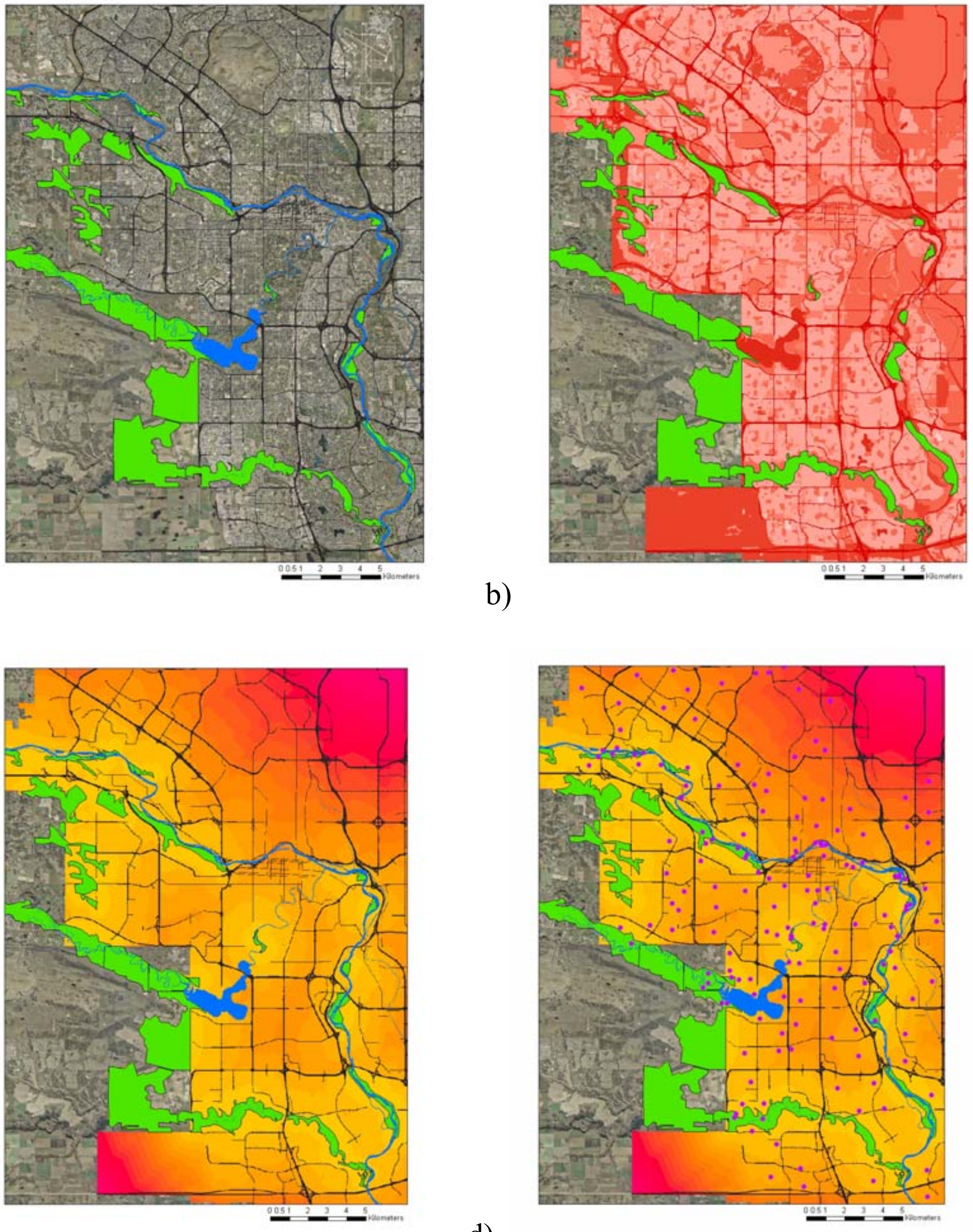
c)


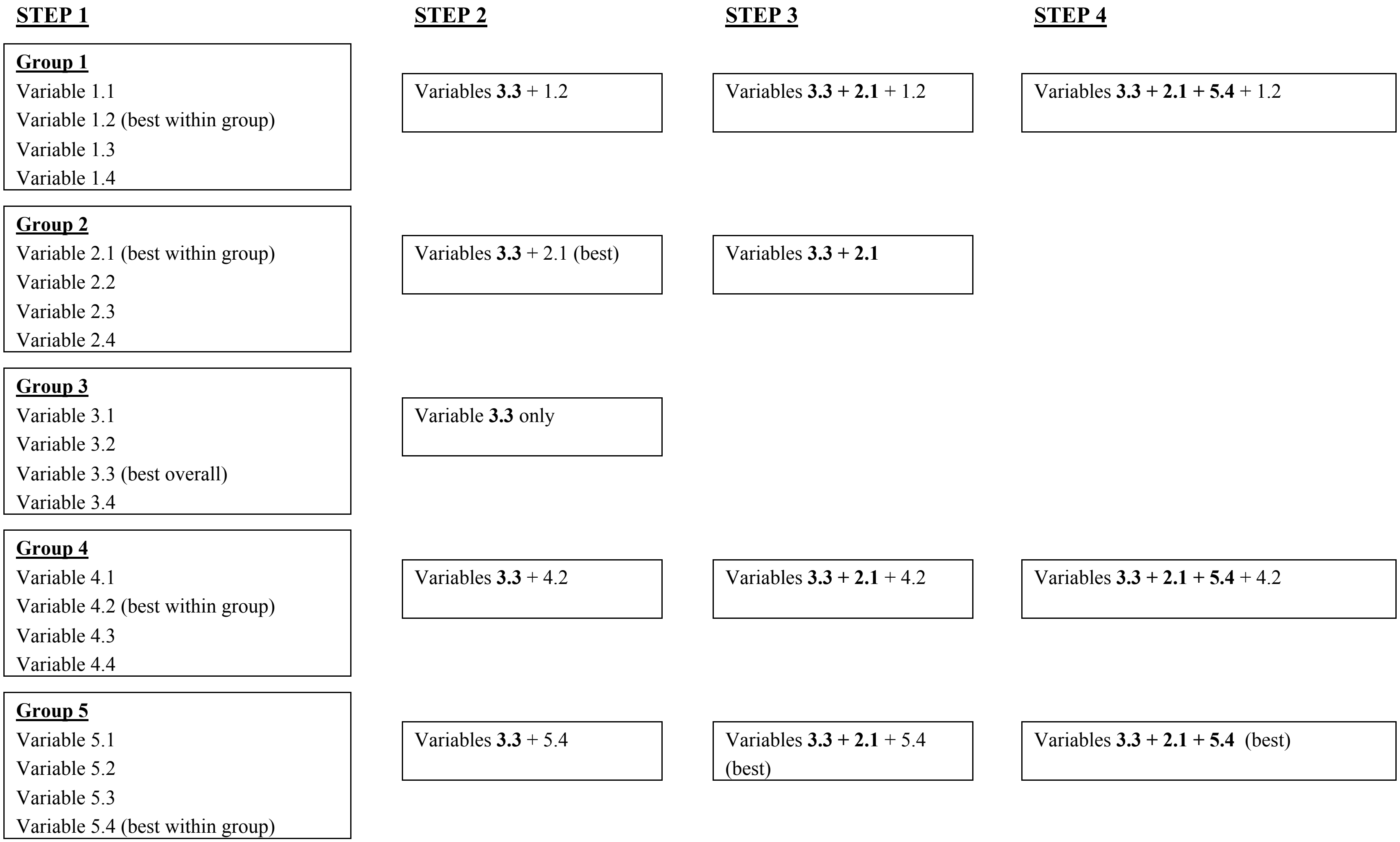
Figure 4-2. Derivation of mean and 'accessible' canopy cover within a given radius (250, 500, or 1000 m) of a survey site. a) A buffer was drawn (turquoise line) around the survey point (red point). b) A canopy cover value was assigned to each land cover polygon within the buffer and mean canopy cover calculated by weighting the canopy cover value of each polygon by its area. c) For canopy cover corrected for accessibility, areas around large barriers (in this case, major road and Bow River) were assigned a canopy value of 0 and the mean recalculated.



a) b)

c) d)

Figure 4-3. Illustration of steps used to derive cost distance to natural features (here, natural areas > 15 ha). a) Forested natural areas were plotted in a geographic information system. b) A friction layer was created using the friction values from Table 4-3 (here, using the chickadee cost surface). c) A cost distance layer was derived using the 'cost distance' function in ArcGIS. d) A cost distance value was assigned to each survey point. Cost distances to nearest water body and Bow River were derived analogously.



STEP 1	**STEP 2**	**STEP 3**	**STEP 4**
Group 1 Variable 1.1 Variable 1.2 (best within group) Variable 1.3 Variable 1.4	Variables **3.3** + 1.2	Variables **3.3 + 2.1** + 1.2	Variables **3.3 + 2.1 + 5.4** + 1.2
Group 2 Variable 2.1 (best within group) Variable 2.2 Variable 2.3 Variable 2.4	Variables **3.3** + 2.1 (best)	Variables **3.3 + 2.1**	
Group 3 Variable 3.1 Variable 3.2 Variable 3.3 (best overall) Variable 3.4	Variable **3.3** only		
Group 4 Variable 4.1 Variable 4.2 (best within group) Variable 4.3 Variable 4.4	Variables **3.3** + 4.2	Variables **3.3 + 2.1** + 4.2	Variables **3.3 + 2.1 + 5.4** + 4.2
Group 5 Variable 5.1 Variable 5.2 Variable 5.3 Variable 5.4 (best within group)	Variables **3.3** + 5.4	Variables **3.3 + 2.1** + 5.4 (best)	Variables **3.3 + 2.1 + 5.4** (best)

Figure 4-4. Flow chart showing the stepwise AIC-based model building and selection process. The best model from each step is subsequently compared, in the following step, to derivatives containing one additional (and uncorrelated) variable. This process is reiterated until model fit can no longer be improved through the addition of variables. Variables carried over from the previous step are in bold font.

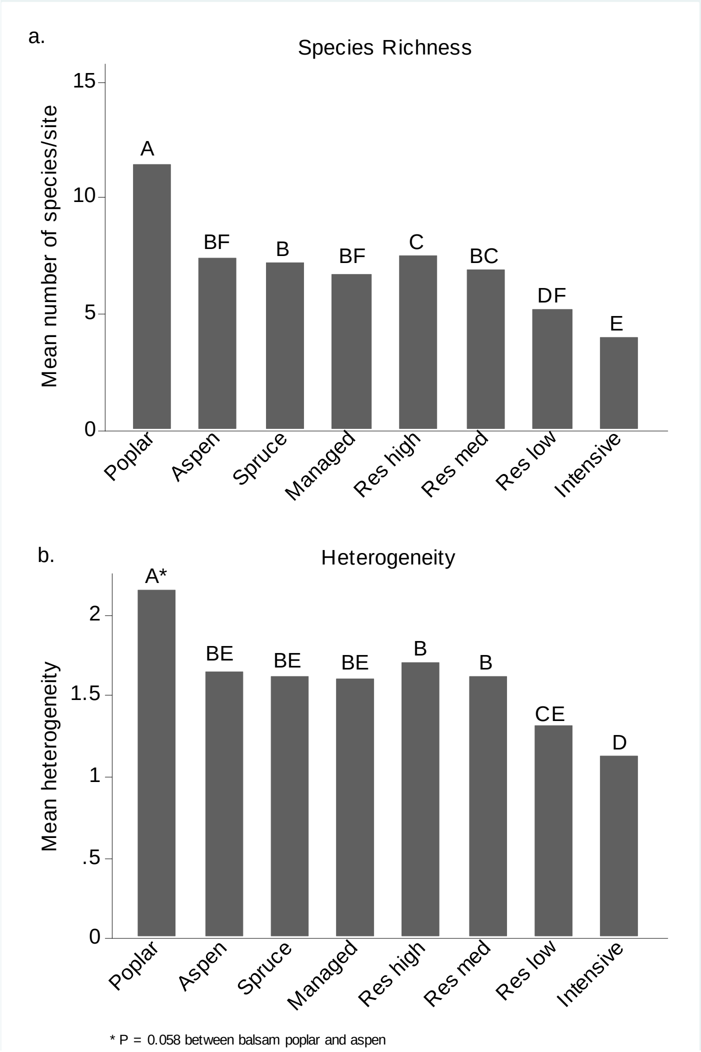


Figure 4-5. Avian species richness (a) and Shannon-Weaver heterogeneity (b) in relation to land cover type in the urban landscape of Calgary, Alberta, Canada. Letters above bars represent groups based on post-hoc comparisons using non-parametric Wilcoxon rank-sum tests ($P < 0.05$ unless specified otherwise). Exploiters, adapters, and avoiders defined as per Table 4-4. Letters above bars represent groups based on post-hoc comparisons using non-parametric Wilcoxon rank-sum tests. Poplar = balsam poplar stands; Managed = managed parks; Res high, med and low = residential areas with high, medium, and low levels of canopy cover, respectively; Intensive = areas of intensive development (commercial or industrial).

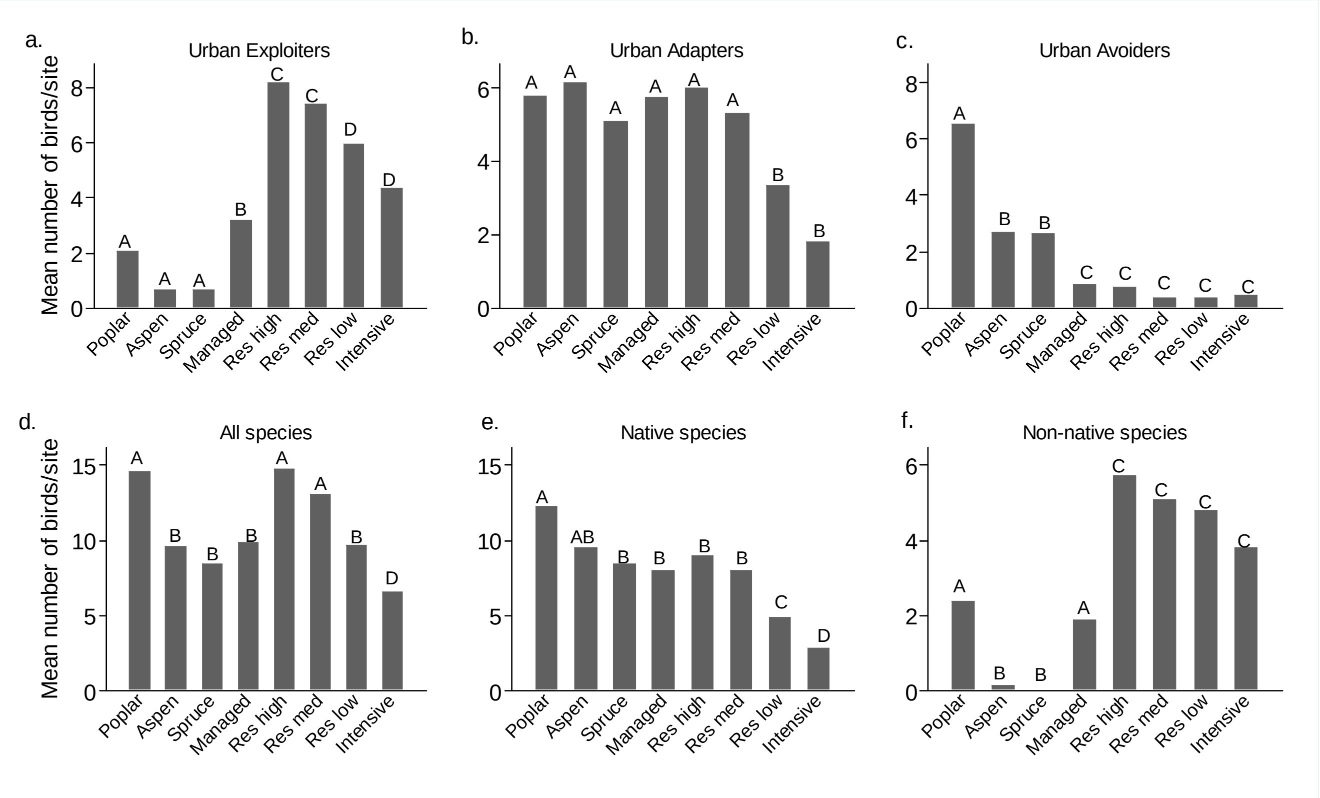


Figure 4-6. Avian abundance in relation to land cover type in the urban landscape of Calgary, Alberta, Canada. Exploiters, adapters, and avoiders defined as per Table 4-4. Letters above bars represent groups based on post-hoc comparisons using non-parametric Wilcoxon rank-sum tests. Land cover abbreviations as in Fig. 4-5.

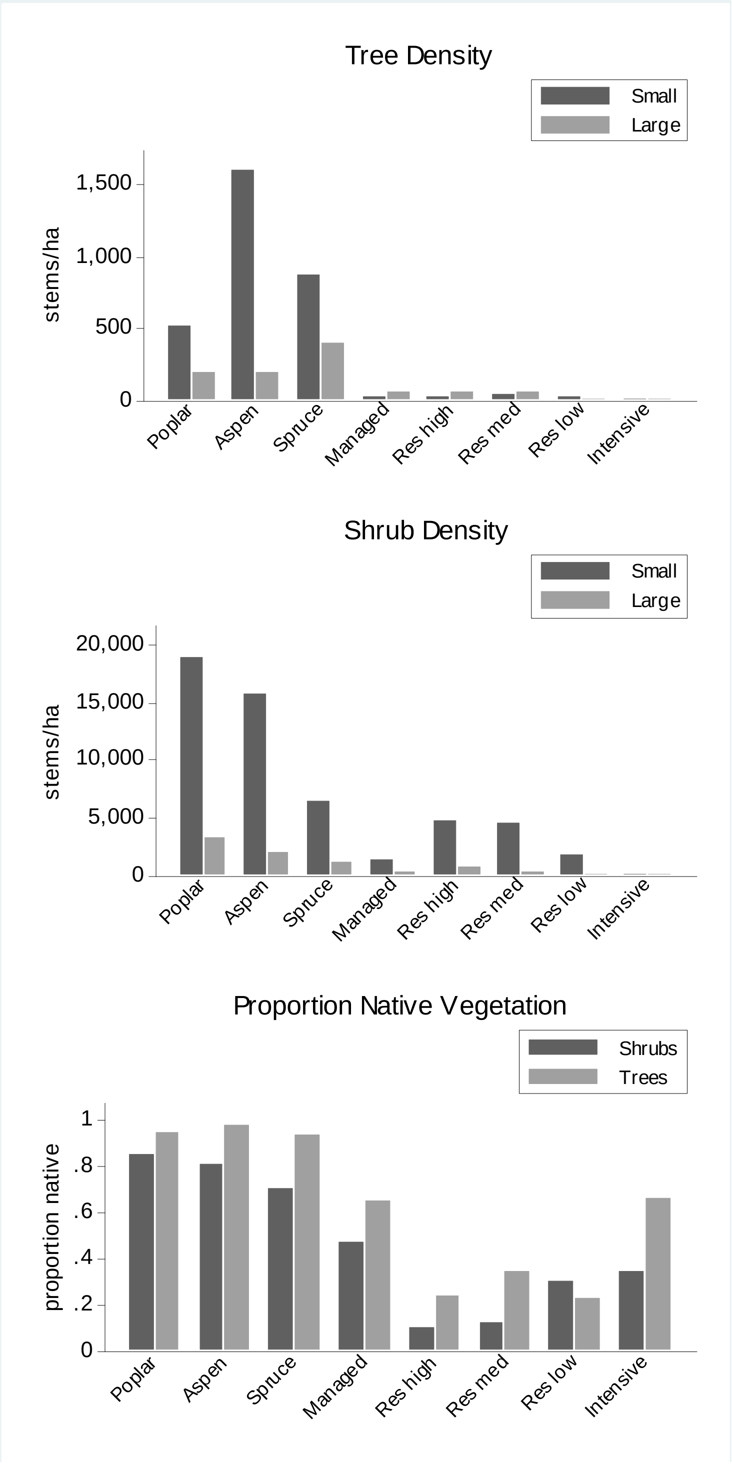


Figure 4-7. Comparison of vegetation characteristics among land cover types in Calgary, Alberta, Canada. Land cover abbreviations as in Fig. 4-5.

