# WHY DID THE CHICKADEE CROSS THE ROAD: EFFECTS OF LINEAR HABITAT GAPS ON THE MOVEMENTS OF BLACK-CAPPED CHICKADEES

by

**Jacob Mackenzie Bailey**

B.Sc. Hons., Thompson Rivers University, 2015

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES (BIOLOGY)

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

September 2017

**Abstract**

I present a novel approach utilizing radio frequency identification (RFID) birdfeeders, coupled with playback experiments, to investigate the gap-crossing decisions of black-capped chickadees (*Poecile atricapillus*). Results from my RFID experiments revealed the best predictors of gap-crossing behaviors were gap-distance, and vegetation density. Birds were less likely to cross as gap distance increased. As the amount of vegetation within gaps increased, birds were more likely to cross. Playback experiments showed a decrease in gap-crossing behaviour after the RFID sampling period. Because birdfeeders were put out during this time, decreases in gap-crossing propensity suggests that birds may be engaging in a tradeoff between energy reserves and risk taking. Results from both experiments confirm that gaps do restrict movements of wintering black-capped chickadees. I recommend the primary way to increase connectivity for birds in fragmented habitats is to reduce the distance across gaps. Furthermore, increasing vegetation within gaps may also increase connectivity.

**Preface**

I directed the design, execution, and analysis of all research in this thesis, and therefore the introductory and concluding chapters are written in first person singular. However, to acknowledge the contributions of collaborators, the two data chapters that constitute the independent studies of this thesis are written in first person plural.

Chapter 2: Bailey JM, Reudink MW, LaZerte SE, Paetkau M, Johnson CJ, Hill DJ, Otter KA (In review). Using radio frequency identification (RFID) to investigate the gap-crossing decisions of black-capped chickadees (*Poecile atricapillus*). The Auk.

Chapter 3: Bailey JM, Reudink MW, Otter KA. Comparing gap-crossing responses in black-capped chickadees (*Poecile atricapillus*) induced by playback to a novel RFID method.

**Table of Contents**

**List of Tables**

**List of Figures**

## Acknowledgements

To be inserted prior to final submission.

**Chapter 1: Introduction**

Habitat loss changes the spatial configuration of the landscape, often resulting in the division of larger habitat patches into smaller and more isolated patches (Didham 2001). Currently, most of the world's forests already lie within 1 km of a forest edge (Haddad et al. 2015). As the earth's population increases, habitat fragmentation is likely to have greater impacts on the planet's ecological systems (Sala et al. 2000, McLaughlin 2011).

Habitat fragmentation can have a number of negative effects on animal populations. Habitat fragmentation increases patch isolation by restricting animal movements among patches (Haddad et al. 2015). Increased patch isolation can result in limited dispersal of juveniles (Beauchamp et al. 1997, With et al. 1997), reduced genetic connectivity among populations (Keller and Largiadèr 2003, Adams and Burg 2015), and decreases in biodiversity (Bregman et al. 2014). Therefore, it is imperative that we understand the impacts of habitat fragmentation in order to implement effective management and conservation strategies.

Gaps in forest habitat, as the result of fragmentation, affect the movement behaviours of a range of taxa (e.g., Villard et al. 1999, Collinge 2000, Harris and Reed 2001, Bélisle and Desrochers 2002, Bakker and Van Vuren 2004, Riley et al. 2006, Janin et al. 2012, Duggan et al. 2012, Smith et al. 2013, Poessel et al. 2014). Yet because of their ability to fly, habitat fragmentation may not be considered a particular threat to birds. However, gaps have been shown to act as significant barriers to the movement of forest songbirds (Desrochers and Hannon 1997; Haddad 1999; Desrochers and Fortin 2000; Bélisle et al. 2001; Harris and Reed 2001; Bélisle and Desrochers 2002), leaving birds susceptible to many of the same adverse effects observed in other taxa.

The primary reason for birds to avoid crossing gaps has generally been attributed to predation risk (e.g., hawks, falcons, and small owls) (Lima and Dill 1990, Rodríguez et al. 2001, Tellería et al. 2001, Desrochers et al. 2002). Because depredation imposes such high fitness costs on an individual, animals should attempt to minimize predation risk even at the sacrifice of other energetic costs. Interestingly, this has been demonstrated in some experimental gap crossing studies (Desrochers and Hannon 1997, St. Clair et al. 1998, Bélisle and Desrochers 2002). St. Clair et al. (1998) used mobbing calls to attract birds from one side of a gap in an attempt to entice the birds to cross. However birds also had the opportunity to fly through a longer forested route, therefore circumventing the gap. Birds were more likely to traverse the forested route (or "detour") that was up to twice the distance of the "direct" gap-crossing route. Presumably this two-to-one threshold is the distance ratio where the energetic costs of taking the longer route outweigh the risk of predation. These results suggest that not only are there clear costs to forest songbirds moving across gaps, but also decision making based on these costs lies within their perceptual range (Lima and Zollner 1996).

Perhaps unsurprisingly, the most prominent factor associated with gap-crossing behaviours is gap distance. Increases in gap distance are consistently related with decreased gap-crossing likelihood in birds (Desrochers and Hannon 1997, St Clair et al. 1998, Rodríguez et al. 2001, Harris and Reed 2001, Bélisle and Desrochers 2002, Tremblay and St. Clair 2009). Increases in gap distance are generally thought to negatively impact gap-crossing likelihoods because crossing larger gaps exposes birds to increased predation risk. A larger gap takes more time to cross, therefore, crossing larger gaps results in greater exposure to predation. Conversely, small gaps pose less exposure, therefore birds are more likely to cross small gaps. This may also

explain why there appears to be a "gap-crossing" threshold distance. If birds perceive a small gap as less risky and a larger gap as more risky, at some distance the risk simply becomes too great.

The vegetation structure within gaps influences the gap-crossing decisions of birds, and helps to facilitate gap-crossing movements (Rodríguez et al. 2001, Tellería et al. 2001, Bélisle and Desrochers 2002). Birds are more likely to cross even moderately sized gaps with some intervening vegetation. This increase in gap-crossing propensity is again likely related to predation risk. If birds have cover to move though within the habitat gap, their exposure to predation is reduced. Vegetation cover may reduce exposure below the threshold risk levels noted above, and allow birds to to move across gaps they otherwise may not.

In addition to the physical attributes of a gap, differences among individual birds can result in varying gap-crossing propensities. For example, differences in gap-crossing behaviour in the hooded warbler (*Setophaga citrina*) have been linked to sex (Norris et al. 2002). In their study, Norris et al. (2002) demonstrated that while the movements of both sexes were negatively impacted by habitat fragmentation, female hooded warblers had a lower propensity to cross gaps than males. The gap-crossing threshold distance for females was also significantly lower than males. Additionally, the pairing status of an individual may play a role in gap-crossing behaviours. Fraser and Stutchbury (2004) demonstrated that paired males were less likely to cross habitat gaps than unpaired males in the scarlet tanager (*Piranga olivacea*). Suggesting that the motivation to find a mate may increase a bird's likelihood to cross gaps. These studies highlight that the differences among individuals can play a role in influencing gap-crossing behaviours.

**1.1     Investigating the Effects of Habitat Fragmentation on Songbirds**

There are a large number of methods for studying animal movements (Rubenstein and Hobson 2004, Kays et al. 2015). One method is translocation or homing experiments (Bélisle et al. 2001, Gobeil and Villard 2002, Desrochers et al. 2010). These experiments are often used to investigate how birds move through fragmented habitats at a landscape scale. Birds are translocated some distance away from their home range or territory. Researchers then compare how long it takes the translocated individuals to return back to their respective territories, and compare these times across landscapes that vary in their degree or type of fragmentation. These studies consistently show that habitat fragmentation constrains the movements of songbirds on the landscape scale (Bélisle et al. 2001, Gobeil and Villard 2002, Castellón and Sieving 2006, Jones et al. 2017). While these studies clearly show that habitat fragmentation has negative impacts on songbird movements, they generally do not track the individual movement paths of the birds in the experiment.  As such, they are limited to making inferences about the specific paths individual birds take through fragmented and non-fragmented habitats. These studies are also limited in sample size to the number of birds that are translocated, but then also detected back in their territories, making this a time and labor intensive method. It is also difficult to use these kinds of experiments to investigate the behaviors of birds as they face each individual gap-crossing decision.