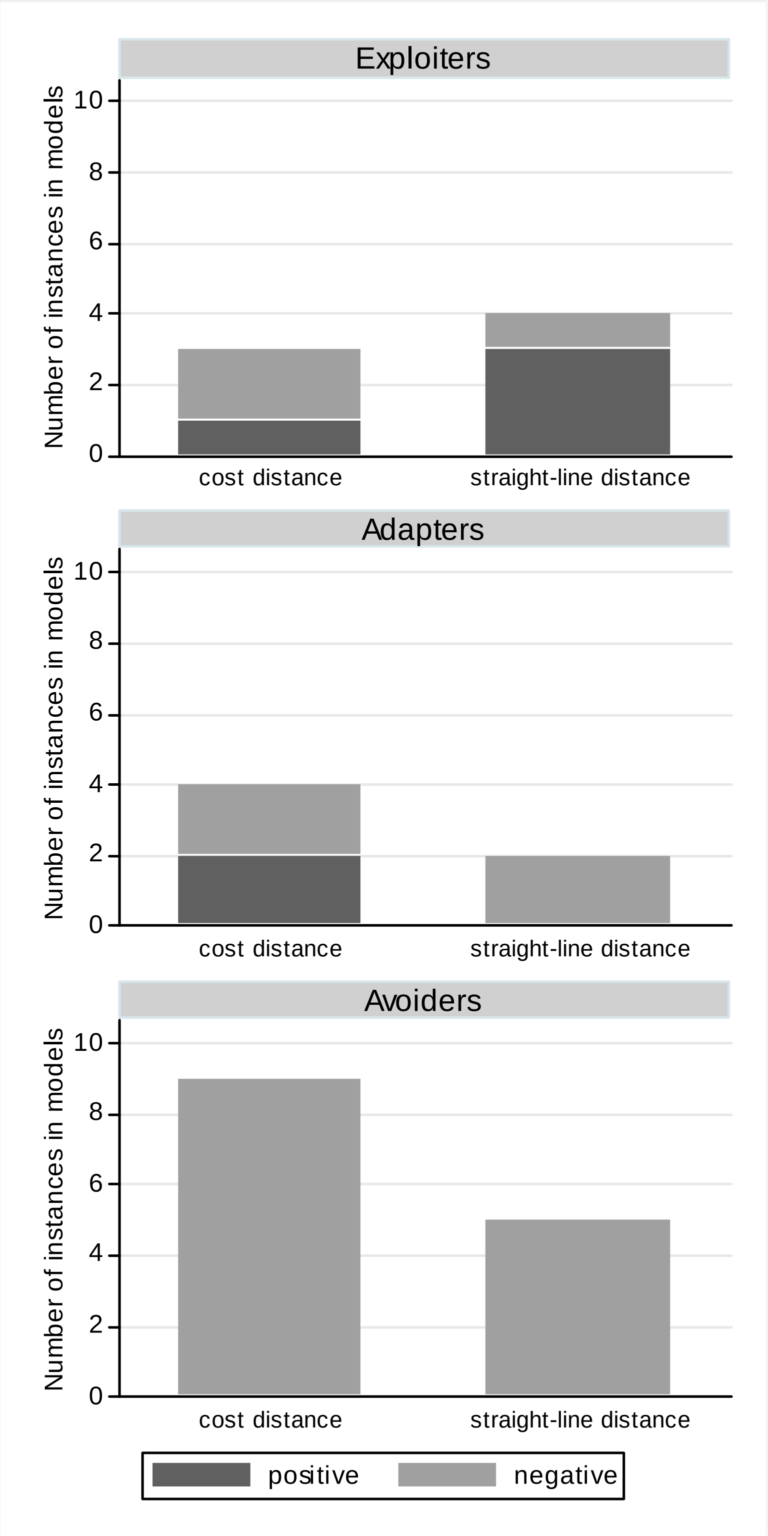


Figure 4-8. Frequency of cost distance versus straight-line distance variables included in models explaining the occurrence of individual focal species.

Appendix 4-1. Scientific names and characteristics of species detected during bird surveys conducted in Calgary, Alberta, Canada, 2005-2007.

Species	**Scientific name**	**Group**	**Origin**	**Residency**	**Nest location**[a]	**Nest Type**	**Diet**[a]
Focal species (detected at > 5% of sites)							
American crow	*Corvus brachyrhynchos*	exploit	native	summer	decid tree, shrub	cup	mixed
Black-billed magpie	*Pica pica*	exploit	native	year-round	decid tree, shrub	sphere	mixed
Blue jay	*Cyanocitta cristata*	exploit	native	year-round	conif tree	cup	mixed
Chipping sparrow	*Spizella passerina*	exploit	native	summer	conif tree, decid tree	cup	insects, seeds
Common grackle	*Quiscalus quiscula*	exploit	native	summer	decid tree, conif tree	cup, cavity	Mixed
House finch	*Carpodacus mexicanus*	exploit	non-native	year-round	decid tree, shrub, building	cup	seeds, fruit, buds, tree sap
House sparrow	*Passer domesticus*	exploit	non-native	year-round	building, tree	cavity	seeds, insects, fruit
Rock pigeon	*Columba livia*	exploit	non-native	year-round	building, cliff	saucer	seeds
American robin	*Turdus migratorius*	adapt	native	summer	decid tree, conif tree	cup	insects, fruit
Black-capped chickadee	*Poecile atricapillus*	adapt	native	year-round	decid tree, snag	cavity	insects, coniferous seeds, fruit
European starling	*Sturnus vulgaris*	adapt	non-native	summer	decid tree, building	cavity	insects, fruit, seeds
House wren	*Troglodytes aedon*	adapt	native	summer	decid tree, snag	cavity	insects, invertebrates
Red-breasted nuthatch	*Sitta canadensis*	adapt	native	year-round	conif tree	cavity	insects
Brown-headed cowbird	*Molothrus ater*	avoid	native	summer	decid trees, shrub, ground	parasite	insects, seeds
Cedar waxwing	*Bombycilla cedrorum*	avoid	native	summer	decid tree, conif tree	cup	berries, insects
Downy woodpecker	*Picoides pubescens*	avoid	native	year-round	snag	cavity	insects
Grey catbird	*Dumatella carolinensis*	avoid	native	summer	shrub	cup	insects, fruit
Least flycatcher	*Empidonax minimus*	avoid	native	summer	decid tree, shrub	cup	insects, berries
Northern flicker	*Colaptes auratus*	avoid	native	summer	snag	cavity	insects
Ruby-crowned kinglet	*Regalus calendula*	avoid	native	summer	conif tree	pendant	insects, tree sap, berries

Red-winged blackbird	*Agelaius phoeniceus*	avoid	native	summer	reeds	cup	insects, seeds
Song sparrow	*Melospiza melodia*	avoid	native	summer	ground, shrub	cup	insects, seeds
Tree swallow	*Tachycineta bicolor*	avoid	native	summer	snag	cavity	insects, berries
Warbling vireo	*Vireo gilvus*	avoid	native	summer	decid tree, shrub	cup	insects, fruit
Yellow warbler	*Dendroica petechia*	avoid	native	summer	shrub, tree	cup	insects
Non-focal species (detected at < 5% of sites)							
Barn swallow	*Hirundo rustica*	exploit	native	summer	building	cup	insects
Mourning dove	*Zenaida macroura*	adapt	native	summer	decid tree, conif tree, ground	saucer	seeds
Pine siskin	*Carduelis pinus*	adapt	native	year-round	conif tree, decid tree	saucer	seeds, insects
Common raven	*Corvus corax*	avoid	native	year-round	cliff, conif tree	cup	mixed
Common nighthawk	*Chordeiles minor*	avoid	native	summer	ground	no nest	insects
Belted kingfisher	*Ceryle alcyon*	avoid	native	summer	bank, snag	burrow	fish
Hairy woodpecker	*Picoides villosus*	avoid	native	year-round	decid tree, snag	cavity	insects
Western wood-peewee	*Contopus sordidulus*	avoid	native	summer	conif tree	cup	insects
Eastern kingbird	*Tyrannus tyrannus*	avoid	native	summer	decid tree, shrub	cup	insects, fruit
Red-eyed vireo	*Vireo olivaceus*	avoid	native	summer	shrub, decid tree	cup	insects, fruit
Northern rough-winged swallow	*Stelgidopteryx serripennis*	avoid	native	summer	bank, cliff, culvert	burrow, crevice	insects
White-breasted nuthatch	*Sitta carolinensis*	avoid	native	year-round	decid tree	cavity	insects
Golden-crowned kinglet	*Regalus calendula*	avoid	native	year-round	conif tree	pendant	insects, tree sap, fruit
Swainson's thrush	*Catharus ustulatus*	avoid	native	summer	shrub, conif tree	cup	insects, fruit
Hermit thrush	*Catharus guttatus*	avoid	native	summer	ground, tree	cup	insects, fruit
Tennessee warbler	*Vermivora peregrina*	avoid	native	summer	ground	cup	insects, fruit
Orange-crowned warbler	*Vermivora celata*	avoid	native	summer	ground	cup	insects, fruit, nectar, tree sap
Yellow-rumped warbler	*Dendroica coronata*	avoid	native	summer	conif tree	cup	insects, berries
Western tanager	*Piranga ludoviciana*	avoid	native	summer	conif tree	cup	insects, fruit
Clay-coloured sparrow	*Spizella pallida*	avoid	native	summer	shrub, ground	cup	insects, seeds
Savannah sparrow	*Passerculus sandwichensis*	avoid	native	summer	ground	cup	insects, seeds, snails

Lincoln's sparrow	*Melospiza lincolnii*	avoid	native	summer	ground	cup	insects, seeds
White-crowned sparrow	*Zonotrichia leucophrys*	avoid	native	summer	shrub, ground	cup	insects, seeds, berries
White-throated sparrow	*Zonotrichia albicollis*	avoid	native	summer	ground, shrub	cup	insects, seeds, fruit
Dark-eyed junco	*Junco hyemalis*	avoid	native	summer	ground, bank	cup	seeds, insects
Rose-breasted grosbeak	*Pheucticus ludovicianus*	avoid	native	summer	decid tree, shrub	cup	insects, seeds, fruit, buds
Yellow-headed blackbird	*Xanthocephalus xanthocephalus*	avoid	native	summer	reeds	cup	insects, seeds
Brewer's blackbird	*Euphagus cyanocephalus*	avoid	native	summer	conif tree, ground, shrub	cup	insects, seeds, fruit
Baltimore oriole	*Icterus galbula*	avoid	native	summer	decid tree	pendant	insects, fruit, nectar
American goldfinch	*Carduelis tristis*	avoid	native	summer	shrub	cup	seeds

* From Erhlich *et al.* (1988).

Appendix 4-2. Correlations among candidate predictor variables used in analyses (continuous variables only; numbers represent Pearson correlation coefficients; bold font indicates coefficients > |0.6|).

LOCAL SHRUB VARIABLES

	shrub_sm_ln	shrub_lg_ln	shrub_tot_ln	shrub_native_ln	shrub_nonnative_ln	shrub_conif_ln	shrub_dec_ln
shrub_sm_ln	1						
shrub_lg_ln	0.5955	1					
shrub_tot_ln	**0.9939**	**0.6623**	1				
shrub_native_ln	**0.6897**	**0.6008**	**0.6986**	1			
shrub_nonnative_ln	**0.7141**	0.3416	**0.7167**	0.1186	1		
shrub_conif_ln	-0.0082	-0.0341	0.0082	-0.0175	0.0109	1	
shrub_dec_ln	**0.7153**	**0.6153**	**0.7277**	**0.7370**	0.378	-0.0411	1
shrub_fruit_ln	**0.8872**	**0.6268**	**0.8926**	0.5885	**0.6566**	-0.1154	0.463

	shrub_fruit_ln
shrub_fruit_ln	1

LOCAL TREE VARIABLES

	can_hgt_ mean_sqrt	can_hgt_ max_sqrt	cancov_ 50_sqrt	tot_tree_ln	tree_lg_ln	tree_sm_ln	veg_struct_ hetero_sqrt
can_hgt__mean_sqrt	1						
can_hgt_max_sqrt	**0.9182**	1					
cancov_50_sqrt	**0.7201**	**0.6882**	1				
tot_tree_ln	0.4130	0.3920	**0.7880**	1			
tree_lg_ln	**0.6721**	**0.6097**	**0.8080**	**0.7344**	1		
tree_sm_ln	0.2361	0.2387	**0.6413**	**0.9603**	0.5587	1	
veg_struct_hetero_sqrt	0.2068	0.1946	0.3199	0.4212	0.3129	0.4139	1
tree_native_sqrt	0.3536	0.3385	**0.7324**	**0.9666**	**0.6789**	**0.9452**	0.4471
tree_nonnative_sqrt	0.0937	0.0856	-0.0294	-0.0665	-0.0047	-0.0831	-0.1552
tree_conif_sqrt	0.3369	0.2878	0.2477	0.3090	0.3982	0.2842	0.1829
tree_decid_sqrt	0.2680	0.2625	**0.6865**	**0.8852**	0.5506	**0.8659**	0.3450
tree_fruit_sqrt	-0.0999	-0.0509	-0.1971	-0.1246	-0.0663	-0.1227	-0.1151
tree_hetero_sqrt	-0.0039	-0.0260	-0.3628	-0.4278	-0.3143	-0.4133	-0.2036
tot_tree_snag_ln	0.1607	0.1411	0.5585	**0.8117**	0.4518	**0.8379**	0.3697
tree_snag_sm_ln	0.2731	0.2666	**0.6513**	**0.8449**	**0.6162**	**0.8242**	0.3707
tree_snag_lg_ln	0.2243	0.2064	**0.6425**	**0.8785**	0.5590	**0.8784**	0.3849

	tree_ native_sqrt	tree_ nonnative_sqrt	tree_ conif_sqrt	tree_ decid_sqrt	tree_ fruit_sqrt	tree_ hetero_sqrt	tot_tree_ snag_ln
tree_native_sqrt	1						
tree_nonnative_sqrt	-0.2566	1					
tree_conif_sqrt	0.2778	0.1256	1				
tree_decid_sqrt	**0.8918**	-0.1273	-0.0985	1			
tree_fruit_sqrt	-0.2650	0.4816	-0.0329	-0.2410	1		
tree_hetero_sqrt	-0.5034	0.5859	0.0950	-0.4253	0.4248	1	

tot_tree_snag_ln	**0.8344**	-0.1517	0.1268	0.7999	-0.1445	-0.3943	1
tree_snag_sm_ln	**0.8436**	-0.0993	0.1459	**0.8092**	-0.1916	-0.4747	**0.7835**
tree_snag_lg_ln	**0.8910**	-0.1544	0.1376	**0.8536**	-0.1815	-0.4665	**0.9625**

	tree_snag_ sm_ln	tree_snag_ lg_ln
tree_snag_sm_ln	1	
tree_snag_lg_ln	**0.9141**	1

LANDSCAPE FOREST COVER VARIABLES

	cancov_ 250_sqrt	cancov_ 500_sqrt	cancov_ 1000_sqrt	access_ cancov_ 250_sqrt	access_ cancov_ 500_sm_sqrt	access_ cancov_ 500_lg_sqrt	access_ cancov_ 1000_sqrt
cancov_250_sqrt	1						
cancov_500_sqrt	**0.9452**	1					
cancov_1000_sqrt	**0.8387**	**0.9420**	1				
access_cancov_250_sqrt	**0.9639**	**0.9097**	**0.7970**	1			
access_cancov_500_sm_sqrt	**0.8524**	**0.8975**	**0.8276**	**0.8846**	1		
access_cancov_500_lg_sqrt	**0.8814**	**0.9377**	**0.8943**	**0.8684**	**0.9533**	1	
access_cancov_1000_sqrt	**0.7155**	**0.8211**	**0.8892**	**0.7111**	**0.8195**	**0.8988**	1

ISOLATION VARIABLES

	dist_ dtown	dist_ water_ln	dist_ bow_sqrt	dist_ nat_sqrt	costdist_ water_ bcch_ln	costdist_ water_ ywar_ln	costdist_ bow_ bcch_sqrt
dist_dtown	1						
dist_water_ln	0.2595	1					
dist_bow_sqrt	0.3429	0.5003	1				
dist_nat_sqrt	-0.0666	**0.6652**	0.3542	1			
costdist_water_bcch_ln	0.2325	**0.9573**	0.4416	**0.6669**	1		
costdist_water_ywar_ln	0.2439	**0.9810**	0.4657	**0.6898**	**0.9747**	1	
costdist_bow_bcch_sqrt	0.3037	0.5221	**0.9745**	0.3693	0.4901	0.4910	1
costdist_bow_ywar_sqrt	0.3427	0.5098	**0.9934**	0.3514	0.4495	0.4796	**0.9769**
costdist_nat_bcch_sqrt	-0.0988	**0.6326**	0.2624	**0.9615**	**0.6589**	**0.6614**	0.3033
costdist_nat_ywar_sqrt	-0.0975	**0.6598**	0.3002	**0.9874**	**0.6651**	**0.6903**	0.3236

	costdist_ bow_ywar_ sqrt	costdist_ nat_bcch_ sqrt	costdist_ nat_ywar_ sqrt
costdist_bow_ywar_sqrt	1		
costdist_nat_bcch_sqrt	0.2675	1	
costdist_nat_ywar_sqrt	0.3070	**0.9804**	1