Radiotracking has been employed to investigate patch use and bird movements in fragmented habitats (Norris et al. 2002, Fraser and Stutchbury 2004, MacIntosh et al. 2011). Radiotracking has the benefit of being a relatively passive technique. Birds do not necessarily need to be physically moved (as in translocation studies), or enticed to move through the use of mobbing calls or other stimuli in order to track their movements. Therefore, this allows for a

more natural observation of bird movements, and minimal interaction from the observer. As with translocations, these studies also have the advantage of being able to track the movements of individuals, and therefore can be used to study how behaviours may vary between individuals of differing age, sex, or condition. However, this method is again somewhat labor intensive, as it typically requires investigators to be in the field actively tracking radiotagged individuals. The number of individuals that can be tracked at any given time is also limited to the amount of time investigators can be in the field tracking tagged individuals.

Playback experiments are one of the most common methods for studying the effects of habitat fragmentation on bird movements (Desrochers and Hannon 1997, Rodríguez et al. 2001, Harris and Reed 2001, Bélisle and Desrochers 2002, Tremblay and St. Clair 2009). These experiments involve calling birds from one location to another using mobbing calls, and then comparing responses between playbacks that involve gap-crossing and those that do not. This method is particularly well suited for looking at the effects of specific types of habitat barriers, or the effects of linear breaks in forest habitat (such as roads, powerlines, or pipelines). Playbacks can be effective for investigating gap-crossing decisions of songbirds, as they are easily repeatable and can be used to sample a large number of individuals across many sites with relative ease. However, it is difficult to use playback experiments to track the movements of individuals. Playback studies are also limited to the range which the mobbing calls can be detected by birds. In addition, because predation risk is one of the main deterrents to gap-crossing in birds, these calls might make birds less likely to cross gaps, as mobbing calls generally function to alert others of nearby predators (Curio et al. 1978). While there is some evidence that mobbing calls do not influence the perception of predation risk in black-capped chickadees (*Poecile atricapillus*) (Desrochers et al. 2002), there is also evidence that mobbing

behaviours may be restricted by territory boundaries (Betts et al. 2005). However, this restriction of mobbing behaviour based on territory boundaries was observed during the breeding season, and in two members of the warbler family (black-throated green warblers, *Setophaga virens*, and black-throated blue warblers, *Setophaga caerulescens*) rather than in black-capped chickadees. Given the conflicting results with respect to how birds respond to and perceive mobbing calls, the extent to which using mobbing calls in playback experiments may be influencing the results of gap-crossing studies remains uncertain.

The goal of my research was to identify the factors influencing the gap-crossing decisions of individual black-capped chickadees when faced with linear gaps in forest habitat. My work differs from several of the previous studies I review above, as many of these studies considered how habitat openings (e.g. clearcuts) fragment the landscape and influence movements to circumvent these gaps. My research focused on fragmentation of the landscape via linear gaps that must be crossed and cannot be circumvented. Therefore, radiotracking and homing experiments were less suited for use in my study. In contrast, playback experiments have been well developed to study the impacts of linear gaps, and have been used extensively to do so (Desrochers and Hannon 1997, Rodríguez et al. 2001, Harris and Reed 2001, Bélisle and Desrochers 2002, Tremblay and St. Clair 2009).

I was interested in how the responses of birds to gaps may differ between individuals, and given the limitations of playbacks outlined above, I also developed a novel technique. This technique was passively tracking the movement of birds visiting feeders fitted with Radio frequency identification (RFID) loggers set in a network on the landscape. RFID is well suited to address many of the limitations associated with the other techniques I have described.

## 1.2   Radio Frequency Identification

RFID is becoming an increasingly popular method to investigate a wide range of phenomena in ornithological studies (reviewed by Bonter and Bridge 2011). RFID loggers detect individuals fitted with passive integrated transponders (PIT tags) that come within range of the system's antenna. RFID has a number of benefits over other songbird tracking techniques (Bonter and Bridge 2011). These benefits lend themselves to investigating the decisions of birds when faced with linear gaps. RFID allows for the automated detection of individuals with minimal disturbance from the observer. Therefore, by tracking sequential reads from multiple RFID readers, it is possible to track the movements of individual birds with minimal disruption of their natural movement patterns. Because the tags that are detected by the reader boards are small and lightweight (~2mm/ < 0.15g), they can be effectively utilized on small animals, such as birds (even as small as humming birds - Hou et al. 2015). The lack of a battery on the tags aids in their small size, and also allows for increased longevity of the tags, as compared to radio-telemetry transmitters. The tags and reader boards (Bridge and Bonter 2011) are also relatively low cost allowing researchers to deploy a large number of tags and readers when compared to other techniques, such as GPS or geolocator tags. Importantly, RFID also has potential for integration with other technologies, instruments, or equipment.

I incorporated RFID reader boards into the base of birdfeeders I constructed from a combination of PVC pipe and 3D printed parts. My RFID system was composed of four main parts: 1) an RFID reader board which interprets and writes the data to an SD card, 2) a scanning antenna, 3) transponder tags, and 4) a power source. The RFID reader boards were built to the specifications outlined by Bonter and Bridge (2010). The scanning antenna in our system was located in the perch of the feeder, and detected tagged birds that landed on the feeder. These tags

are mounted within standard leg bands and attached to the bird. When a tag is detected by the bird feeder, it records the date, time, and ID number of the tag, thus giving precise information about a specific bird's location at a given time.

## 1.3    Study Species

Black-capped chickadees are a forest-dwelling species resident in the winter months when birds are most active at feeders. Black-capped chickadees range in size from roughly 10–14 grams, and between 12–15 cm in length (Foote et al. 2010). Black-capped chickadees can be found across most of North America, and as far north as Alaska and as far south as northern New Mexico. Black-capped chickadees are abundant and highly gregarious in winter making catching and banding large numbers of individuals practical (Foote et al. 2010). Gap-crossing behaviours have also been extensively studied in black-capped chickadees (Desrochers and Hannon 1997, St Clair et al. 1998, Desrochers and Fortin 2000, Bélisle et al. 2001, Bélisle and Desrochers 2002, Turcotte and Desrochers 2003, Groom 2009, Tremblay and St. Clair 2009, St-Louis et al. 2014, Adams and Burg 2015) making them a useful subject to determine the relative capacity of RFID tracking to investigate gap-crossing behaviour compared to other techniques, such as playbacks.

## 1.4    Study site

I conducted field work within Prince George BC, Canada (53°55′ N, 122°44′ W) at three separate study areas located within the sub-boreal spruce ecosystem common for the area (Figure 1.1). Study sites were selected among areas of mature (Figure 1.1 A, C) and young (Figure 1.1 B) growth local forest consisting of a mix of conifers (Douglas Fir, *Pseudotsuga menziesii*, Sub-boreal Spruce, *Picea sp.*, Lodgepole Pine, *Pinus contorta*) and deciduous species (Trembling

Aspen, *Populus tremuloides*, Cottonwood, *Populus sp.*, Birch, *Betula sp.*, Willow, *Salix sp.*),

which were intersected by gaps ranging from: walking trails; roads of varying size and activity

level; and, major powerline transmission corridors. Field work took place between November

2015–March 2016 and October 2016–March 2017, beginning roughly when birds settled into

winter flocks and ending near the disbanding of winter flocks prior to the onset of breeding.