ALL VARIABLES

	shrub_sm_ln	shrub_lg_ln	shrub_tot_ln	shrub_native_ln	shrub_nonnative_ln	shrub_conif_ln	shrub_decid_ln
shrub_sm_ln	1						
shrub_lg_ln	0.5955	1					
shrub_tot_ln	**0.9939**	**0.6623**	1				
shrub_native_ln	**0.6897**	**0.6008**	**0.6986**	1			
shrub_nonnative_ln	**0.7141**	0.3416	**0.7167**	0.1186	1		
shrub_conif_ln	-0.0082	-0.0341	0.0082	-0.0175	0.0109	1	
shrub_dec_ln	**0.7153**	**0.6153**	**0.7277**	**0.7370**	0.3780	-0.0411	1
shrub_fruit_ln	**0.8872**	**0.6268**	**0.8926**	0.5885	**0.6566**	-0.1154	0.4630
can_hgt__mean_sqrt	0.5103	0.4465	0.5372	0.3255	0.4077	0.1071	0.3030
can_hgt_max_sqrt	0.4851	0.4601	0.5131	0.3165	0.3773	0.0703	0.3316
cancov_50_sqrt	**0.6637**	0.5715	**0.6848**	**0.6607**	0.3540	0.0173	0.5449
tot_tree_ln	**0.6186**	0.5279	**0.6312**	**0.7446**	0.2426	0.0434	0.5345
tree_lg_ln	0.5442	0.3885	0.5559	0.5779	0.2691	0.0680	0.4124
tree_sm_ln	0.5290	0.4743	0.5395	0.7015	0.1693	0.0488	0.4958
veg_struct_hetero_sqrt	-0.2455	0.3975	-0.1806	0.2118	-0.3778	0.0341	0.0479
tree_native_sqrt	0.5563	0.5030	0.5689	**0.7356**	0.1570	-0.0119	0.4963
tree_nonnative_sqrt	-0.0029	-0.1354	-0.0073	-0.2586	0.2943	0.1010	-0.0673
tree_conif_sqrt	0.0798	-0.0071	0.0887	0.0771	0.0640	0.4462	0.0378
tree_decid_sqrt	**0.6047**	0.5453	**0.6119**	**0.7268**	0.2333	-0.2205	0.5393
tree_fruit_sqrt	-0.0985	-0.1456	-0.1004	-0.2806	0.1708	0.1269	-0.1416
tree_hetero_sqrt	-0.2090	-0.2905	-0.2134	-0.5276	0.2424	0.1057	-0.2789
tot_tree_snag_ln	0.4450	0.3808	0.4520	**0.6183**	0.1160	-0.0976	0.3846
tree_snag_sm_ln	0.5197	0.5022	0.5326	**0.7146**	0.1324	-0.0688	0.4608
tree_snag_lg_ln	0.5198	0.4589	0.5291	**0.7123**	0.1356	-0.0934	0.4533
cancov_250_sqrt	**0.6043**	0.5140	**0.6327**	0.5024	0.4094	0.0662	0.4812
cancov_500_sqrt	0.5731	0.4782	**0.6003**	0.4474	0.3969	0.1241	0.4553
cancov_1000_sqrt	0.5495	0.4490	0.5746	0.3862	0.4285	0.0900	0.4261
access_cancov_250_sqrt	0.4927	0.4341	0.5214	0.3972	0.3451	0.0827	0.3902

access_cancov_500_sm_sqrt	0.3962	0.3658	0.4243	0.2727	0.3080	0.1657	0.2906
access_cancov_500_lg_sqrt	0.4757	0.4420	0.5047	0.3273	0.3779	0.1230	0.3593
access_cancov_1000_sqrt	0.3946	0.3703	0.4197	0.2214	0.3682	0.0818	0.2871
dist_dtown	-0.3973	-0.3468	-0.4092	-0.1547	-0.4181	0.2427	-0.2664
dist_water_ln	-0.5146	-0.4630	-0.5204	**-0.6944**	-0.0699	0.1083	-0.5231
dist_bow_sqrt	-0.2811	-0.2045	-0.2708	-0.2634	-0.0903	0.1848	-0.2510
dist_nat_sqrt	-0.4308	-0.2834	-0.4289	-0.5545	-0.0624	-0.0156	-0.4001
costdist_water_bcch_ln	-0.5019	-0.4443	-0.5093	**-0.6669**	-0.0887	0.1340	-0.5172
costdist_water_ywar_ln	-0.5138	-0.4424	-0.5179	**-0.7020**	-0.0706	0.1244	-0.5221
costdist_bow_bcch_sqrt	-0.2705	-0.2183	-0.2630	-0.2916	-0.0517	0.1912	-0.2622
costdist_bow_ywar_sqrt	-0.2651	-0.2054	-0.2547	-0.2775	-0.0498	0.1991	-0.2509
costdist_nat_bcch_sqrt	-0.3842	-0.2470	-0.3804	-0.5393	-0.0249	-0.0164	-0.3589
costdist_nat_ywar_sqrt	-0.3958	-0.2671	-0.3932	-0.5602	-0.0157	-0.0191	-0.3806

	shrub_fruit_ln	can_hgt_mean_sqrt	can_hgt_max_sqrt	cancov_50_sqrt	tot_tree_ln	tree_lg_ln	tree_sm_ln
shrub_fruit_ln	1						
can_hgt__mean_sqrt	0.5506	1					
can_hgt_max_sqrt	0.5187	**0.9125**	1				
cancov_50_sqrt	**0.6532**	**0.7181**	**0.6774**	1			
tot_tree_ln	**0.6133**	0.4206	0.3934	**0.7897**	1		
tree_lg_ln	0.5511	**0.6600**	0.5874	**0.8163**	**0.7812**	1	
tree_sm_ln	0.5210	0.2452	0.2439	**0.6479**	**0.9597**	**0.6130**	1
veg_struct_hetero_sqrt	-0.0877	0.1677	0.1694	0.3247	0.4325	0.3381	0.4322
tree_native_sqrt	0.5811	0.3597	0.3374	**0.7343**	**0.9665**	0.7332	0.9432
tree_nonnative_sqrt	-0.0774	0.0687	0.0726	-0.0709	-0.0993	-0.0808	-0.0998
tree_conif_sqrt	0.0601	0.3767	0.3161	0.2694	0.3501	0.3987	0.3367

tree_decid_sqrt	**0.6062**	0.2606	0.2529	**0.6890**	**0.8711**	**0.6003**	**0.8449**
tree_fruit_sqrt	-0.1137	-0.1225	-0.0542	-0.2457	-0.1581	-0.1205	-0.1463
tree_hetero_sqrt	-0.2373	-0.0369	-0.0448	-0.3864	-0.4408	-0.3876	-0.4120
tot_tree_snag_ln	0.4644	0.1664	0.1425	0.5642	**0.7974**	0.4922	**0.8213**
tree_snag_sm_ln	0.5419	0.2681	0.2604	**0.6714**	**0.8678**	**0.6263**	**0.8500**
tree_snag_lg_ln	0.5401	0.2306	0.2084	**0.6551**	**0.8759**	**0.5940**	**0.8734**
cancov_250_sqrt	0.5722	**0.6692**	**0.6409**	**0.8363**	**0.6178**	**0.6256**	0.4925
cancov_500_sqrt	0.5191	**0.6341**	**0.6257**	**0.7586**	0.5773	0.5789	0.4682
cancov_1000_sqrt	0.4838	0.5804	0.5807	**0.6889**	0.5293	0.5367	0.4332
access_cancov_250_sqrt	0.4670	0.6331	0.5950	**0.7626**	0.5313	0.5726	0.4077
access_cancov_500_sm_sqrt	0.3664	0.5159	0.5045	**0.6065**	0.4391	0.4627	0.3505
access_cancov_500_lg_sqrt	0.4286	0.5314	0.5347	**0.6509**	0.5120	0.4892	0.4261
access_cancov_1000_sqrt	0.3373	0.4375	0.4539	0.5298	0.4264	0.4111	0.3664
dist_dtown	-0.4095	-0.3901	-0.4566	-0.4034	-0.1419	-0.2102	-0.0501
dist_water_ln	-0.4904	-0.4234	-0.4106	**-0.6675**	**-0.6652**	**-0.6310**	-0.5884
dist_bow_sqrt	-0.2809	-0.2295	-0.2291	-0.2773	-0.1572	-0.1806	-0.0909
dist_nat_sqrt	-0.3839	-0.3002	-0.2610	-0.4762	-0.5681	-0.4767	-0.5215
costdist_water_bcch_ln	-0.4660	-0.3873	-0.3589	**-0.6300**	**-0.6235**	-0.5548	-0.5593
costdist_water_ywar_ln	-0.4916	-0.4001	-0.3767	**-0.6627**	**-0.6792**	**-0.6132**	**-0.6102**
costdist_bow_bcch_sqrt	-0.2582	-0.2126	-0.2021	-0.2911	-0.1682	-0.1802	-0.1056
costdist_bow_ywar_sqrt	-0.2679	-0.2026	-0.1965	-0.2736	-0.1695	-0.1774	-0.1081
costdist_nat_bcch_sqrt	-0.3338	-0.2450	-0.2078	-0.4235	-0.5237	-0.4363	-0.4838
costdist_nat_ywar_sqrt	-0.3517	-0.2615	-0.2190	-0.4547	-0.5600	-0.4666	-0.5176
	veg_struct_hetero_sqrt	tree_native_sqrt	tree_nonnative_sqrt	tree_conif_sqrt	tree_decid_sqrt	tree_fruit_sqrt	tree_hetero_sqrt

veg_struct_hetero_sqrt	1						
tree_native_sqrt	0.4633	1					
tree_nonnative_sqrt	-0.1964	-0.2805	1				
tree_conif_sqrt	0.2230	0.3267	0.0762	1			
tree_decid_sqrt	0.3302	**0.8739**	-0.1267	-0.0803	1		
tree_fruit_sqrt	-0.1025	-0.2842	0.4449	-0.0977	-0.2512	1	
tree_hetero_sqrt	-0.3162	-0.5054	0.5788	0.0508	-0.4112	0.4255	1
tot_tree_snag_ln	0.3868	**0.8206**	-0.1662	0.1525	**0.7812**	-0.1587	-0.3891
tree_snag_sm_ln	0.4059	**0.8693**	-0.1469	0.1496	**0.8379**	-0.2329	-0.5243
tree_snag_lg_ln	0.4066	**0.8894**	-0.1829	0.1559	**0.8497**	-0.2087	-0.4832
cancov_250_sqrt	0.2257	0.5653	-0.0037	0.2836	0.5181	-0.1074	-0.1776
cancov_500_sqrt	0.1777	0.5202	0.0354	0.3118	0.4650	-0.0458	-0.0979
cancov_1000_sqrt	0.1211	0.4717	0.0718	0.2796	0.4286	-0.0033	-0.0399
access_cancov_250_sqrt	0.2405	0.4834	0.0050	0.2903	0.4290	-0.0955	-0.1345
access_cancov_500_sm_sqrt	0.1939	0.3977	0.0308	0.3072	0.3303	0.0331	-0.0067
access_cancov_500_lg_sqrt	0.1953	0.4628	0.0355	0.2767	0.4186	0.0231	-0.0298
access_cancov_1000_sqrt	0.1393	0.3746	0.0865	0.2350	0.3477	0.0647	0.0500
dist_dtown	0.1033	-0.0957	-0.1342	0.2085	-0.2435	0.0096	0.0262
dist_water_ln	-0.2959	-0.6540	0.2407	-0.1418	**-0.6007**	0.2558	0.5392
dist_bow_sqrt	0.0343	-0.1333	-0.0535	0.1558	-0.2124	0.1803	0.2917
dist_nat_sqrt	-0.1878	-0.5710	0.2229	-0.2579	-0.4481	0.1061	0.3776
costdist_water_bcch_ln	-0.2470	**-0.6170**	0.2341	-0.0941	-0.5947	0.2581	0.4818
costdist_water_ywar_ln	-0.2888	**-0.6716**	0.2386	-0.1183	**-0.6338**	0.2528	0.5260
costdist_bow_bcch_sqrt	0.0151	-0.1502	-0.0299	0.1706	-0.2408	0.2220	0.3059
costdist_bow_ywar_sqrt	0.0089	-0.1485	-0.0415	0.1637	-0.2316	0.1983	0.3109
costdist_nat_bcch_sqrt	-0.1627	-0.5357	0.2585	-0.2534	-0.4143	0.1356	0.3497
costdist_nat_ywar_sqrt	-0.2051	-0.5692	0.2586	-0.2569	-0.4436	0.1255	0.3938

	tot_tree_snag_ln	tree_snag_sm_ln	tree_snag_lg_ln	cancov_250_sqrt	cancov_500_sqrt	cancov_1000_sqrt	access_cancov_250_sqrt
tot_tree_snag_ln	1						
tree_snag_sm_ln	**0.7933**	1					
tree_snag_lg_ln	**0.9602**	**0.9246**	1				
cancov_250_sqrt	0.4627	0.4871	0.5101	1			
cancov_500_sqrt	0.4053	0.4264	0.4430	**0.9427**	1		
cancov_1000_sqrt	0.3844	0.3772	0.4024	**0.8490**	**0.9492**	1	
access_cancov_250_sqrt	0.3946	0.4021	0.4327	**0.9562**	**0.9013**	**0.8022**	1
access_cancov_500_sm_sqrt	0.3295	0.3024	0.3416	**0.8402**	**0.8893**	**0.8313**	**0.8742**
access_cancov_500_lg_sqrt	0.3927	0.3649	0.4029	**0.8741**	**0.9360**	**0.9089**	**0.8531**
access_cancov_1000_sqrt	0.3522	0.2873	0.3376	**0.7176**	**0.8261**	**0.8982**	**0.7085**
dist_dtown	-0.1252	-0.1385	-0.1414	-0.4223	-0.3832	-0.4300	-0.3577
dist_water_ln	-0.4966	**-0.6219**	-0.5938	-0.4945	-0.4741	-0.4392	-0.3916
dist_bow_sqrt	-0.0635	-0.2300	-0.1568	-0.0905	0.0019	0.0417	-0.0474
dist_nat_sqrt	-0.4665	-0.4907	-0.5188	-0.4772	-0.4775	-0.4173	-0.4308
costdist_water_bcch_ln	-0.5143	-0.5887	-0.5900	-0.5010	-0.4834	-0.4520	-0.4049
costdist_water_ywar_ln	-0.5475	**-0.6424**	**-0.6356**	-0.5122	-0.4919	-0.4496	-0.4184
costdist_bow_bcch_sqrt	-0.0822	-0.2480	-0.1750	-0.1021	-0.0213	0.0175	-0.0611
costdist_bow_ywar_sqrt	-0.0843	-0.2477	-0.1778	-0.0889	0.0042	0.0483	-0.0473
costdist_nat_bcch_sqrt	-0.4509	-0.4614	-0.4950	-0.4466	-0.4489	-0.4004	-0.3969
costdist_nat_	-0.4711	-0.4937	-0.5225	-0.4636	-0.4618	-0.3989	-0.4176

ywar_sqrt

	access_cancov_500_sm_sqrt	access_cancov_500_lg_sqrt	access_cancov_1000_sqrt	dist_dtown	dist_water_ln	dist_bow_sqrt	dist_nat_sqrt
access_cancov_500_sm_sqrt	1						
access_cancov_500_lg_sqrt	**0.9442**	1					
access_cancov_1000_sqrt	**0.8171**	**0.9069**	1				
dist_dtown	-0.2461	-0.3606	-0.3751	1			
dist_water_ln	-0.2533	-0.3426	-0.2764	0.2437	1		
dist_bow_sqrt	0.1340	0.1366	0.2003	0.2786	0.4839	1	
dist_nat_sqrt	-0.3705	-0.3719	-0.2749	-0.0313	**0.7178**	0.3966	1
costdist_water_bcch_ln	-0.2846	-0.3697	-0.3049	0.2261	**0.9562**	0.4262	**0.7185**
costdist_water_ywar_ln	-0.2903	-0.3674	-0.2900	0.2248	**0.9818**	0.4501	**0.7400**
costdist_bow_bcch_sqrt	0.1032	0.1083	0.1657	0.2407	0.5040	**0.9756**	0.4083
costdist_bow_ywar_sqrt	0.1306	0.1351	0.2018	0.2746	0.5012	**0.9934**	0.4014
costdist_nat_bcch_sqrt	-0.3572	-0.3655	-0.2881	-0.0621	**0.6797**	0.2945	**0.9634**

costdist_nat_ ywar_sqrt	-0.3656	-0.3660	-0.2689	-0.0607	**0.7165**	0.3433	**0.9884**

	costdist_ water_ bcch_ln	costdist_ water_ ywar_ln	costdist_ bow_ bcch_sqrt	costdist_ bow_ ywar_sqrt	costdist_ nat_ bcch_sqrt	costdist_ nat_ ywar_sqrt
costdist_water_bcch_ln	1					
costdist_water_ywar_ln	**0.9769**	1				
costdist_bow_bcch_sqrt	0.4718	0.4756	1			
costdist_bow_ywar_sqrt	0.4438	0.4719	**0.9793**	1		
costdist_nat_bcch_sqrt	**0.7019**	**0.7067**	0.3265	0.3070	1	
costdist_nat_ywar_sqrt	**0.7219**	**0.7438**	0.3638	0.3567	**0.9833**	1

Appendix 4-3. Details of models presented in Table 4-5 describing local vegetation factors explaining composition of avian communities in Calgary, Alberta. All models were derived from linear regression except for the urban avoider model, which was derived using ordered probit regression for a categorical response variable.

TOTAL SPECIES RICHNESS - STRUCTURAL

regress total_pa_ln2 for_cov_tot_sqrt

Source	SS	df	MS	Number of obs	=	183
				F(1, 181)	=	104.43
Model	10.5740733	1	10.57407	Prob > F	=	0
Residual	18.3277939	181	0.101259	R-squared	=	0.3659
				Adj R-squared	=	0.3624
Total	28.9018671	182	0.158801	Root MSE	=	0.31821

total_pa_ln	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_50_sqrt	0.092	0.009	10.220	0.000	0.075	0.110
_cons	1.590	0.046	34.900	0.000	1.500	1.680

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-90.79519	-49.11808	2	102.2362	108.6551

TOTAL SPECIES RICHNESS - COMPOSITIONAL

regress total_pa_ln2 tot_tree_dec_dens_corr_sqrt tot_shrub_fruit_dens_corr_ln2

Source	SS	df	MS	Number of obs =	183	
				F(2, 180) =		42.71
Model	9.3009221	2	4.650461	Prob > F =		0
Residual	19.600945	180	0.108894	R-squared =		0.3218
				Adj R-squared =		0.3143
Total	28.9018671	182	0.158801	Root MSE		0.32999

=

total_pa_ln2	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
shrub_fruit_ln	0.111	0.017	6.650	0.000	0.078	0.144
tree_decid_sqrt	0.042	0.027	1.570	0.118	-0.011	0.096
_cons	1.667	0.043	38.680	0.000	1.582	1.752

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-90.79519	-55.26314	3	116.5263	126.1547

SHANNON-WEAVER HETEROGENEITY - STRUCTURAL

regress sw_hetero_bird sw_hetero_struct_sqrt for_cov_tot_sqrt

Source	SS	df	MS	Number of obs	=	183
				F(2, 180)	=	45.89
Model	13.6780507	2	6.839025	Prob > F	=	0
Residual	26.8264344	180	0.149036	R-squared	=	0.3377
				Adj R-squared	=	0.3303
Total	40.5044851	182	0.222552	Root MSE	=	0.38605

sw_hetero_~d	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_50_sqrt	0.109	0.012	9.430	0.000	0.086	0.132
veg_struct_hetero_sqrt	-0.173	0.120	-1.440	0.152	-0.410	0.064
_cons	1.232	0.094	13.170	0.000	1.047	1.416

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-121.677	-83.97675	3	173.9535	183.582

TOTAL ABUNDANCE - COMPOSITIONAL

```
regress total_abun tot_shrub_fruit_dens_corr_ln2
```

Source	SS	df	MS			
				Number of obs	=	183
				F(1, 181)	=	32.92
Model	650.828828	1	650.8288	Prob > F	=	0
Residual	3578.52363	181	19.77085	R-squared	=	0.1539
				Adj R-squared	=	0.1492
Total	4229.35246	182	23.2382	Root MSE	=	4.4464

total_abun	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
shrub_fruit_ln	1.070	0.187	5.740	0.000	0.702	1.438
_cons	8.624	0.580	14.860	0.000	7.478	9.769

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-547.0049	-531.7153	2	1067.431	1073.85

ABUNDANCE OF NATIVE BIRDS - STRUCTURAL

```
regress total_abun_native2_sqrt for_cov_tot_sqrt
```

Source	SS	df	MS			
				Number of obs	=	183
				F(1, 181)	=	120.35
Model	48.3602727	1	48.36027	Prob > F	=	0
Residual	72.7290022	181	0.401818	R-squared	=	0.3994
				Adj R-squared	=	0.3961
Total	121.089275	182	0.665326	Root MSE	=	0.63389

total~2_sqrt	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_50_	0.198	0.018	10.970	0.000	0.162	0.233

```
sqrt
_cons                 1.723        0.091       18.980            0.000        1.544        1.902


Model           Obs            ll(null)       ll(model)    df                 AIC          BIC

                                      -              -
.                     183      221.8801      175.2345                 2     354.469      360.888
```

ABUNDANCE OF NATIVE BIRDS - COMPOSITIONAL

```
regress total_abun_native2_sqrt tot_tree_dec_dens_corr_sqrt ///
                    tot_shrub_fruit_dens_corr_ln2

                                                        Number of
Source            SS               df           MS          obs           =                183
                                                        F( 2,   180)   =               36.6
Model             35.0067758            2     17.50339   Prob > F       =                  0
Residual          86.082499           180     0.478236   R-squared      =             0.2891
                                                        Adj R-
                                                        squared        =             0.2812
Total             121.089275          182     0.665326   Root MSE       =            0.69155


                                                                        [95%
total~2_sqrt      Coef.            Std. Err.    t              P>t             Conf.        Interval]

shrub_fruit_ln            0.196        0.035        5.590          0.000        0.127        0.265
tree_decid_sqrt           0.125        0.057        2.210          0.028        0.013        0.237
_cons                     1.965        0.090       21.760          0.000        1.787        2.143

Model             Obs              ll(null)       ll(model)      df                AIC           BIC

                                           -              -
.                         183      221.8801       190.6583                3     387.3166      396.945
```