## 1.5    Outline of Thesis

The goal of this thesis was to quantify the effects gaps have on the movements of black-capped

chickadees, and to identify factors that influenced their gap-crossing decisions. Furthermore, I

also developed and evaluated a novel methodology for investigating these phenomena. I

organized this thesis into four chapters, consisting of an introduction, two data chapters, and a

concluding chapter. In Chapter 2, I used RFID to investigate the gap-crossing decisions of black-

capped chickadees, and model what factors best predict their gap-crossing decisions. In Chapter

3, I use playbacks to further assess the permeability of habitat gaps to black-capped chickadee

movements, and to evaluate and verify the results from the experiments described in Chapter 2.

This thesis concludes with Chapter 4, where I provide context for the research I have conducted,

provide suggestions for future research directions, and outline the potential conservation and

management implications of my work.

## 1.6 Literature Cited

Adams, R. V., and T. M. Burg (2015). Gene flow of a forest-dependent bird across a fragmented landscape. PLoS ONE 10:e0140938.

Bakker, V. J., and D. H. Van Vuren (2004). Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. Conservation Biology 18:689–697.

Beauchamp, G., M. Belisle, and L.-A. Giraldeau (1997). Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. Journal of Animal Ecology 66:671–682.

Bélisle, M., and A. Desrochers (2002). Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17:219–231.

Bélisle, M., A. Desrochers, and M.-J. Fortin (2001). Influence of forest cover on the movements of forest birds: a homing experiment. Ecology 82:1893–1904.

Betts, M. G., A. S. Hadley, and P. J. Doran (2005). Avian mobbing response is restricted by territory boundaries: experimental evidence from two species of forest warblers. Ethology 111:821–835.

Bonter, D. N., and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. Journal of Field Ornithology 82:1–10.

Bregman, T. P., C. H. Sekercioglu, and J. A. Tobias (2014). Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation. Biological Conservation 169:372–383.

Bridge, E. S., and D. N. Bonter (2011). A low-cost radio frequency identification device for ornithological research: Low-cost RFID reader. Journal of Field Ornithology 82:52–59.

Castellón, T. D., and K. E. Sieving (2006). An experimental test of matrix permeability and corridor use by an endemic understory bird. Conservation Biology 20:135–145.

Collinge, S. K. (2000). Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81:2211–2226.

Curio, E., U. Ernst, and W. Vieth (1978). The adaptive significance of avian mobbing. Zeitschrift für Tierpsychologie 48:184–202.

Desrochers, A., M. Bélisle, and J. Bourque (2002). Do mobbing calls affect the perception of predation risk by forest birds? Animal Behaviour 64:709–714.

Desrochers, A., M. Bélisle, J. Morand-Ferron, and J. Bourque (2010). Integrating GIS and homing experiments to study avian movement costs. Landscape Ecology 26:47–58.

Desrochers, A., and M.-J. Fortin (2000). Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. Oikos 91:376–384.

Desrochers, A., and S. J. Hannon (1997). Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204–1210.

Didham, R. K. (2001). Ecological consequences of habitat fragmentation. In eLS. John Wiley & Sons, Ltd.

Duggan, J. M., E. J. Heske, and R. L. Schooley (2012). Gap-crossing decisions by adult Franklin's ground squirrels in agricultural landscapes. Journal of Mammalogy 93:1231–1239.

Foote, Jennifer R., Daniel J. Mennill, Laurene M. Ratcliffe and Susan M. Smith.(2010). Black-capped chickadee (*Poecile atricapillus*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna-org.prxy.lib.unbc.ca/Species-Account/bna/species/bkcchi

Fraser, G. S., and B. J. M. Stutchbury (2004). Area-sensitive forest birds move extensively among forest patches. Biological Conservation 118:377–387.

Gobeil, J.-F., and M.-A. Villard (2002). Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. Oikos 98:447–458.

Griffith, S. C., I. P. F. Owens, and K. A. Thuman (2002). Extra pair paternity in birds: a review of interspecific variation and adaptive function. Molecular Ecology 11:2195–2212.