ABUNDANCE OF NON-NATIVE BIRDS - STRUCTURAL

```
regress total_abun_nonnative_sqrt tot_tree_sm_dens_corr_ln2

Source                                          Number of obs
SS               df              MS             =                  183
                                                           F( 1,
                                                           181) =            62.45
                                                           Prob > F
Model            42.784546            1         42.78455   =                     0
```

Residual	123.99405	181	0.68505	R-squared =	0.2565
				Adj R-squared =	0.2524
Total	166.778597	182	0.916366	Root MSE =	0.82768

total~e_sqrt	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
tree_small_ln	-0.613	0.078	-7.900	0.000	-0.766	-0.460
_cons	2.119	0.077	27.680	0.000	1.968	2.270

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-251.1728	-224.0491	2	452.0983	458.5173

ABUNDANCE OF NON-NATIVE BIRDS - COMPOSITIONAL

regress total_abun_nonnative_sqrt tot_tree_native_dens_corr_sqrt

Source	SS	df	MS	Number of obs	=	183
				F(1, 181)	=	61.28
Model	42.1858043	1	42.1858	Prob > F	=	0
Residual	124.592792	181	0.688358	R-squared	=	0.2529
				Adj R-squared	=	0.2488
Total	166.778597	182	0.916366	Root MSE	=	0.82967

total~e_sqrt	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
tree_native_sqrt	-0.409	0.052	-7.830	0.000	-0.512	-0.306
_cons	2.138	0.078	27.250	0.000	1.983	2.293

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-251.1728	-224.4899	2	452.9798	459.3988

ABUNDANCE OF URBAN EXPLOITERS - STRUCTURAL

regress exploit_abun2_sqrt tot_shrub_sm_dens_corr_ln2 tot_tree_sm_dens_corr_ln2

```
                                                    Number of
Source          SS            df        MS          obs            =         183
                                                    F( 2,  180)    =       35.56
Model             48.50048         2    24.25024    Prob > F       =           0
Residual        122.754371       180    0.681969    R-squared      =      0.2832
                                                    Adj R-
                                                    squared        =      0.2752
Total           171.254851       182    0.940961    Root MSE       =     0.82581


                                                                   [95%
exploit_ab~t    Coef.         Std. Err.  t           P>t           Conf.      Interval]

tree_small_ln       -0.733       0.091     -8.020         0.000     -0.913      -0.553
shrub_small_
ln                   0.087       0.042      2.060         0.041      0.004       0.169
_cons                2.251       0.122     18.410         0.000      2.009       2.492


Model           Obs           ll(null)   ll(model)   df            AIC        BIC

                                     -           -
.                     183     253.5963    223.1297              3  452.2595   461.8879
```

ABUNDANCE OF URBAN EXPLOITERS - COMPOSITIONAL

regress exploit_abun2_sqrt tot_tree_native_dens_corr_sqrt

```
Source                                   Number of obs
SS              df            MS         =                  183
                                                     F(  1,
                                                     181) =          77.68
                                                     Prob > F
Model           51.4284796         1        51.42848 =                   0
                                                     R-squared
Residual        119.826372       181        0.662024 =              0.3003
                                                     Adj R-
                                                     squared =      0.2964
                                                     Root
Total           171.254851       182        0.940961 MSE      =     0.81365
```

exploit_ab~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
tree_native_sqrt	-0.451	0.051	-8.810	0.000	-0.553	-0.350
_cons	2.495	0.077	32.430	0.000	2.343	2.647

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-253.5963	-220.9208	2	445.8416	452.2605

ABUNDANCE OF URBAN ADAPTERS - STRUCTURAL

```
regress adapt_abun_sqrt for_cov_tot_sqrt
```

Source	SS	df	MS			
				Number of obs	=	183
				F(1, 181)	=	46.32
Model	19.6102867	1	19.61029	Prob > F	=	0
Residual	76.6277611	181	0.423358	R-squared	=	0.2038
				Adj R-squared	=	0.1994
Total	96.2380478	182	0.52878	Root MSE	=	0.65066

adapt_abun~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_50_sqrt	0.126	0.018	6.810	0.000	0.089	0.162
_cons	1.473	0.093	15.810	0.000	1.289	1.657

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-200.8622	-180.0126	2	364.0251	370.4441

ABUNDANCE OF URBAN ADAPTERS - COMPOSITIONAL

```
regress adapt_abun_sqrt
tot_shrub_fruit_dens_corr_ln2
```

Source	SS	df	MS	Number of obs	=	183
				F(1, 181)	=	29.86
Model	13.626567	1	13.62657	Prob > F	=	0
Residual	82.6114809	181	0.456417	R-squared	=	0.1416
				Adj R-squared	=	0.1368
Total	96.2380478	182	0.52878	Root MSE	=	0.67559

adapt_abun~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
shrub_fruit_ln	0.155	0.028	5.460	0.000	0.099	0.211
_cons	1.619	0.088	18.350	0.000	1.445	1.793

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-200.8622	-186.8924	2	377.7847	384.2037

ABUNDANCE OF URBAN AVOIDERS - STRUCTURAL

oprobit avoid_abun_cat3 tot_tree_dens_corr_ln2

Ordered probit	regression	Number of obs	=	183
		LR chi2(1)	=	64.47
		Prob > chi2	=	0
Log likelihood	-154.54839	Pseudo R2	=	0.1726

avoid_abu~t3	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_total_ln	0.9476	0.1267	7.4800	0.0000	0.6992	1.1960
/cut1	0.7861	0.1357			0.5202	1.0520
/cut2	1.5867	0.1642			1.2649	1.9085

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-186.7846	-154.5484	3	315.0968	324.7252

ABUNDANCE OF URBAN AVOIDERS - COMPOSITIONAL

```
oprobit avoid_abun_cat3 tot_shrub_native_dens_corr_ln2
```

Ordered probit	regression	Number of obs	=	183
		LR chi2(1)	=	72.88
		Prob > chi2	=	0
Log likelihood	-150.34234	Pseudo R2	=	0.1951

avoid_abu~t3	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	0.438	0.055	8.030	0.000	0.331	0.545
/cut1	0.772	0.132			0.514	1.031
/cut2	1.612	0.165			1.288	1.936

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-186.7846	-150.3423	3	306.6847	316.3131

NATIVE SPECIES RICHNESS - STRUCTURAL (DEVELOPED SITES ONLY)

```
regress total_pa_native2_sqrt tot_shrub_dens_corr_ln2 sw_hetero_struct_sqrt ///
                        tot_tree_lg_dens_corr_ln2 if developed ==1
```

Source	SS	df	MS	Number of obs	=	131
				F(3, 127)	=	26.25
Model	13.3557369	3	4.451912	Prob > F	=	0
Residual	21.5391044	127	0.169599	R-squared	=	0.3827
				Adj R-squared	=	0.3682
Total	34.8948412	130	0.268422	Root MSE	=	0.41182

total_pa_n~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]

tree_large_ln	0.963	0.223	4.320	0.000	0.522	1.405
shrub_total_ln	0.112	0.035	3.180	0.002	0.042	0.181
veg_struct_hetero_ sqrt	0.387	0.182	2.130	0.035	0.027	0.748
_cons	1.145	0.176	6.500	0.000	0.796	1.493

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	131	-99.23373	-67.63201	4	143.264	154.7648

NATIVE SPECIES RICHNESS - COMPOSITIONAL (DEVELOPED SITES ONLY)

```
regress total_pa_native2_sqrt tot_tree_nonnative_dens_corr_sq ///
                    tot_shrub_nonnat_dens_corr_ln2 if developed ==1
```

Source	SS	df	MS			
				Number of obs	=	131
				F(2, 128)	=	27.52
Model	10.4941323	2	5.247066	Prob > F	=	0
Residual	24.4007089	128	0.190631	R-squared	=	0.3007
				Adj R-squared	=	0.2898
Total	34.8948412	130	0.268422	Root MSE	=	0.43661

total_pa_n~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
shrub_nonnative _ln	0.117	0.030	3.950	0.000	0.058	0.175
tree_nonnative_ sqrt	0.486	0.162	3.010	0.003	0.166	0.806
_cons	1.387	0.091	15.190	0.000	1.206	1.567

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	131	-99.23373	-75.80262	3	157.6052	166.2308

ABUNDANCE OF NATIVE SPECIES - STRUCTUAL (DEVELOPED SITES ONLY)

```
regress total_abun_native3_sqrt for_cov_tot_sqrt if developed ==1
```

```
                                              Number of
Source         SS           df        MS      obs           =          131
                                              F(  1,   129) =         73.3
Model          28.8286959        1   28.8287  Prob > F      =            0
Residual        50.732079      129  0.393272  R-squared     =       0.3623
                                              Adj R-squared =       0.3574
Total          79.5607749      130  0.612006  Root MSE      =      0.62711


                                                            [95%
total~3_sqrt   Coef.        Std. Err.  t          P>t       Conf.     Interval]

cancov_50_
sqrt                0.272      0.032      8.560      0.000     0.209      0.334
_cons               1.512      0.112     13.490      0.000     1.290      1.733


Model          Obs          ll(null)   ll(model)  df        AIC       BIC

                                   -          -
.                     131   153.2177   123.7451          2  251.4902  257.2406
```

ABUNDANCE OF NATIVE SPECIES - COMPOSITIONAL (DEVELOPED SITES ONLY)

```
regress total_abun_native3_sqrt tot_tree_nonnative_dens_corr_sq ///
                       tot_shrub_nonnat_dens_corr_ln2 if developed
                       ==1
```

```
                                                   Number
Source              SS          df        MS       of obs     =          131
                                                   F(  2,
                                                   128)       =        27.22
Model               23.7433058        2  11.87165  Prob > F   =            0
Residual            55.8174691      128  0.436074  R-squared  =       0.2984
                                                   Adj R-
                                                   squared    =       0.2875
Total               79.5607749      130  0.612006  Root MSE   =      0.66036


                                                              [95%
total~3_sqrt        Coef.       Std. Err.  t        P>t       Conf.     Interval]
```

shrub_nonnative_ln	0.179	0.045	4.000	0.000	0.090	0.267
tree_nonnative_sqrt	0.711	0.245	2.910	0.004	0.227	1.195
_cons	1.487	0.138	10.780	0.000	1.214	1.761

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	131	-153.2177	-130.0022	3	266.0044	274.63

Appendix 4-4. Details of logistic regression models presented in Table 4-6 describing local vegetation factors explaining the presence or absence of individual focal species of songbirds in Calgary, Alberta.

AMERICAN CROW - STRUCTURAL

logit amcr_pa tot_shrub_dens_corr_ln2 tot_tree_sm_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	4.77
	Prob > chi2	=	0.0922
Log likelihood = -122.74865	Pseudo R2	=	0.0191

amcr_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_small_ln	-0.503	0.242	-2.070	0.038	-0.978	-0.028
shrub_total_ln	0.151	0.104	1.460	0.145	-0.052	0.354
_cons	-0.455	0.314	-1.450	0.147	-1.070	0.160

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-125.1329	-122.749	3	251.4973	261.1258

Area under ROC curve:	0.6128

AMERICAN CROW - COMPOSITIONAL

logit amcr_pa tot_shrub_native_dens_corr_ln2 tot_tree_nonnative_dens_corr_sq

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	10.74
	Prob > chi2	=	0.0046
Log likelihood = -119.76164	Pseudo R2	=	0.0429

amcr_pa	Coef.	Std. Err.	z	P>z	[95%	Interval]

					Conf.	
tree_nonnative_sqrt	0.968	0.404	2.390	0.017	0.175	1.760
shrub_native_ln	-0.156	0.088	-1.770	0.077	-0.329	0.017
_cons	-0.526	0.315	-1.670	0.095	-1.144	0.091

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-125.1329	-119.7616	3	245.5233	255.1517

Area under ROC curve:	0.6187

AMERICAN ROBIN - STRUCTURAL

logit amro_pa sw_hetero_struct_sqrt tot_shrub_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	11.1
	Prob > chi2	=	0.0039
Log likelihood = -55.465818	Pseudo R2	=	0.0909

amro_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_total_ln	0.425	0.148	2.870	0.004	0.135	0.715
veg_struct_hetero_sqrt	1.702	0.944	1.800	0.071	-0.148	3.552
_cons	-0.210	0.835	-0.250	0.802	-1.845	1.426

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-61.01353	-55.4658	3	116.9316	126.5601

Area under ROC curve:	0.6999

AMERICAN ROBIN - COMPOSITIONAL

logit amro_pa tot_shrub_coni_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	7.43
	Prob > chi2	=	0.0064
Log likelihood = -57.299072	Pseudo R2	=	0.0609

amro_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_conif_ln	1.923	0.977	1.970	0.049	0.007	3.839
_cons	1.746	0.269	6.480	0.000	1.218	2.273

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-61.01353	-57.29907	2	118.5981	125.0171

Area under ROC curve: 0.6648

BLACK-BILLED MAGPIE - STRUCTURAL

logit bbma_pa sw_hetero_struct_sqrt tot_tree_sm_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	7.32
	Prob > chi2	=	0.0258
Log likelihood = -120.54926	Pseudo R2	=	0.0295

bbma_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_total_ln	-0.553	0.216	-2.550	0.011	-0.977	-0.129

veg_struct_hetero_sqrt	1.167	0.673	1.730	0.083	-0.153	2.486
_cons	-0.208	0.489	-0.430	0.670	-1.166	0.750

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-124.2075	-120.549	3	247.0985	256.727

Area under ROC curve:	0.5987

BLACK-BILLED MAGPIE - COMPOSITIONAL

logit bbma_pa tot_shrub_native_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	7.87
	Prob > chi2	=	0.005
Log likelihood = -120.27353	Pseudo R2	=	0.0317

bbma_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	-0.2271305	0.0823459	-2.76	0.006	-0.388526	-0.0657355
_cons	0.7635613	0.2177295	3.51	0.000	0.3368194	1.190303

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-124.2075	-120.2735	2	244.5471	250.966

Area under ROC curve:	0.6249

BLACK-CAPPED CHICKADEE - STRUCTURAL

logit bcch_pa sw_hetero_struct_sqrt for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	70.86
	Prob > chi2	=	0
Log likelihood = -79.617268	Pseudo R2	=	0.308

bcch_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.727	0.115	6.340	0.000	0.502	0.952
veg_struct_hetero_sqrt	-1.870	0.854	-2.190	0.029	-3.544	-0.196
_cons	-0.488	0.663	-0.740	0.462	-1.787	0.812

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-115.0463	-79.6173	3	165.2345	174.863

Area under ROC curve:	0.858

BLACK-CAPPED CHICKADEE - COMPOSITIONAL

logit bcch_pa tot_tree_native_dens_corr_sqrt tot_shrub_fruit_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	38.7
	Prob > chi2	=	0
Log likelihood = -95.696392	Pseudo R2	=	0.1682

bcch_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_fruit_ln	0.517	0.127	4.060	0.000	0.267	0.767

tree_native_sqrt	0.385	0.281	1.370	0.171	-0.166	0.935
_cons	-0.682	0.289	-2.360	0.018	-1.249	-0.115

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-115.0463	-95.69639	3	197.3928	207.0212

Area under ROC curve:	0.7747

BROWN-HEADED COWBIRD - STRUCTURAL

logit bhco_pa tot_tree_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	13.83
	Prob > chi2	=	0.0002
Log likelihood = -66.061527	Pseudo R2	=	0.0947

bhco_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_total_ln	0.852	0.226	3.770	0.000	0.409	1.295
_cons	-2.745	0.364	-7.550	0.000	-3.458	-2.032

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-72.97406	-66.0615	2	136.1231	142.542

Area under ROC curve:	0.7137

BROWN-HEADED COWBIRD - COMPOSITIONAL

logit bhco_pa tot_shrub_native_dens_corr_ln2

Logistic	Number of	=	183

regression	obs		
	LR chi2(1)	=	24.72
	Prob > chi2	=	0
Log likelihood = -60.612934	Pseudo R2	=	0.1694

bhco_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	0.552	0.119	4.660	0.000	0.320	0.785
_cons	-3.235	0.444	-7.290	0.000	-4.105	-2.365

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-72.97406	-60.61293	2	125.2259	131.6448

Area under ROC curve:	0.7695

BLUE JAY - STRUCTURAL

logit blja_pa tot_shrub_sm_dens_corr_ln2 tot_tree_sm_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	5.38
	Prob > chi2	=	0.0679
Log likelihood = -49.19993	Pseudo R2	=	0.0518

blja_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_small_ln	0.364	0.199	1.830	0.067	-0.025	0.753
tree_small_ln	-1.057	0.623	-1.700	0.090	-2.278	0.164
_cons	-3.062	0.665	-4.600	0.000	-4.366	-1.758

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.88926	-49.1999	3	104.3999	114.0283

Area under ROC curve:	0.6698

BLUE JAY - COMPOSITIONAL

```
logit blja_pa sw_hetero_tree_sqrt
```

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	3.06
	Prob > chi2	=	0.0804
Log likelihood = -50.360561	Pseudo R2	=	0.0295

blja_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_hetero_sqrt	1.396	0.909	1.540	0.124	-0.385	3.177
_cons	-3.744	0.967	-3.870	0.000	-5.640	-1.848

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.88926	-50.36056	2	104.7211	111.1401

Area under ROC curve:	0.6444

CEDAR WAXWING - STRUCTURAL

```
logit cewx_pa tot_shrub_sm_dens_corr_ln2
```

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	17.71
	Prob > chi2	=	0
Log likelihood = -40.581639	Pseudo R2	=	0.1791

cewx_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_small_ln	0.923	0.273	3.390	0.001	0.389	1.457

```
_cons                     -6.059        1.260      -4.810       0.000       -8.528       -3.589

Model               Obs            ll(null)      ll(model)   df           AIC          BIC

                                        -
.                          183    49.43628    -40.5816            2    85.16328     91.58225

Area under ROC
curve:                    0.8149
```

CEDAR WAXWING - COMPOSITIONAL

```
logit cewx_pa tot_shrub_native_dens_corr_ln2

                      Number of
Logistic regression   obs            =              183
                      LR chi2(1)     =            15.58
                      Prob > chi2    =           0.0001
Log likelihood = -
41.646088             Pseudo R2      =           0.1576


                                                              [95%
cewx_pa               Coef.          Std. Err.    z           P>z       Conf.        Interval]

shrub_native_ln            0.555          0.150       3.690      0.000       0.260        0.850
_cons                     -3.991          0.613      -6.510      0.000      -5.192       -2.790


Model                 Obs            ll(null)     ll(model)   df          AIC          BIC

.                          183     -49.43628    -41.64609          2    87.29218     93.71115

Area under ROC
curve:                     0.7959
```

CHIPPING SPARROW - STRUCTURAL

```
logit chsp_pa
tot_tree_sm_dens_corr_ln2

                      Number of
Logistic regression   obs            =              183
                      LR chi2(1)     =            13.47
                      Prob > chi2    =           0.0002
```

```
Log likelihood = -
117.80433            Pseudo R2      =              0.0541


                                                            [95%
chsp_pa              Coef.          Std. Err.   z           P>z        Conf.        Interval]

tree_small_ln               -0.837       0.266      -3.150      0.002       -1.358       -0.316
_cons                        0.115       0.193       0.600      0.551       -0.263        0.493


Model                Obs            ll(null)    ll(model)   df         AIC          BIC

                                                -
.                              183    124.5384   -117.804          2    239.6087     246.0276

Area under ROC
curve:                      0.6097
```

CHIPPING SPARROW - COMPOSITIONAL

```
logit chsp_pa tot_shrub_native_dens_corr_ln2
sw_hetero_tree_sqrt

Logistic             Number of
regression           obs            =                183
                     LR chi2(2)     =              24.22
                     Prob > chi2    =                  0
Log likelihood =
-112.43036           Pseudo R2      =             0.0972


                                                            [95%
chsp_pa              Coef.          Std. Err.   z           P>z        Conf.        Interval]

tree_hetero_sqrt             1.544       0.500       3.090      0.002        0.565        2.524
shrub_native_ln             -0.189       0.105      -1.800      0.072       -0.396        0.017
_cons                       -1.408       0.573      -2.460      0.014       -2.531       -0.286

Model                Obs            ll(null)    ll(model)   df         AIC          BIC

                                           -           -
.                              183    124.5384    112.4304          3    230.8607     240.4892

Area under ROC
curve:                      0.6802
```

COMMON GRACKLE - STRUCTURAL

logit cogk_pa tot_tree_sm_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	1.17
	Prob > chi2	=	0.2801
Log likelihood = -53.686393	Pseudo R2	=	0.0107

cogk_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_small_ln	-0.434	0.449	-0.970	0.334	-1.315	0.446
_cons	-2.130	0.322	-6.610	0.000	-2.761	-1.498

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-54.26958	-53.6864	2	111.3728	117.7918

Area under ROC curve:	0.4789

COMMON GRACKLE - COMPOSITIONAL

logit cogk_pa tot_tree_fruit_dens_corr_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	7.89
	Prob > chi2	=	0.005
Log likelihood = -50.326676	Pseudo R2	=	0.0727

cogk_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_fruit_sqrt	2.239	0.787	2.850	0.004	0.697	3.780
_cons	-3.186	0.451	-7.060	0.000	-4.070	-2.302

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-54.26958	-50.32668	2	104.6534	111.0723

Area under ROC curve: 0.7071

DOWNY WOODPECKER - STRUCTURAL

logit dowo_pa sw_hetero_struct_sqrt for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	32.73
	Prob > chi2	=	0
Log likelihood = -35.522728	Pseudo R2	=	0.3154

dowo_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.958	0.249	3.840	0.000	0.469	1.446
veg_struct_hetero_sqrt	-3.532	1.600	-2.210	0.027	-6.668	-0.396
_cons	-5.569	1.310	-4.250	0.000	-8.136	-3.001

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.88926	-35.5227	3	77.04546	86.67392

Area under ROC curve: 0.8956

DOWNY WOODPECKER - COMPOSITIONAL

logit dowo_pa snag_tree_lg_dens_corr_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	20.47

	Prob > chi2	=	0
Log likelihood = -41.65493	Pseudo R2	=	0.1972

dowo_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_snag_large_sqrt	1.880	0.443	4.240	0.000	1.011	2.748
_cons	-3.265	0.413	-7.900	0.000	-4.074	-2.455

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.88926	-41.65493	2	87.30986	93.72883

Area under ROC curve:	0.7873

EUROPEAN STARLING - STRUCTURAL

logit eust_pa tot_tree_lg_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	4.12
	Prob > chi2	=	0.0423
Log likelihood = -113.71485	Pseudo R2	=	0.0178

eust_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_large_ln	0.679	0.335	2.030	0.043	0.022	1.335
_cons	-1.030	0.225	-4.570	0.000	-1.472	-0.589

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-115.7766	-113.715	2	231.4297	237.8487

Area under ROC curve:	0.5797

EUROPEAN STARLING - COMPOSITIONAL

logit eust_pa sw_hetero_tree_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	16.38
	Prob > chi2	=	0.0001
Log likelihood = -107.58867	Pseudo R2	=	0.0707

eust_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_hetero_sqrt	-1.517	0.386	-3.930	0.000	-2.274	-0.760
_cons	0.545	0.355	1.530	0.125	-0.151	1.242

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-115.7766	-107.5887	2	219.1773	225.5963

Area under ROC curve:	0.6735

GREY CATBIRD - STRUCTURAL

logit grca_pa tot_shrub_sm_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	28.48
	Prob > chi2	=	0
Log likelihood = -24.549258	Pseudo R2	=	0.3671

grca_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_small_ln	1.895	0.535	3.540	0.000	0.847	2.942
_cons	-11.195	2.747	-4.080	0.000	-16.578	-5.812

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-38.79067	-24.5493	2	53.09852	59.51749

Area under ROC curve:	0.9208

GREY CATBIRD - COMPOSITIONAL

logit grca_pa tot_shrub_native_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	35.6
	Prob > chi2	=	0
Log likelihood = -20.989362	Pseudo R2	=	0.4589

grca_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	1.436	0.428	3.350	0.001	0.596	2.276
_cons	-8.425	2.211	-3.810	0.000	-12.758	-4.091

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-38.79067	-20.98936	2	45.97872	52.3977

Area under ROC curve:	0.9538

HOUSE FINCH - STRUCTURAL

logit hofi_pa tot_shrub_lg_dens_corr_ln2 tot_tree_sm_dens_corr_ln2 sw_hetero_struct_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(3)	=	32.07
	Prob > chi2	=	0
Log likelihood = -94.094534	Pseudo R2	=	0.1456

hofi_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_small_ln	-2.689	0.757	-3.550	0.000	-4.174	-1.205
shrub_large_ln	0.452	0.179	2.530	0.011	0.102	0.802
veg_struct_hetero_sqrt	-0.182	0.758	-0.240	0.810	-1.667	1.303
_cons	-0.338	0.580	-0.580	0.560	-1.475	0.799

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-110.131	-94.0945	4	196.1891	209.027

Area under ROC curve:	0.7379

HOUSE FINCH - COMPOSITIONAL

```
logit hofi_pa tot_tree_native_dens_corr_sqrt
```

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	28.97
	Prob > chi2	=	0
Log likelihood = -95.648257	Pseudo R2	=	0.1315

hofi_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_native_sqrt	-1.553	0.467	-3.330	0.001	-2.468	-0.639
_cons	0.015	0.258	0.060	0.954	-0.490	0.520

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-110.131	-95.64826	2	195.2965	201.7155

Area under ROC curve:	0.6782

HOUSE SPARROW - STRUCTURAL

```
logit hosp_pa tot_tree_dens_corr_ln2

                       Number of
Logistic regression    obs            =           183
                       LR chi2(1)     =          53.8
                       Prob > chi2    =             0
Log likelihood = -
75.175123              Pseudo R2      =        0.2635


                                                           [95%
hosp_pa                Coef.      Std. Err.   z       P>z  Conf.     Interval]

tree_total_ln           -1.610      0.261   -6.170  0.000   -2.121    -1.099
_cons                    2.715      0.335    8.090  0.000    2.057     3.372



Model                  Obs        ll(null)  ll(model)  df    AIC       BIC

                                         -
.                          183  102.0751   -75.1751     2  154.3502  160.7692

Area under ROC
curve:                  0.7856
```

HOUSE SPARROW - COMPOSITIONAL

```
logit hosp_pa tot_tree_native_dens_corr_sqrt

                      Number of
Logistic regression   obs            =           183
                      LR chi2(1)     =         63.46
                      Prob > chi2    =             0
Log likelihood = -
70.345614             Pseudo R2      =        0.3108


                                                          [95%
hosp_pa               Coef.      Std. Err.   z       P>z  Conf.     Interval]

tree_native_sqrt       -1.301      0.211   -6.150  0.000   -1.715    -0.887
_cons                   2.559      0.311    8.220  0.000    1.949     3.169
```

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-102.0751	-70.34561	2	144.6912	151.1102

Area under ROC curve:	0.8539

HOUSE WREN - STRUCTURAL

```
logit howr_pa sw_hetero_struct_sqrt tot_shrub_sm_dens_corr_ln2
```

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	18.76
	Prob > chi2	=	0.0001
Log likelihood = -85.425605	Pseudo R2	=	0.0989

howr_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_small_ln	0.496	0.130	3.810	0.000	0.241	0.751
veg_struct_hetero_sqrt	1.350	0.800	1.690	0.091	-0.218	2.917
_cons	-4.000	0.859	-4.660	0.000	-5.683	-2.318

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-94.80395	-85.4256	3	176.8512	186.4797

Area under ROC curve:	0.7057

HOUSE WREN - COMPOSITIONAL

```
logit howr_pa snag_tree_lg_dens_corr_sqrt tot_shrub_fruit_dens_corr_ln2
```

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	23.18
	Prob > chi2	=	0
Log likelihood = -83.213387	Pseudo R2	=	0.1223

howr_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_fruit_ln	0.333	0.140	2.380	0.017	0.059	0.608
tree_snag_large_sqrt	0.791	0.405	1.950	0.051	-0.002	1.585
_cons	-2.530	0.442	-5.720	0.000	-3.397	-1.664

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-94.80395	-83.21339	3	172.4268	182.0552

Area under ROC curve:	0.7275

LEAST FLYCATCHER - STRUCTURAL

logit lefl_pa sw_hetero_struct_sqrt for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	52.68
	Prob > chi2	=	0
Log likelihood = -27.931343	Pseudo R2	=	0.4853

lefl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	1.628	0.421	3.870	0.000	0.803	2.454
veg_struct_hetero_sqrt	-5.379	2.154	-2.500	0.013	-9.601	-1.157
_cons	-9.049	2.201	-4.110	0.000	-13.363	-4.735

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-54.26958	-27.9313	3	61.86269	71.49114

Area under ROC curve:	0.9528

LEAST FLYCATCHER - COMPOSITIONAL

logit lefl_pa tot_shrub_native_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	48.51
	Prob > chi2	=	0
Log likelihood = -30.013416	Pseudo R2	=	0.447

lefl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	1.196	0.263	4.550	0.000	0.682	1.711
_cons	-6.491	1.257	-5.160	0.000	-8.954	-4.027

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-54.26958	-30.01342	2	64.02683	70.4458

Area under ROC curve:	0.939

NORTHERN FLICKER - STRUCTURAL

logit nofl_pa for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	21.82
	Prob > chi2	=	0
Log likelihood = -63.883511	Pseudo R2	=	0.1459

nofl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.402	0.094	4.260	0.000	0.217	0.587
_cons	-3.908	0.617	-6.330	0.000	-5.118	-2.698

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-74.79486	-63.8835	2	131.767	138.186

Area under ROC curve:	0.7805

NORTHERN FLICKER - COMPOSITIONAL

logit nofl_pa tot_shrub_fruit_dens_corr_ln2 sw_hetero_tree_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	20.5
	Prob > chi2	=	0
Log likelihood = -64.546704	Pseudo R2	=	0.137

nofl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_hetero_sqrt	-1.517	0.484	-3.130	0.002	-2.467	-0.568
shrub_fruit_ln	0.310	0.131	2.360	0.018	0.052	0.568
_cons	-1.570	0.629	-2.500	0.013	-2.803	-0.338

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-74.79486	-64.5467	3	135.0934	144.7219

Area under ROC curve:	0.7501

RED-BREASTED NUTHATCH - STRUCTURAL

logit rbnu_pa tot_shrub_dens_corr_ln2 canhgt_wgtmn_n_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	23.77
	Prob > chi2	=	0

```
Log likelihood = -
100.82139             Pseudo R2     =          0.1054


                                                                  [95%
rbnu_pa               Coef.         Std. Err.   z          P>z     Conf.      Interval]

max_canopy_hgt_sqrt         0.899       0.257      3.500    0.000      0.396       1.403
shrub_total_ln              0.160       0.113      1.410    0.159     -0.063       0.382
_cons                      -4.344       0.865     -5.020    0.000     -6.039      -2.649


Model                 Obs           ll(null)    ll(model)  df      AIC        BIC

                                           -
.                             183   112.7045    -100.821        3  207.6428   217.2712

Area under ROC
curve:                     0.7212
```

RED-BREASTED NUTHATCH - COMPOSITIONAL

```
logit rbnu_pa tot_shrub_nonnat_dens_corr_ln2 tot_tree_coni_dens_corr_sqrt
```

```
                      Number of
Logistic regression   obs           =             183
                      LR chi2(2)    =           29.68
                      Prob > chi2   =               0
Log likelihood = -
97.866955             Pseudo R2     =          0.1317


                                                                  [95%
rbnu_pa               Coef.         Std. Err.   z          P>z     Conf.      Interval]

shrub_nonnative_ln          0.400       0.125      3.210    0.001      0.156       0.645
tree_conif_sqrt             1.178       0.382      3.080    0.002      0.428       1.927
_cons                      -2.433       0.424     -5.740    0.000     -3.263      -1.603


Model                 Obs           ll(null)    ll(model)  df      AIC        BIC

                                           -           -
.                             183   112.7045    97.86696        3  201.7339   211.3624


Area under ROC
curve:                     0.7262
```

ROCK PIGEON - STRUCTURAL

```
logit ropi_pa for_cov_tot_sqrt

                      Number of
Logistic regression   obs            =          183
                      LR chi2(1)     =          7.7
                      Prob > chi2    =       0.0055
Log likelihood =  -
72.72226              Pseudo R2      =       0.0503


                                                            [95%
ropi_pa               Coef.        Std. Err.   z         P>z      Conf.       Interval]

cancov_50_sqrt            -0.244       0.094    -2.590    0.010      -0.429       -0.059
_cons                     -0.835       0.374    -2.230    0.026      -1.568       -0.101


Model                 Obs          ll(null)    ll(model)  df       AIC         BIC

                                           -
.                            183   76.57083    -72.7223        2  149.4445    155.8635

Area under ROC
curve:                    0.6586
```

ROCK PIGEON - COMPOSITIONAL

```
logit ropi_pa snag_tree_tot_dens_corr_sqrt

                     Number of
Logistic regression  obs            =          183
                     LR chi2(1)     =         8.15
                     Prob > chi2    =       0.0043
Log likelihood = -
72.495961            Pseudo R2      =       0.0532


                                                           [95%
ropi_pa              Coef.        Std. Err.   z         P>z      Conf.       Interval]

tree_snag_total_sqrt     -1.457       0.768    -1.900    0.058      -2.962        0.048
_cons                    -1.488       0.220    -6.770    0.000      -1.918       -1.057
```

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-76.57083	-72.49596	2	148.9919	155.4109

Area under ROC curve:	0.5978

RUBY-CROWNED KINGLET - STRUCTURAL

logit rcki_pa can_hgt_max_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	7.06
	Prob > chi2	=	0.0079
Log likelihood = -40.762183	Pseudo R2	=	0.0797

rcki_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
max_can_hgt_sqrt	0.871	0.347	2.510	0.012	0.191	1.550
_cons	-6.356	1.608	-3.950	0.000	-9.507	-3.205

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-44.29262	-40.7622	2	85.52437	91.94334

Area under ROC curve:	0.7317

RUBY-CROWNED KINGLET - COMPOSITIONAL

logit rcki_pa tot_shrub_coni_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	18.75
	Prob > chi2	=	0
Log likelihood = -34.919851	Pseudo R2	=	0.2116

rcki_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_conif_ln	1.452	0.362	4.010	0.000	0.743	2.161
_cons	-3.702	0.485	-7.630	0.000	-4.653	-2.751

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-44.29262	-34.91985	2	73.8397	80.25867

Area under ROC curve:	0.806

RED-WINGED BLACKBIRD - STRUCTURAL

logit rwbl_pa sw_hetero_struct_sqrt for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	16.95
	Prob > chi2	=	0.0002
Log likelihood = -33.117357	Pseudo R2	=	0.2037

rwbl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.672	0.214	3.140	0.002	0.253	1.092
veg_struct_hetero_qrt	-2.271	1.596	-1.420	0.155	-5.399	0.856
_cons	-4.929	1.253	-3.930	0.000	-7.384	-2.473

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-41.59007	-33.1174	3	72.23471	81.86317

Area under ROC curve:	0.8399

RED-WINGED BLACKBIRD - COMPOSITIONAL

logit rwbl_pa tot_shrub_native_dens_corr_ln2 tot_tree_coni_dens_corr_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	24.97
	Prob > chi2	=	0
Log likelihood = -29.103217	Pseudo R2	=	0.3002

rwbl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_conif_sqrt	-5.503	2.625	-2.100	0.036	-10.648	-0.359
shrub_native_ln	0.358	0.179	2.000	0.045	0.008	0.708
_cons	-2.686	0.814	-3.300	0.001	-4.281	-1.091

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-41.59007	-29.10322	3	64.20643	73.83489

Area under ROC curve:	0.8776

SONG SPARROW - STRUCTURAL

logit sosp_pa sw_hetero_struct_sqrt for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	23.99
	Prob > chi2	=	0
Log likelihood = -29.595051	Pseudo R2	=	0.2884

sosp_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.906	0.275	3.290	0.001	0.366	1.445
veg_struct_hetero_sqrt	-2.726	1.794	-1.520	0.129	-6.242	0.790

_cons	-6.261	1.577	-3.970	0.000	-9.351	-3.170

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-41.59007	-29.5951	3	65.1901	74.81856

Area under ROC curve:	0.8842

SONG SPARROW - COMPOSITIONAL

logit sosp_pa sw_hetero_tree_sqrt tot_shrub_native_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	28.84
	Prob > chi2	=	0
Log likelihood = -27.169038	Pseudo R2	=	0.3467

sosp_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	0.659	0.250	2.640	0.008	0.170	1.149
tree_hetero_sqrt	-1.663	0.951	-1.750	0.080	-3.528	0.201
_cons	-3.889	1.349	-2.880	0.004	-6.533	-1.245

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-41.59007	-27.16904	3	60.33808	69.96654

Area under ROC curve:	0.9228

TREE SWALLOW - STRUCTURAL

logit tesw_pa tot_tree_lg_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	6.42

	Prob > chi2	=	0.0113
Log likelihood = -43.695411	Pseudo R2	=	0.0684

tesw_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_large_ln	1.311	0.494	2.660	0.008	0.343	2.279
_cons	-3.330	0.465	-7.160	0.000	-4.241	-2.418

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-46.90589	-43.6954	2	91.39082	97.80979

Area under ROC curve:	0.6774

TREE SWALLOW - COMPOSITIONAL

logit tesw_pa tot_shrub_native_dens_corr_ln2 sw_hetero_tree_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	26.49
	Prob > chi2	=	0
Log likelihood = -33.660862	Pseudo R2	=	0.2824

tesw_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_hetero_sqrt	-2.445	0.807	-3.030	0.002	-4.026	-0.864
shrub_native_ln	0.316	0.166	1.900	0.057	-0.010	0.642
_cons	-1.971	0.828	-2.380	0.017	-3.594	-0.347

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-46.90589	-33.66086	3	73.32172	82.95018

Area under ROC curve:	0.8462

WARBLING VIREO - STRUCTURAL

logit wavi_pa for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	21.73
	Prob > chi2	=	0
Log likelihood = -41.024418	Pseudo R2	=	0.2094

wavi_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.543	0.139	3.910	0.000	0.271	0.815
_cons	-5.550	1.010	-5.490	0.000	-7.529	-3.570

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.88926	-41.0244	2	86.04884	92.46781

Area under ROC curve:	0.8246

WARBLING VIREO - COMPOSITIONAL

logit wavi_pa tot_shrub_native_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	17.99
	Prob > chi2	=	0
Log likelihood = -42.892848	Pseudo R2	=	0.1734

wavi_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	0.583	0.149	3.920	0.000	0.291	0.874
_cons	-4.006	0.609	-6.570	0.000	-5.200	-2.811

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.88926	-42.89285	2	89.7857	96.20467

Area under ROC curve:	0.7954

YELLOW WARBLER - STRUCTURAL

logit yewb_pa for_cov_tot_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	61.32
	Prob > chi2	=	0
Log likelihood = -61.463608	Pseudo R2	=	0.3328

yewb_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.682	0.111	6.140	0.000	0.464	0.900
_cons	-5.098	0.735	-6.940	0.000	-6.538	-3.659

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-92.12544	-61.4636	2	126.9272	133.3462

Area under ROC curve:	0.8691

YELLOW WARBLER - COMPOSITIONAL

logit yewb_pa tot_shrub_native_dens_corr_ln2

Logistic regression	Number of obs	=	183
	LR chi2(1)	=	100.25
	Prob > chi2	=	0
Log likelihood =	Pseudo R2	=	0.5441

-41.999679

yewb_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_native_ln	1.294	0.195	6.640	0.000	0.912	1.677
_cons	-4.976	0.715	-6.960	0.000	-6.377	-3.575

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-92.12544	-41.99968	2	87.99936	94.41833

Area under ROC curve:	0.9354

Appendix 4-5. Details of models presented in Table 4-7 describing local and landscape-level factors explaining the composition of avian communities in Calgary, Alberta. All models were derived from linear regression except for the urban avoider model, which was derived using ordered probit regression for a categorical response variable.

TOTAL SPECIES RICHNESS

regress total_pa_ln2 dist_bow_sqrt for_cov_tot_sqrt

Source	SS	df	MS	Number of obs	=	183
				F(2, 180)	=	62.29
Model	11.8219	2	5.91096	Prob > F	=	0
Residual	17.0799	180	0.09489	R-squared	=	0.409
				Adj R-squared	=	0.4025
Total	28.9019	182	0.1588	Root MSE	=	0.30804

total_pa_ln2	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
dist_bow_sqrt	-0.003	0.001	-3.630	0.000	-0.005	-0.002
cancov_50_sqrt	0.083	0.009	9.000	0.000	0.064	0.101
_cons	1.792	0.071	25.200	0.000	1.652	1.933

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-90.795	-42.666	3	91.3321	100.9606

SHANNON-WEAVER HETEROGENEITY

regress sw_hetero_bird dist_bow_sqrt for_cov_tot_sqrt

Source	SS	df	MS	Number of obs	=	183
				F(2, 180)	=	53.58
Model	15.1152	2	7.55759	Prob > F	=	0
Residual	25.3893	180	0.14105	R-squared	=	0.3732
				Adj R-squared	=	0.3662
Total	40.5045	182	0.22255	Root MSE	=	0.37557

sw_hetero_~d	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_50_sqrt	0.092	0.011	8.250	0.000	0.070	0.114
dist_bow_sqrt	-0.004	0.001	-3.520	0.001	-0.006	-0.002
_cons	1.362	0.087	15.710	0.000	1.191	1.534

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-121.68	-78.939	3	163.878	173.506

TOTAL ABUNDANCE

```
regress total_abun tot_tree_dec_dens_corr_sqrt tot_shrub_dens_corr_ln2 dist_bow_sqrt ///
                          canhgt_wgtmn_n_sqrt
```

Source	SS	df	MS	Number of obs	=	183
				F(4, 178)	=	16.7
Model	1154.27	4	288.568	Prob > F	=	0
Residual	3075.08	178	17.2757	R-squared	=	0.2729
				Adj R-squared	=	0.2566
Total	4229.35	182	23.2382	Root MSE	=	4.1564

total_abun	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
shrub_total_ln	1.050	0.232	4.520	0.000	0.591	1.508
dist_bow_sqrt	-0.039	0.012	-3.110	0.002	-0.063	-0.014
mean_can_hgt_sqrt	1.220	0.441	2.770	0.006	0.350	2.090
tree_dec_sqrt	-0.707	0.342	-2.070	0.040	-1.382	-0.033
_cons	6.646	1.547	4.300	0.000	3.594	9.699

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-547	-517.84	5	1045.68	1061.732

ABUNDANCE OF NATIVE BIRDS

```
regress total_abun_native2_sqrt dist_dtown forcov_wgt_mn250_sqrt dist_hydro_ln2 ///
                          tot_shrub_fruit_dens_corr_ln2 dist_bow_sqrt
```

Source	SS	df	MS	Number of obs	=	183
				F(5, 177)	=	36.8
Model	61.7146	5	12.3429	Prob > F	=	0
Residual	59.3747	177	0.33545	R-squared	=	0.5097
				Adj R-squared	=	0.4958
Total	121.089	182	0.66533	Root MSE	=	0.57918

total~2_sqrt	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_250_sqrt	0.245	0.034	7.140	0.000	0.177	0.313
shrub_fruit_ln	0.081	0.031	2.660	0.009	0.021	0.141
dist_bow_sqrt	-0.005	0.002	-2.560	0.011	-0.009	-0.001
dist_dtown	0.00003	0.000	2.500	0.013	0.000	0.000
dist_water_sqrt	-0.082	0.040	-2.030	0.043	-0.162	-0.002
_cons	1.970	0.327	6.020	0.000	1.325	2.615

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-221.88	-156.67	6	325.343	344.6004

ABUNDANCE OF NON-NATIVE BIRDS

```
regress total_abun_nonnative_sqrt  forcov_wgt_mn500_sqrt tot_tree_sm_dens_corr_ln2 ///
                          dist_nat_sqrt tot_shrub_sm_dens_corr_ln2 cd_bcchpb2_b_10_sqrt
                          sw_hetero_struct_sqrt
```

Source	SS	df	MS	Number of obs	=	183
				F(6, 176)	=	20.77
Model	69.1344	6	11.5224	Prob > F	=	0
Residual	97.6442	176	0.5548	R-squared	=	0.4145
				Adj R-squared	=	0.3946
Total	166.779	182	0.91637	Root MSE	=	0.74485

total~e_sqrt	Coef.	Std.	t	P>t	[95%	Interval]

		Err.			Conf.	
tree_small_ln	-0.726	0.106	-6.840	0.000	-0.936	-0.517
dist_nat_sqrt	0.012	0.003	4.190	0.000	0.007	0.018
shrub_small_ln	0.231	0.050	4.590	0.000	0.132	0.331
veg_hetero_struct_sqrt	0.680	0.283	2.400	0.017	0.122	1.238
costdist_bow_bcch_sqrt	-0.004	0.002	-2.380	0.018	-0.007	-0.001
cancov_500_sqrt	-0.103	0.053	-1.950	0.052	-0.207	0.001
_cons	1.155	0.320	3.610	0.000	0.524	1.785

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-251.17	-202.19	7	418.379	440.8453

ABUNDANCE OF URBAN EXPLOITERS

```
regress exploit_abun2_sqrt dist_bow_sqrt tot_tree_native_dens_corr_sqrt ///
                           dist_nat_sqrt tot_shrub_sm_dens_corr_ln2 sw_hetero_struct_sqrt
```

Source	SS	df	MS			
				Number of obs	=	183
				F(5, 177)	=	26.74
Model	73.6956	5	14.7391	Prob > F	=	0
Residual	97.5592	177	0.55118	R-squared	=	0.4303
				Adj R-squared	=	0.4142
Total	171.255	182	0.94096	Root MSE	=	0.74242

exploit_ab~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
tree_native_sqrt	-0.495	0.075	-6.560	0.000	-0.644	-0.346
dist_nat_sqrt	0.015	0.003	5.250	0.000	0.009	0.020
shrub_small_ln	0.155	0.044	3.550	0.001	0.069	0.241
veg_struct_hetero_sqrt	0.654	0.283	2.310	0.022	0.096	1.213
dist_bow_sqrt	-0.005	0.002	-2.210	0.029	-0.010	-0.001
_cons	1.254	0.305	4.100	0.000	0.651	1.856

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-253.6	-202.11	6	416.22	435.4766

ABUNDANCE OF URBAN ADAPTERS

```
regress adapt_abun_sqrt sw_hetero_struct_sqrt forcov_wgt_mn250_sqrt dist_hydro_ln2 ///
                        dist_dtown
```

Source	SS	df	MS	Number of obs	=	183
				F(4, 178)	=	18.38
Model	28.1285	4	7.03214	Prob > F	=	0
Residual	68.1095	178	0.38264	R-squared	=	0.2923
				Adj R-squared	=	0.2764
Total	96.238	182	0.52878	Root MSE	=	0.61858

adapt_abun~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
cancov_250_sqrt	0.207	0.032	6.530	0.000	0.145	0.270
dist_water_ln	-0.101	0.038	-2.610	0.010	-0.177	-0.025
dist_dtown	0.00002	0.000	1.970	0.051	0.000	0.000
veg_struct_hetero	-0.315	0.197	-1.600	0.112	-0.704	0.074
_cons	1.916	0.376	5.100	0.000	1.175	2.657

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-200.86	-169.23	5	348.46	364.5073

ABUNDANCE OF URBAN AVOIDERS

```
oprobit avoid_abun_cat3 sw_hetero_struct_sqrt cd_yewbtr2_h_10_ln2 tot_shrub_dens_corr_ln2
```

Ordered probit	regression	Number of obs	=	183
		LR chi2(3)	=	94.62
		Prob > chi2	=	0
Log likelihood	-139.47	Pseudo R2	=	0.2533

avoid_abu~t3	Coef.	Std.	z	P>z	[95%	Interval]

		Err.			Conf.	
costdist_water_ywar_ln	-0.570	0.087	-6.520	0.000	-0.741	-0.399
shrub_total_ln	0.178	0.060	2.990	0.003	0.062	0.295
veg_struct_hetero	0.646	0.397	1.630	0.104	-0.132	1.424
/cut1	-3.378	0.909			-5.160	-1.596
/cut2	-2.447	0.895			-4.201	-0.693

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-186.78	-139.47	5	288.946	304.9932

NATIVE SPECIES RICHNESS - DEVELOPED SITES ONLY

```
regress total_pa_native2_sqrt tot_tree_lg_dens_corr_ln2 forcov_wgt_mn250_ac_sqrt ///
                             dist_nat_sqrt tot_shrub_nonnat_dens_corr_ln2
                             sw_hetero_struct_sqrt dist_dtown ///
                             if developed ==1
```

Source	SS	df	MS			
				Number of obs	=	131
				F(6, 124)	=	20.9
Model	17.5436	6	2.92394	Prob > F	=	0
Residual	17.3512	124	0.13993	R-squared	=	0.5028
				Adj R-squared	=	0.4787
Total	34.8948	130	0.26842	Root MSE	=	0.37407

total_pa_n~t	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
dist_nat_sqrt	-0.006	0.002	-3.590	0.000	-0.009	-0.003
access_cancov_250_sqrt	0.114	0.036	3.210	0.002	0.044	0.185
shrub_nonnative_ln	0.103	0.032	3.230	0.002	0.040	0.166
dist_dtown	0.00002	0.000	2.230	0.027	0.000	0.000
veg_struct_hetero_sqrt	0.338	0.165	2.050	0.043	0.011	0.665
tree_large_ln	0.488	0.255	1.920	0.058	-0.016	0.993
_cons	1.091	0.203	5.360	0.000	0.689	1.494

Model	Obs	ll(null)	ll(model)	df	AIC	BIC

.	131	-99.234	-53.47	7	120.941	141.0671

ABUNDANCE OF NATIVE SPECIES - DEVELOPED SITES ONLY

```
regress total_abun_native3_sqrt sw_hetero_struct_sqrt forcov_wgt_mn250_ac_sqrt ///
                                 dist_nat_sqrt tot_shrub_nonnat_dens_corr_ln2 dist_dtown if
                                developed ==1
```

Source	SS	df	MS			
				Number of obs	=	131
				F(5, 125)	=	28.95
Model	42.6897	5	8.53794	Prob > F	=	0
Residual	36.8711	125	0.29497	R-squared	=	0.5366
				Adj R-squared	=	0.518
Total	79.5608	130	0.61201	Root MSE	=	0.54311

total~3_sqrt	Coef.	Std. Err.	t	P>t	[95% Conf.	Interval]
access_cancov_250_sqrt	0.298	0.044	6.820	0.000	0.211	0.384
shrub_nonnative_ln	0.149	0.043	3.470	0.001	0.064	0.234
dist_nat_sqrt	-0.008	0.002	-3.200	0.002	-0.013	-0.003
dist_dtown	0.00004	0.000	2.650	0.009	0.000	0.000
veg_struct_hetero_sqrt	0.412	0.237	1.740	0.085	-0.057	0.881
_cons	0.817	0.293	2.790	0.006	0.238	1.397

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	131	-153.22	-102.84	6	217.684	234.9353

Appendix 4-6. Details of logistic regression models presented in Table 4-8 describing local and landscape factors explaining the presence or absence of individual focal species of songbirds in Calgary, Alberta.

AMERICAN CROW

```
logit amcr_pa  forcov_wgt_mn1000_sqrt dist_hydro_ln2 dist_dtown ///
                    cd_bcchpb2_n_10_sqrt
```

Logistic regression	Number of obs	=	183
	LR chi2(4)	=	31.52
	Prob > chi2	=	0
Log likelihood = -109.37077	Pseudo R2	=	0.126

amcr_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
costdist_nat_bcch_sqrt	0.017	0.006	2.800	0.005	0.005	0.029
cancov_1000_sqrt	0.395	0.170	2.330	0.020	0.062	0.728
dist_water_ln	0.248	0.167	1.490	0.137	-0.079	0.576
dist_dtown	0.000	0.000	-1.370	0.171	0.000	0.000
_cons	-3.754	1.272	-2.950	0.003	-6.248	-1.260

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-125.1	-109.37	5	228.74	244.79

Area under ROC curve: 0.7384

AMERICAN ROBIN

```
logit amro_pa tot_shrub_coni_dens_corr_ln2 tot_shrub_dens_corr_ln2 dist_dtown ///
                    forcov_wgt_mn250_sqrt cd_bcchpb2_n_10_sqrt
```

Logistic regression	Number of obs	=	183
	LR chi2(5)	=	28.35
	Prob > chi2	=	0
Log likelihood = -46.840302	Pseudo R2	=	0.2323

amro_pa	Coef.	Std.	z	P>z	[95%	Interval]

		Err.			Conf.	
dist_dtown	0.000	0.000	2.770	0.006	0.000	0.000
cancov_250_sqrt	0.479	0.246	1.940	0.052	-0.004	0.962
costdist_nat_bcch_sqrt	-0.015	0.009	-1.740	0.082	-0.032	0.002
shrub_conif_ln	1.367	1.008	1.360	0.175	-0.608	3.341
shrub_total_ln	0.155	0.192	0.810	0.418	-0.221	0.532
_cons	-0.628	1.232	-0.510	0.610	-3.044	1.787

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-61.01	-46.84	6	105.68	124.94

Area under ROC curve: 0.8357

BLACK-BILLED MAGPIE

```
logit bbma_pa sw_hetero_struct_sqrt cd_bcchpb2_b_10_sqrt tot_shrub_native_dens_corr_ln2
///
                                              dist_dtown
```

Logistic regression	Number of obs	=	183
	LR chi2(4)	=	34.29
	Prob > chi2	=	0
Log likelihood = -107.06371	Pseudo R2	=	0.138

bbma_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
costdist_bow_bcch_sqrt	-0.018	0.005	-3.550	0.000	-0.028	-0.008
shrub_native_ln	-0.428	0.103	-4.140	0.000	-0.630	-0.225
dist_dtown	0.000	0.000	-2.210	0.027	0.000	0.000
veg_struct_hetero_sqrt	1.246	0.708	1.760	0.078	-0.141	2.634
_cons	2.235	0.712	3.140	0.002	0.841	3.630

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-124.2	-107.06	5	224.13	240.17

Area under ROC curve: 0.7344

BLACK-CAPPED CHICKADEE

```
logit bcch_pa sw_hetero_struct_sqrt forcov_wgt_mn250_sqrt ///
                              cd_bcchpb2_n_10_sqrt

                              Number of
Logistic regression           obs            =          183
                              LR chi2(3)     =       103.64
                              Prob >
                              chi2           =            0
Log likelihood = -63.225437   Pseudo R2      =       0.4504


                                        Std.                           [95%
bcch_pa                       Coef.     Err.        z          P>z     Conf.     Interval]

cancov_250_sqrt                1.311    0.209       6.280      0.000    0.902       1.720
costdist_nat_bcch_sqrt        -0.025    0.007      -3.410      0.001   -0.040      -0.011
veg_struct_hetero_sqrt        -1.681    0.945      -1.780      0.075   -3.533       0.170
_cons                         -0.692    0.958      -0.720      0.470   -2.569       1.186


Model                         Obs       ll(null)   ll(model)   df      AIC       BIC

.                               183      -115      -63.225        4    134.45     147.29

Area under ROC curve:          0.9116
```

BROWN-HEADED COWBIRD

```
. logit bhco_pa forcov_wgt_mn250_sqrt tot_shrub_native_dens_corr_ln2 dist_nat_sqrt

                              Number of
Logistic regression           obs            =          183
                              LR chi2(3)     =        34.78
                              Prob >
                              chi2           =            0
Log likelihood = -55.581962   Pseudo R2      =       0.2383


                                        Std.                           [95%
bhco_pa                       Coef.     Err.        z          P>z     Conf.     Interval]

shrub_native_ln                0.497    0.156       3.180      0.001    0.190       0.803
dist_nat_sqrt                 -0.043    0.016      -2.750      0.006   -0.074      -0.013
cancov_250_sqrt               -0.387    0.187      -2.070      0.039   -0.754      -0.020
_cons                         -0.247    1.017      -0.240      0.808   -2.240       1.747
```

```
Model                          Obs        ll(null)   ll(model)   df        AIC       BIC

.                                   183    -72.97     -55.582         4    119.16        132

area under ROC curve   =          0.8428
```

BLUE JAY

```
logit blja_pa tot_tree_sm_dens_corr_ln2 sw_hetero_struct_sqrt ///
forcov_wgt_mn1000_sqrt dist_dtown
```

```
                               Number of
Logistic regression            obs           =          183
                               LR chi2(4)    =        16.84
                               Prob >
                               chi2          =       0.0021
Log likelihood = -43.471606    Pseudo R2     =       0.1622


                                            Std.                            [95%
blja_pa                        Coef.        Err.       z          P>z       Conf.      Interval]

cancov_1000_sqrt                   0.843    0.294      2.870      0.004     0.267      1.420
dist_dtown                        0.0002    0.000      2.610      0.009     0.000      0.000
veg_struct_hetero_sqrt            -2.081    1.163     -1.790      0.073    -4.360      0.198
tree_small_ln                     -0.898    0.609     -1.470      0.141    -2.092      0.296
_cons                             -5.246    1.553     -3.380      0.001    -8.290     -2.202


Model                          Obs        ll(null)   ll(model)   df        AIC       BIC

.                                   183    -51.89     -43.472         5    96.943    112.99

Area under ROC curve   =          0.8206
```

CEDAR WAXWING

```
. logit cewx_pa tot_shrub_sm_dens_corr_ln2
```

```
                               Number of
Logistic regression            obs           =          183
                               LR chi2(1)    =        17.71
                               Prob >
                               chi2          =            0
Log likelihood = -40.581639    Pseudo R2     =       0.1791
```

cewx_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
shrub_sm_ln	0.923	0.273	3.390	0.001	0.389	1.457
_cons	-6.059	1.260	-4.810	0.000	-8.528	-3.589

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-49.44	-40.582	2	85.163	91.582

area under ROC curve = 0.81

CHIPPING SPARROW

```
logit chsp_pa  forcov_wgt_mn1000_sqrt sw_hetero_tree_sqrt tot_tree_sm_dens_corr_ln2
```

Logistic regression	Number of obs	=	183
	LR chi2(3)	=	32.75
	Prob > chi2	=	0
Log likelihood = -108.16233	Pseudo R2	=	0.1315

chsp_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_hetero_sqrt	1.388	0.497	2.790	0.005	0.414	2.361
tree_small_ln	-0.891	0.321	-2.780	0.005	-1.519	-0.263
cancov_1000_sqrt	0.410	0.153	2.680	0.007	0.111	0.710
_cons	-2.479	0.685	-3.620	0.000	-3.822	-1.136

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-124.5	-108.16	4	224.32	237.16

Area under ROC curve = 0.7398

COMMON GRACKLE

```
logit cogk_pa tot_shrub_coni_dens_corr_ln2 tot_tree_fruit_dens_corr_sqrt ///
                              cd_bcchpb2_b_10_sqrt tot_tree_sm_dens_corr_ln2
```

Logistic regression	Number of	=	183

	obs		
	LR chi2(4)	=	16.57
	Prob > chi2	=	0.0023
Log likelihood = -45.982331	Pseudo R2	=	0.1527

cogk_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
tree_fruit_sqrt	2.796	0.956	2.920	0.003	0.922	4.669
costdist_bow_bcch_sqrt	-0.020	0.009	-2.290	0.022	-0.038	-0.003
shrub_conif_ln	0.594	0.389	1.530	0.127	-0.169	1.357
tree_small_ln	-0.980	0.712	-1.380	0.168	-2.375	0.415
_cons	-1.928	0.670	-2.880	0.004	-3.241	-0.615

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-54.27	-45.982	5	101.96	118.01

Area under ROC curve = 0.7897

DOWNY WOODPECKER

```
logit dowo_pa forcov_wgt_mn250_sqrt cd_yewbtr2_h_10_ln2 cd_yewbtr2_b_10_sqrt
```

Logistic regression	Number of obs	=	183
	LR chi2(3)	=	37.9
	Prob > chi2	=	0
Log likelihood = -32.936826	Pseudo R2	=	0.3652

dowo_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
costdist_water_ywar_ln	-0.970	0.351	-2.760	0.006	-1.658	-0.282
costdist_bow_ywar_sqrt	-0.016	0.007	-2.230	0.025	-0.029	-0.002
cancov_250_sqrt	0.377	0.265	1.420	0.155	-0.142	0.897
_cons	3.286	2.828	1.160	0.245	-2.258	8.829

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-51.89	-32.937	4	73.874	86.712

```
area under ROC curve   =              0.9175
```

EUROPEAN STARLING

```
logit eust_pa can_hgt_max_sqrt sw_hetero_tree_sqrt dist_bow_sqrt ///
                               cd_bcchpb2_n_10_sqrt tot_shrub_native_dens_corr_ln2
                               forcov_wgt_mn500_sqrt ///
                               can_hgt_max_sqrt

                               Number of
Logistic regression            obs           =          183
                               LR chi2(6)    =        43.55
                               Prob >
                               chi2          =            0
Log likelihood = -94.001203    Pseudo R2     =       0.1881


                                             Std.                          [95%
eust_pa                        Coef.         Err.      z          P>z      Conf.     Interval]

cancov_500_sqrt                   -0.519     0.184     -2.810     0.005    -0.881     -0.158
tree_hetero_sqrt                  -1.312     0.489     -2.690     0.007    -2.270     -0.354
shrub_native_ln                    0.328     0.133      2.470     0.014     0.067      0.588
max_can_hgt_sqrt                   0.620     0.254      2.440     0.015     0.122      1.117
costdist_nat_bcch_sqrt             0.013     0.006      2.200     0.028     0.001      0.025
dist_bow_sqrt                     -0.015     0.008     -1.750     0.081    -0.031      0.002
_cons                             -0.983     0.987     -1.000     0.319    -2.918      0.952


Model                          Obs           ll(null)  ll(model)  df       AIC       BIC

.                                 183        -115.8    -94.001          7       202     224.47

Area under ROC curve   =              0.7847
```

GREY CATBIRD

```
logit grca_pa cd_yewbtr2_b_10_sqrt dist_hydro_ln2 tot_shrub_sm_dens_corr_ln2

                               Number of
Logistic regression            obs           =          183
                               LR chi2(3)    =         43.5
                               Prob >
                               chi2          =            0
Log likelihood = -17.040989    Pseudo R2     =       0.5607


grca_pa                        Coef.         Std.      z          P>z      [95%      Interval]
```

		Err.			Conf.	
dist_water_ln	-1.880	0.969	-1.940	0.052	-3.779	0.020
shrub_small_ln	0.887	0.571	1.550	0.120	-0.231	2.005
costdist_bow_ywar_sqrt	-0.013	0.009	-1.380	0.168	-0.031	0.005
_cons	3.002	5.383	0.560	0.577	-7.549	13.554

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-38.79	-17.041	4	42.082	54.92

Area under ROC curve = 0.9665

HOUSE FINCH

logit hofi_pa tot_tree_sm_dens_corr_ln2 dist_hydro_ln2 forcov_wgt_mn500_sm_ac_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(3)	=	76.27
	Prob > chi2	=	0
Log likelihood = -71.995009	Pseudo R2	=	0.3463

hofi_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
dist_water_ln	1.358	0.290	4.680	0.000	0.789	1.927
assess_cancov_500_sm_sqrt	0.869	0.195	4.460	0.000	0.488	1.251
tree_small_ln	-2.021	0.816	-2.480	0.013	-3.621	-0.421
_cons	-12.392	2.462	-5.030	0.000	-17.218	-7.567

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-110.1	-71.995	4	151.99	164.83

Area under ROC curve = 0.88

HOUSE SPARROW

logit hosp_pa forcov_wgt_mn250_sqrt dist_hydro_ln2 dist_dtown

Logistic regression	Number of obs	=	183

```
                              LR chi2(3)   =          79.12
                              Prob >
                              chi2         =              0
Log likelihood = -62.512912   Pseudo R2    =         0.3876


                                           Std.                           [95%
hosp_pa                       Coef.        Err.      z          P>z       Conf.     Interval]

dist_water_ln                      1.225     0.213      5.750     0.000     0.807      1.642
dist_dtown                       -0.0002     0.000     -2.500     0.012     0.000      0.000
cancov_250_sqrt                   -0.313     0.153     -2.050     0.040    -0.612     -0.014
_cons                             -3.765     1.507     -2.500     0.012    -6.718     -0.812


Model                         Obs          ll(null)  ll(model)  df        AIC       BIC

                                                                          133.0258
.                                    183    -102.1    -62.513          4  145.8638

Area under ROC curve   =            0.8755
```

HOUSE WREN

```
logit howr_pa dist_dtown dist_hydro_ln2 tot_shrub_fruit_dens_corr_ln2
```

```
                              Number of
Logistic regression           obs          =            183
                              LR chi2(3)   =          31.37
                              Prob >
                              chi2         =              0
Log likelihood = -79.121174   Pseudo R2    =         0.1654


                                           Std.                           [95%
howr_pa                       Coef.        Err.      z          P>z       Conf.     Interval]

dist_water_ln                     -0.467     0.156     -3.000     0.003    -0.772     -0.162
shrub_fruit_ln                     0.380     0.138      2.750     0.006     0.109      0.651
dist_dtown                         0.000     0.000      1.940     0.053     0.000      0.000
_cons                             -0.336     1.252     -0.270     0.788    -2.789      2.117


Model                         Obs          ll(null)  ll(model)  df        AIC       BIC

.                                    183     -94.8    -79.121          4   166.24    179.08

Area under ROC curve   =            0.7658
```

LEAST FLYCATCHER

logit lefl_pa tot_shrub_sm_dens_corr_ln2 cd_yewbtr2_h_10_ln2

Logistic regression	Number of obs	=	183
	LR chi2(2)	=	61.44
	Prob > chi2	=	0
Log likelihood = -23.550919	Pseudo R2	=	0.566

lefl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
costdist_water_ywar_ln	-1.930838	0.6341	-3.05	0.002	-3.1736	-0.688
shrub_small_ln	0.6255733	0.4273	1.46	0.143	-0.212	1.4631
_cons	7.330043	4.7116	1.56	0.12	-1.9044	16.565

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-54.27	-23.551	3	53.102	62.73

Area under ROC curve = 0.9656

NORTHERN FLICKER

logit nofl_pa sw_hetero_tree_sqrt for_cov_tot_sqrt cd_yewbtr2_b_10_sqrt ///
dist_dtown

Logistic regression	Number of obs	=	183
	LR chi2(4)	=	35.17
	Prob > chi2	=	0
Log likelihood = -57.208997	Pseudo R2	=	0.2351

nofl_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
cancov_50_sqrt	0.250	0.106	2.360	0.018	0.042	0.457
costdist_bow_ywar_sqrt	-0.010	0.006	-1.760	0.079	-0.021	0.001

```
dist_dtown                      0.000    0.000    -1.660   0.096    0.000     0.000
tree_hetero_sqrt               -0.827    0.570    -1.450   0.147   -1.945     0.291
_cons                          -0.979    1.000    -0.980   0.327   -2.939     0.980


Model                    Obs           ll(null)  ll(model)  df        AIC       BIC

.                                 183   -74.79    -57.209       5   124.42    140.47

area under ROC curve   =          0.8187
```

RED-BREASTED NUTHATCH

```
logit rbnu_pa cd_bcchpb2_h_10_ln2 forcov_wgt_mn500_sqrt ///
                         tot_tree_coni_dens_corr_sqrt

                         Number of
Logistic regression      obs           =             183
                         LR chi2(3)    =           69.78
                         Prob >
                         chi2          =               0
Log likelihood = -77.812079  Pseudo R2 =          0.3096


                                       Std.                        [95%
rbnu_pa                  Coef.         Err.      z         P>z     Conf.     Interval]

cancov_500_sqrt                 1.278    0.227     5.640   0.000    0.834     1.722
costdist_water_bcch_ln          0.346    0.171     2.020   0.043    0.010     0.681
tree_conif_sqrt                 0.852    0.498     1.710   0.087   -0.124     1.828
                                                                        -
_cons                          -8.761    1.861    -4.710   0.000   12.408    -5.113


Model                    Obs           ll(null)  ll(model)  df        AIC       BIC

.                                 183   -112.7    -77.812       4   163.62    176.46


Area under ROC curve   =          0.8605
```

ROCK PIGEON

```
logit ropi_pa dist_nat_sqrt snag_tree_tot_dens_corr_sqrt dist_bow_sqrt

                         Number of
Logistic regression      obs           =             183
```

```
                                LR chi2(3)    =          24.68
                                Prob >
                                chi2          =              0
Log likelihood = -64.233054     Pseudo R2     =         0.1611


                                              Std.                               [95%
ropi_pa                         Coef.         Err.       z           P>z         Conf.      Interval]

dist_bow_sqrt                        -0.056     0.017      -3.410      0.001     -0.089       -0.024
dist_nat_sqrt                         0.046     0.017       2.720      0.007      0.013        0.080
tree_snag_total_sqrt                 -2.276     0.972      -2.340      0.019     -4.181       -0.371
_cons                                -0.967     0.604      -1.600      0.109     -2.152        0.217


Model                           Obs           ll(null)   ll(model)   df          AIC        BIC

.                                       183    -76.57     -64.233           4    136.47        149.3

Area under ROC curve   =              0.7481
```

RUBY-CROWNED KINGLET

```
logit rcki_pa can_hgt_max_sqrt tot_shrub_coni_dens_corr_ln2 ///
                                forcov_wgt_mn500_lg_ac_sqrt cd_yewbtr2_h_10_ln2
                                sw_hetero_struct_sqrt

                                Number of
Logistic regression             obs           =            183
                                LR chi2(5)    =          35.42
                                Prob >
                                chi2          =              0
Log likelihood = -26.581986     Pseudo R2     =         0.3999


                                              Std.                               [95%
rcki_pa                         Coef.         Err.       z           P>z         Conf.      Interval]

shrub_conif_ln                        1.318     0.399       3.310      0.001      0.537        2.099
access_cancov_500_lg_sqrt             0.872     0.384       2.270      0.023      0.120        1.625
veg_struct_hetero_sqrt               -2.607     1.525      -1.710      0.087     -5.596        0.382
max_can_hgt                           0.905     0.558       1.620      0.105     -0.188        1.999
costdist_water_ywar_ln                0.521     0.372       1.400      0.162     -0.209        1.250
                                                                                      -
_cons                               -13.288     4.726      -2.810      0.005     22.552       -4.025



Model                           Obs           ll(null)   ll(model)   df          AIC        BIC
```

```
.                                 183    -44.29    -26.582         6   65.164    84.421

area under ROC curve   =       0.9318
```

RED-WINGED BLACKBIRD

```
logit rwbl_pa dist_dtown dist_bow_sqrt tot_tree_coni_dens_corr_sqrt ///
                                dist_nat_sqrt

                                Number of
Logistic regression             obs          =        183
                                LR chi2(4)   =      41.36
                                Prob >
                                chi2         =          0
Log likelihood = -20.909494     Pseudo R2    =     0.4972


                                             Std.                               [95%
rwbl_pa                         Coef.        Err.      z            P>z        Conf.      Interval]

dist_nat_sqrt                       -0.055    0.024      -2.320     0.020     -0.102     -0.009
dist_bow_sqrt                       -0.060    0.030      -2.010     0.045     -0.119     -0.001
dist_dtown                           0.000    0.000      -1.600     0.110     -0.001      0.000
tree_conif_sqrt                     -2.858    2.286      -1.250     0.211     -7.340      1.623
_cons                                2.322    1.251       1.860     0.063     -0.129      4.774


Model                           Obs          ll(null)  ll(model)    df         AIC        BIC

.                                 183    -41.59    -20.909         5   51.819    67.866

area under ROC curve   =       0.9223
```

SONG SPARROW

```
logit sosp_pa cd_yewbtr2_b_10_sqrt dist_hydro_ln2

                                Number of
Logistic regression             obs          =        183
                                LR chi2(2)   =      47.79
                                Prob >
                                chi2         =          0
Log likelihood = -17.697075     Pseudo R2    =     0.5745


                                             Std.                               [95%
sosp_pa                         Coef.        Err.      z            P>z        Conf.      Interval]
```

dist_water_ln	-2.553	0.972	-2.630	0.009	-4.457	-0.648
costdist_bow_ywar_sqrt	-0.024	0.013	-1.890	0.059	-0.049	0.001
_cons	10.611	4.158	2.550	0.011	2.462	18.759

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-41.59	-17.697	3	41.394	51.023

area under ROC curve = 0.9672

TREE SWALLOW

logit tesw_pa sw_hetero_tree_sqrt dist_bow_sqrt cd_yewbtr2_n_10_sqrt ///
forcov_wgt_mn1000_ac_sqrt

Logistic regression	Number of obs	=	183
	LR chi2(4)	=	46.39
	Prob > chi2	=	0
Log likelihood = -23.710646	Pseudo R2	=	0.4945

tesw_pa	Coef.	Std. Err.	z	P>z	[95% Conf.	Interval]
costdist_nat_ywar_sqrt	-0.043	0.016	-2.770	0.006	-0.074	-0.013
access_cancov_1000_sqrt	-1.163	0.504	-2.310	0.021	-2.152	-0.175
tree_hetero_sqrt	-1.881	0.838	-2.240	0.025	-3.524	-0.238
dist_bow_sqrt	-0.015	0.021	-0.730	0.465	-0.055	0.025
_cons	3.876	1.447	2.680	0.007	1.040	6.712

Model	Obs	ll(null)	ll(model)	df	AIC	BIC
.	183	-46.91	-23.711	5	57.421	73.469

area under ROC curve = 0.9448

WARBLING VIREO

logit wavi_pa cd_yewbtr2_h_10_ln2

Logistic regression	Number of obs	=	183

```
                                 LR chi2(1)   =          24.18
                                 Prob >
                                 chi2         =              0
Log likelihood = -39.799841      Pseudo R2    =          0.233


                                              Std.                               [95%
wavi_pa                          Coef.        Err.       z            P>z        Conf.      Interval]

costdist_water_ywar_ln              -1.041      0.250      -4.160      0.000     -1.532       -0.550
_cons                                4.771      1.592       3.000      0.003      1.651        7.891



Model                            Obs          ll(null)   ll(model)    df         AIC        BIC

.                                      183     -51.89        -39.8          2        83.6      90.019


area under ROC curve   =               0.819
```

YELLOW WARBLER

```
logit yewb_pa cd_yewbtr2_b_10_sqrt cd_yewbtr2_h_10_ln2 tot_shrub_dens_corr_ln2

                                 Number of
Logistic regression              obs          =            183
                                 LR chi2(3)   =         118.64
                                 Prob >
                                 chi2         =              0
Log likelihood = -32.806037      Pseudo R2    =         0.6439


                                              Std.                               [95%
yewb_pa                          Coef.        Err.       z            P>z        Conf.      Interval]

costdist_water_ywar_ln              -1.740      0.374      -4.650      0.000     -2.473       -1.007
costdist_bow_ywar_sqrt              -0.016      0.007      -2.380      0.017     -0.029       -0.003
shrub_total_ln                       0.498      0.223       2.240      0.025      0.062        0.935
_cons                                9.970      2.833       3.520      0.000      4.417       15.522



Model                            Obs          ll(null)   ll(model)    df         AIC        BIC

.                                      183     -92.13      -32.806          4      73.612       86.45

area under ROC curve   =              0.9674
```

CHAPTER 5

GENERAL DISCUSSION

A major goal of this research project was to generate practical information that could be used to inform management guidelines aimed at conserving avian diversity within urban areas. Although responses to habitat and landscape changes induced by urban development are bound to be species-specific, managing landscapes for biodiversity requires a multi-species focus (Clevenger and Waltho 2005). A major challenge for applied ecologists is to strike the right balance between complexity and generality in order to draw principles that can be translated into useful management guidelines (Shanahan and Possingham 2009). For this reason I chose to explore functional landscape connectivity within a multi-species system. Analyses of my playback experiments included the responses of four year-round resident birds: black-capped chickadee, red- and white-breasted nuthatch, and downy woodpecker. For my translocation experiments, I chose 2 species with contrasting migratory behaviours and adaptabilities to urban development: black-capped chickadee (resident; urban-adaptable) and yellow-warbler (Neotropical migrant; urban-sensitive) with the expectation that the responses of these contrasting species would represent those of other forest songbirds present in my study area. In this section, I discuss some of the general principles that can be drawn from the findings described in the three previous chapters with particular emphasis on their relevance to the conservation of birds in urban and other fragmented landscapes. I then reflect on the merit and limitations of some of the approaches I took in conducting my research and analyzing my data. I conclude by identifying promising directions for future research.

General principles

Gap width is the primary determinant of movement across urban features

To date, most studies of bird movements across gaps have taken place in relatively natural settings like agricultural or timber harvested landscapes (e.g. Machtans *et al.* 1996, Desrochers and Hannon 1997, Rail *et al.* 1997, St. Clair *et al.* 1998, Doherty and Grubb 2000, Develey and Stouffer 2001, Robichaud *et al.* 2002, St. Clair 2003, Laurance *et al.* 2004, Creegan and Osborne 2005). To my knowledge, my study was the first to assess the permeability of linear features to the movements of songbirds in an urban context. Although the urban landscape represented a challenging system for exploring the effects of habitat fragmentation, it also provided an ideal testing ground for assessing the effects of roads on bird movements. By selecting a variety of roads of varying widths and traffic volumes, I was able to disentangle the effects of road width, traffic volume, noise, and the characteristics of adjacent vegetation on movement behaviour. My playback experiments revealed that, of these factors, the width of the gap in vegetation was the primary contributor to the barrier effect of transportation corridors for forest songbirds. Gap sensitivity by forest songbirds has been documented in several other studies using playback (Sieving *et al.* 1996, Rail *et al.* 1997, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Bélisle and Desrochers 2002, St. Clair. 2003) and passive observation (Laurance *et al.* 2004) techniques.

My playback experiments further showed a clear threshold beyond which movement became increasingly unlikely. Although the birds in my study crossed small gaps without hesitation, as the gap in vegetation exceeded 30 m, the likelihood of movement decreased dramatically and by 45 m, birds were only half as likely to move across gaps as they were to move an equivalent distance in continuous tree cover. This threshold seemed to hold for all species included in my playback analyses, which showed a consistent aversion to crossing gaps > 50 m. Other studies have also observed a reluctance by birds to cross gaps exceeding > 50 m (Desrochers & Hannon 1997; St. Clair *et al.* 1998; Bélisle & Desrochers 2002, Awade and Metzger 2008). My translocation experiments provided additional support for a non-linear relationship between gap width and movement probability. Chickadees, in particular, responded more strongly to the 'barrier' effect of linear features (based on the non-linear crossing probabilities from my playback experiments) than to gap width alone. Thresholds in responses to landscape conditions can be useful for identifying conservation or management targets (Guénette and Villard 2005, Betts *et al.* 2007). This particular threshold suggests that gaps in vegetation associated with transportation corridors should ideally be kept below 50 m in order to allow for unfettered movements by birds. This can be achieved through the strategic placement of trees either along them or in forested medians, which represents a simple and cost-effective measure for improving habitat connectivity for birds in landscapes fragmented by human infrastructures.

Understanding behavioural responses to anthropogenic structures is vital to mitigating their barrier effects on wildlife movements

Another innovative aspect of my research was its focus on the movement behaviour of birds in relation to bridges. The importance of riparian corridors to birds and other wildlife has been well documented in the literature (Knopf *et al.* 1988, Knopf and Samson 1994, Skagen *et al.* 1998, Akresh *et al.* 2009). Although transportation bridges represent major interruptions along these natural conduits of movement, very little is known about how they might affect the movements of birds. The birds in my study showed a strong preference for flying over, rather than under, bridges even though this was the less direct route between the origin and destination speakers. Birds appeared motivated to cross underneath bridges only if this resulted in a substantially shorter gap crossing or if adjacent vegetation was lower than the bridge. Other studies of wildlife movements across wildlife underpasses and overpasses have also revealed striking species-specific responses to human-built structures (Gloyne and Clevenger 2000, Clevenger and Waltho 2005). For example, whereas black bears and cougars preferred constricted wildlife crossing structures for traversing the Trans-Canada Highway in Banff National Park, grizzly bears, elk and deer showed a strong preference for more open structures (Clevenger and Waltho 2005). Similarly, species-specific responses to culverts were observed in small mammals (McDonald and St. Clair 2004). In our study, the preference by birds to move over bridges suggests that their barrier effect can be most effectively mitigated by the placement of tall trees on either side to provide safe passage well above moving traffic.

Motivation affects movement behaviour and functional landscape connectivity

Several ecologists have recognized the importance of motivation as a factor influencing and movement decisions by organisms (Lima and Zolner 1996, Bélisle 2005). This has resulted in the development of experimental approaches for assessing landscape connectivity that provide a standardized incentive for movement. Examples of such techniques include translocation (Bélisle *et al.* 2001, Bélisle and St. Clair 2001, Gobeil and Villard 2002, Castellon and Sieving 2006, Gillies and St. Clair 2008), playback (Sieving *et al.* 1996, Rail *et al.* 1997, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Bélisle and Desrochers 2002, St. Clair 2003), and food-titration (Todd and Cowie 1990) experiments. The two techniques used in my study, playbacks and translocations, involved very different incentives for movement. Whereas in playback experiments, birds were motivated to join a predator-deterring mobbing scene, in translocation experiments, the incentive was to return to the breeding territory (Table 5-1). The two methods also incorporated very different time frames (6 minutes and 5 days for playback and translocation experiments, respectively), which I expected would affect my ability to draw inferences regarding the relative or absolute permeability of features. In light of these differences, I purposely incorporated some overlap in features (e.g. single roads, bridges, and rivers) and species (black-capped chickadee) to provide a basis for comparing how the two techniques assessed permeability and, more specifically, to assess the importance of motivation in movement decisions.

I found both similarities and differences in how playback and translocation experiments assessed permeability. For example, both methods revealed that gaps constrained movement; however, the effect size was generally smaller in translocation than in playback experiments. Indeed, whereas in my playback experiments the propensity of birds to cross gaps dropped precipitously as gap width exceeded 30 m, my translocation experiments showed that even gaps much wider than this did not act as absolute barriers to movement, as evidenced by return rates of at least 60% across all treatments.

This apparent discrepancy can best be explained by considering trade-offs between risk and potential fitness gain (Bélisle 2005). Although birds involved in my playback experiments consistently showed strong interest in participating in a mobbing scene (e.g. aggressive vocalizing and posturing), once a gap exceeded a critical threshold, the cost (or perceived risk) of crossing the gap apparently outweighed the benefits of joining the mobbing event. By comparison, my translocation experiments provided a much stronger incentive for movement. In these experiments, the fitness benefits of returning to the breeding territory must have generally outweighed the costs of travelling across large gaps or otherwise inhospitable terrain. Perceived predation risk has been shown to impact the willingness of forest birds to feed in the open (Desrochers *et al.* 2002). In the Desrochers *et al.* study, researchers manipulated perceived risk through the use of a stuffed merlin and mobbing calls. They found that birds rarely ventured into the open in the presence of the merlin decoy whereas the mobbing call did not alter their behaviour compared to a control.

From a conservation perspective, a question that remains at issue is whether the results of movement experiments, which are generally performed on adult birds, are generalizable to the context of dispersal movements, considered to be of primary importance to the persistence of populations in fragmented landscapes. The motivation for movement and risk tolerance of a dispersing bird is almost certainly higher than that of a bird exposed to an apparent mobbing scene as per my playback experiments (Table 5-2). Conversely, dispersing birds are probably more exploratory, less directional, and more risk-averse in their movements than translocated adults seeking to return to an established breeding territory. Accordingly, the barrier effects demonstrated by playback and translocation experiments are likely liberal and conservative, respectively, relative to the corresponding effects on dispersal movements.

In sum, by providing a standardized incentive for movement, both playback and translocation methods provided a legitimate basis for assessing the relative permeability of features or landscape sections. However, because the incentive was different for each technique, one must apply caution when comparing results across methods. Caution is also required when generalizing the results of such movement experiments to the context of dispersing birds.

Natural areas are essential for maintaining biodiversity in urban areas

One of the most striking results from my study was the disproportionately large contribution natural areas made to the overall diversity of avian species within my study area. Remarkably, almost three quarters of species detected were primarily associated with natural areas. Moreover, 38% of detected species were found exclusively in these sites even though they represented only 22% of sites surveyed. Other studies of avian distributions in urban or exurban areas have also found that natural sites contain many species that are highly intolerant of urban development (Bolger *et al.* 1991, Friesen *et al.* 1995, Crooks *et al.* 2004, Blair 1996, 2004, Fraterrigo and Wiens 2005, Hansen *et al.* 2005, Croci *et al.* 2008). While balsam poplar stands contained by far the most species, aspen and spruce stands also made unique contributions to regional avian diversity. The relative importance of natural areas to the native bird community can best be explained by their radically higher tree and shrub densities as demonstrated by our vegetation surveys. A more complex vegetation structure likely leads to greater abundance of food resources (i.e. insects), more diverse nesting materials and substrates, and greater cover from predators compared to more developed sites (Jokimaki and Huhta 2000). Isolation from natural areas negatively affected the distribution of all 4 native urban-adapted species (black-capped chickadee, red-breasted nuthatch, house wren, and American robin), suggesting that such areas were important not only for harbouring urban-avoiding birds but also for sustaining the presence of native urban-adapted species within the urban matrix. From a management standpoint, this implies that the preservation of the most biologically diverse natural areas should be the main focus of an urban biodiversity conservation plan. As well, because different vegetation communities make different contributions to regional diversity, it may be important to preserve examples of a variety of vegetation communities in order to capture as much of the regional species pool as possible.

Functional connectivity affects the distribution of birds

The burgeoning field of conservation behaviour is predicated on the expectation that behavioural processes operating on individuals can explain patterns of distribution and abundance and ultimately, the persistence of species (Lima and Zolner 1996, Caro 1998, Blumstein and Fernandez-Juricic 2004, Bélisle 2005). More specifically, the concept of functional landscape connectivity is rooted in the notion that the ability of an organism to move between habitat patches is not determined solely by the inter-patch distance but also by the biophysical nature of the routes between the patches and the biology and behaviour of the organism (Taylor *et al.* 1993). Thus, functional connectivity describes the landscape from an organism's rather than a structural perspective (With 2002) and thus, must be measured at the scale at which organisms of interest perceive and respond to the landscape (Wiens 2006).

Fine-scale behavioural studies are viewed with skepticism by some conservation biologists who question whether population viability, rather than movement *per se*, should be the ecological function of interest in studies of habitat fragmentation. Is it enough to ensure the animals can move from one patch to another through a fragmented landscape? Should more effort be made to elucidate the implications of such movements on the viability of populations? While theory (e.g. Taylor *et al.* 1993) and simulation-based studies (e.g. With and Crist 1995, Schumaker 1996, With *et al.* 1999, Bender *et al.* 2003, Tischendorf *et al.* 2003) have long predicted that functional connectivity should affect the distribution of organisms, empirical evidence supporting this prediction has been slow to emerge (Carroll 2006). The gulf between theory and field observations is in part attributable to the fact that population responses to landscape change can take decades to manifest themselves, which tends to obscure links between process and pattern. Nonetheless, such links are becoming increasingly apparent. For example, recent studies in genetics show that disruptions in functional landscape connectivity can lead to the genetic isolation of populations and the loss of genetic diversity in grizzly bears (Proctor *et al.* 2005) and birds (Lindsay *et al.* 2008, Ortega *et al.* 2008).

From a behavioural perspective, although many studies have demonstrated that fragmentation can impede the movements of individuals (Sieving *et al.* 1996, Rail *et al.* 1997, Desrochers and Hannon 1997, St. Clair *et al.* 1998, Bélisle *et al.* 2001, Bélisle and St. Clair 2001, Gobeil and Villard 2002, Bélisle and Desrochers 2002, St. Clair. 2003, Castellon and Sieving 2006) very few studies have been able to ‘scale up’ from movement behaviour to explain occupancy patterns in the landscape (Desrochers *et al.* 1999). Perhaps one of the most important contributions of my research was to provide novel, empirically based evidence of the link between the behavioural process of movement at the scale of individual birds and population-level patterns of species distributions within a highly heterogeneous and fragmented landscape (but see Awade and Metzger 2008). In my study, functional connectivity appeared to affect not only the movements of songbirds but their settlement patterns as well, presumably by constraining dispersal. Hence, considering the permeability of specific features and land cover types to the movements of individuals can lead to better predictions of the occurrence of species in heterogeneous landscapes. Moreover, that functional connectivity can affect the movements of a highly vagile taxon like songbirds underscores the importance of considering this attribute of the landscape when studying the effects of fragmentation on less vagile taxa, particularly in heterogeneous landscapes.

Reflections on experimental and analytical approaches used in this study

The urban landscape: a lesson in complexity and realism

In urban areas, humans are clearly outcompeting many other species for use of some of the most productive lands on the planet, leading many ecologists to view urbanization as one of the most serious threats to biodiversity worldwide (Marzluff *et al.* 2001). Despite this obvious threat, ecologists have generally eschewed the urban landscape either out of personal preference for working in more natural settings or in search of simpler systems in which to test ecological theory. Yet, the world is rarely as simple as the binary landscapes of conventional studies of habitat fragmentation. Even timber harvested landscapes do not fit the ‘habitat island’ model very well because habitat conditions in clearcuts change quickly as a result of forest regeneration (Norton *et al.* 2000). In reality, complex, mosaic landscapes like those found in urban areas may be more the norm than the exception, leading some ecologists to advocate for a gradient-based approach to describing the movements and habitat use of animals in heterogeneous landscapes (Chetkiewicz *et al.* 2006, Carroll 2006, Hansbauer *et al.* 2009). My study provided a number of examples of how such a gradient-based approach can be used to describe functional connectivity in a heterogeneous landscape:

- Consistent with other gradient-based studies of avian distributions in urban landscapes (Blair 1996, 2004, Melles *et al.* 2003, Crooks *et al.* 2004), I examined the distribution of birds across the entire gradient of urbanization as opposed to limiting my comparison to 2 or 3 land cover types.
- Whereas landscape level forest cover is typically expressed in terms of percent forested area (Bélisle *et al.* 2001, Bélisle and St. Clair 2001, Gobeil and Villard 2002), I devised a way of calculating mean canopy cover by assigning a canopy cover value to different polygons and then calculating the mean canopy cover value weighted by the area of each polygon, a method that had not been previously described in the literature.
- Realizing that developed sites vary widely in their vegetation characteristics, I chose to conduct detailed vegetation surveys to quantify these differences.
- Rather than considering the permeability of one road type, I considered a full range of road types of varying widths and traffic volumes.

- By using a regression rather than an ANOVA experimental design, I was able to go beyond simply showing differences between treatments and describe the slope of relationships between predictor and response variables. Such information is of particular value for making predictions and identifying thresholds in a complex world (Gotelli and Ellison 2004).

Learning to think like a bird

Landscape ecologists have a tendency to view the world as a series of mappable units. Yet, animals' perception of the landscape may be quite different, depending on perceptual range, perceived predation risk, and the presence of conspecifics (Lima and Zolner 1996, Chetkiewicz 2006, Stamps 1988). Although popular fragmentation software packages like FRAGSTATS can quickly and efficiently generate a myriad of fragmentation metrics, the realism of such fragmentation indices and metrics has been questioned by many (Jaeger 2000, Bender *et al.* 2003, Tischendorf *et al.* 2003, Neel *et al.* 2004). For example, 'mean nearest neighbour', a commonly used metric for describing landscape connectivity, describes 'mean' gap conditions even though individuals moving through a fragmented landscape may be more sensitive to the maximum gap width encountered along a specific travel route (Bélisle *et al.* 2001). Similarly, Eigenbrod *et al.* (2008) showed that habitat amount within a given radius was not as useful a metric as the amount of 'accessible' habitat (i.e. habitat accessible without having to cross a major highway) for explaining distribution patterns of amphibians in ponds.

In my research, I explored various ways of portraying the landscape as it might be perceived by my study organisms. In Chapter 3, I found that moving birds responded more strongly to minimum rather than mean levels of canopy cover. As well, in Chapter 4, I strove to describe landscape connectivity from an organism-based, functional approach rather than a structural approach based entirely on patch or landscape attributes. Consistent with Awade and Metzger (2008), I was able to demonstrate that functional connectivity was often a better predictor of the distribution of organisms in a fragmented landscape than structural connectivity.

Null-hypothesis testing vs AIC

In the past decade, null-hypothesis testing (NHT) has been heavily criticized, primarily by proponents of information theoretic approaches to model selection and inference (Johnson 1999, Anderson *et al.* 2000, Burnham and Anderson 2002, Whittingham *et al.* 2006, Hurlbert and Lombardi 2009). The primary criticisms of NHT include: (1) it is based on an uninformative null hypothesis that is almost always known *a priori* to be false; (2) it relies on an arbitrary *P*-value, which is largely dependent on sample size; (3) the assumption of random sampling is rarely met in observational studies; and (4) NHT is poorly suited to model or variable selection; (5) in step-wise model-building procedures, the order in which variables are entered into the model can influence the selected model, particularly when predictors are correlated.

In response to some of the shortcomings of NHT, information theoretic approaches such as that based on Akaike's Information Criterion (AIC) have been proposed (Burnham and Anderson 2002). AIC evaluates competing hypotheses based on how well different models fit the data. AIC differences and weights are then used to assess the likelihood that a given model is the best one from a suite of candidate models.

Major strengths of AIC are that it allows the testing of multiple hypotheses and is better suited for situations involving multiple predictor variables. It also provides a powerful means of finding the most parsimonious, best-fitting model among a suite of candidate models. However, like NHT, AIC also has some shortcomings. A commonly voiced problem with AIC is the difficulty in identifying ‘a priori’ models, particularly from a large set of candidate variables. In response to this problem, some authors have advocated comparing all possible subsets (Quinn and Keough 2002) while others reject this idea as a form of ‘model dredging’ (Stephens *et al.* 2005). Another criticism of AIC is that although it allows one to identify a best-fitting model among a suite of candidate models, it does not provide information on how well the model fits the data. Researchers who use AIC are often content to rank a series of alternative models and their AIC scores (Stephens *et al.* 2005), which provides little information on effect sizes or the strength of relationships among predictor and response variables.

In light of the limitations described above, I opted for a hybrid approach to model building, selection, and interpretation. I used an AIC-based step-wise approach to model building as a strategy to group and reduce the number of candidate variables (after Wiens *et al.* 2008). At each step, I used AIC to identify variables with the most explanatory power. By doing so, I allowed variables to compete against each other for inclusion in the best model rather than subjecting each variable to an arbitrary test based on *P*-values. This proved particularly useful for dealing with highly correlated variables. I also used AIC differences and weights to assess the support for my best-fit models. As a final step, I used coefficients and *P*-values to interpret effect sizes and the strength of the relationship between each covariate and the response variable (after Gillies 2008). In the absence of a ‘perfect’ approach to model building, selection, and interpretation, I believe the best approach is one that draws on the strengths of multiple methods, as long as the researcher is aware of the limitations posed by each (see also Stephens *et al.* 2005, Murtaugh 2009, Hurlbert and Lombardi 2009).

Directions for future research

While this project advanced our understanding of how urbanization affects the movements and distributions of songbirds, it also brought to light at least four information gaps that warrant further investigation. First, there is a need to better understand possible source-sink dynamics operating in the urban landscape. My results suggest that populations of native urban-adapted species (e.g. black-capped chickadees, red-breasted nuthatches) within the urban matrix may be sustained by the influx of dispersers emanating from natural areas. A study comparing the reproductive success of urban-adapted species within natural areas and the matrix would help clarify such dynamics, which may have important conservation implications. Secondly, while I selected songbirds as my study system because of their high visibility and well-documented sensitivity to habitat fragmentation, other less vagile taxa are likely to exhibit even greater effects of fragmentation. Such taxa represent worthy targets for the investigation of the effects of fragmentation on individuals and populations. Thirdly, whereas my translocation experiments only allowed me to determine the return time of translocated individuals, it would have been interesting to know which route returning birds actually followed. For example, did a chickadee that took four days to return to its territory spend that time waiting on one side of a freeway before mustering enough courage to cross it or did it undertake a long detour in order to locate a more suitable crossing point? Understanding how birds actually cross barriers would aid in the formulation of mitigation measures aimed at increasing their permeability. Finally, there is a need to better understand the effects of barriers on dispersal movements. This could be achieved through the telemetry-assisted observation of the trajectories of dispersing individuals. Another approach might be to translocate breeding-aged individuals into habitats that are unsuitable for breeding and then record their residency time in this unsuitable habitat (see Castellon and Sieving 2006), or document their movement paths as they search for a suitable breeding patch.

Conclusions

My research provided novel insights into the effects of urbanization on songbirds, drawn from the perspective of three different spatial scales. At the finest scale, my playback experiments identified factors affecting the permeability of linear features associated with transportation or riparian corridors (< 170 m wide). I then used translocation experiments to measure the relative permeability of landscape sections up to 1.5 km in length. At the broadest scale, I examined the role of land cover type, local vegetation characteristics, and landscape composition and configuration on the composition of avian communities and on the occurrence of individual species. I found that the urban landscape contained significant impediments to the movements of songbirds and that these barriers likely affected not only the movements of birds but their settlement patterns as well. My study also highlighted the importance of preserving a functionally connected network of natural areas for conserving both urban-avoiding birds that inhabit them as well as populations of native birds within the urban matrix.

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Table 5-1. Comparison of experimental techniques used to assess the permeability of urban features to the movements of forest songbirds.

Attribute	**Mobbing-based playback experiments**	**Translocation experiments**
Spatial scale	< 200 m	300 – 1500 m
Spatial scale relative to territory	Within or immediately adjacent to territory	Outside of territory
Observational time frame	6 minutes	5 days
Incentive	Participate in a predator mobbing scene	Return to breeding territory
Inferred motivation level	Moderate	Very high
Type of permeability measured	Relative	- Relative (returning birds) - Near-absolute (non-returning birds

Table 5-2. Estimated risk tolerance associated with different types of movement.

Movement type	Destination	Relative risk tolerance
Intra-range movements	Sources of food, water, shelter, mates	Low
Exploratory movements	Mates, new territory	Moderate
Dispersal	New territory	High
Return to territory following translocation	Breeding site	Very high