Groom, J. D. (2009). Patch colonization dynamics in Carolina chickadees (*Poecile carolinensis*) in a fragmented landscape: A manipulative study. The Auk 123:1149–1160.

Haddad, N. M. (1999). Corridor use predicted from behaviors at habitat boundaries. The American Naturalist 153:215–227.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

Harris, R. J., and J. M. Reed (2001). Territorial movements of black-throated blue warblers in a landscape fragmented by forestry. The Auk 118:544–549.

Hou, L., M. Verdirame, and K. C. Welch (2015). Automated tracking of wild hummingbird mass and energetics over multiple time scales using radio frequency identification (RFID) technology. Journal of Avian Biology 46:1–8.

Janin, A., J.-P. Léna, and P. Joly (2012). Habitat fragmentation affects movement behavior of migrating juvenile common toads. Behavioral Ecology and Sociobiology 66:1351–1356.

Jones, C. D., K. W. Stodola, J. Coombs, M. P. Ward, and R. J. Cooper (2017). Responses of Bachman's sparrows and prairie warblers to fragmentation. The Journal of Wildlife Management 81:347–355.

Kays, R., M. C. Crofoot, W. Jetz, and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

Keller, I., and C. R. Largiadèr (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London B: Biological Sciences 270:417–423.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Lima, S. L., and P. A. Zollner (1996). Towards a behavioral ecology of ecological landscapes. Trends in Ecology & Evolution 11:131–135.

MacIntosh, T., B. J. M. Stutchbury, and M. L. Evans (2011). Gap-crossing by wood thrushes (*Hylocichla mustelina*) in a fragmented landscape. Canadian Journal of Zoology 89:1091–1097.

McLaughlin, D. W. (2011). Land, food, and biodiversity. Conservation Biology 25:1117–1120.

Norris, D. R., B. J. M. Stutchbury, and F. Thompson III (2002). Sexual differences in gap-crossing ability of a forest songbird in a fragmented landscape revealed through radiotracking. The Auk 119:528–532.

Poessel, S. A., C. L. Burdett, E. E. Boydston, L. M. Lyren, R. S. Alonso, R. N. Fisher, and K. R. Crooks (2014). Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. Biological Conservation 180:224–232.

Ricketts, T. H. (2001). The Matrix Matters: Effective Isolation in Fragmented Landscapes. The American Naturalist 158:87–99.

Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne (2006). A southern California freeway is a physical and social barrier to gene flow in carnivores: Physical and social barrier to gene flow. Molecular Ecology 15:1733–1741.

Rodríguez, A., H. Andrén, and G. Jansson (2001). Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95:383–396.

Rubenstein, D. R., and K. A. Hobson (2004). From birds to butterflies: animal movement patterns and stable isotopes. Trends in Ecology & Evolution 19:256–263.

Sala, O. E., F. S. Chapin, Iii, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, et al. (2000). Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Smith, M. J., G. J. Forbes, and M. G. Betts (2013). Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). Biological Conservation 168:176–183.

St Clair, C. C., M. Bélisle, A. Desrochers, and S. Hannon (1998). Winter responses of forest birds to habitat corridors and gaps. Conservation Ecology 2:13.

St-Louis, V., J. D. Forester, D. Pelletier, M. Bélisle, A. Desrochers, B. Rayfield, M. A. Wulder, and J. A. Cardille (2014). Circuit theory emphasizes the importance of edge-crossing decisions in dispersal-scale movements of a forest passerine. Landscape Ecology 29:831–841.

Tellería, J. L., E. Virgós, R. Carbonell, J. Pérez-Tris, and T. Santos (2001). Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. Oikos:253–264.

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.

Turcotte, Y., and A. Desrochers (2003). Landscape-dependent response to predation risk by forest birds. Oikos 100:614–618.

Villard, M. A., M. K. Trzcinski, and G. Merriam (1999). Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13:774–783.

With, K. A., R. H. Gardner, and M. G. Turner (1997). Landscape connectivity and population distributions in heterogeneous environments. Oikos:151–169.

## 1.7 Figures
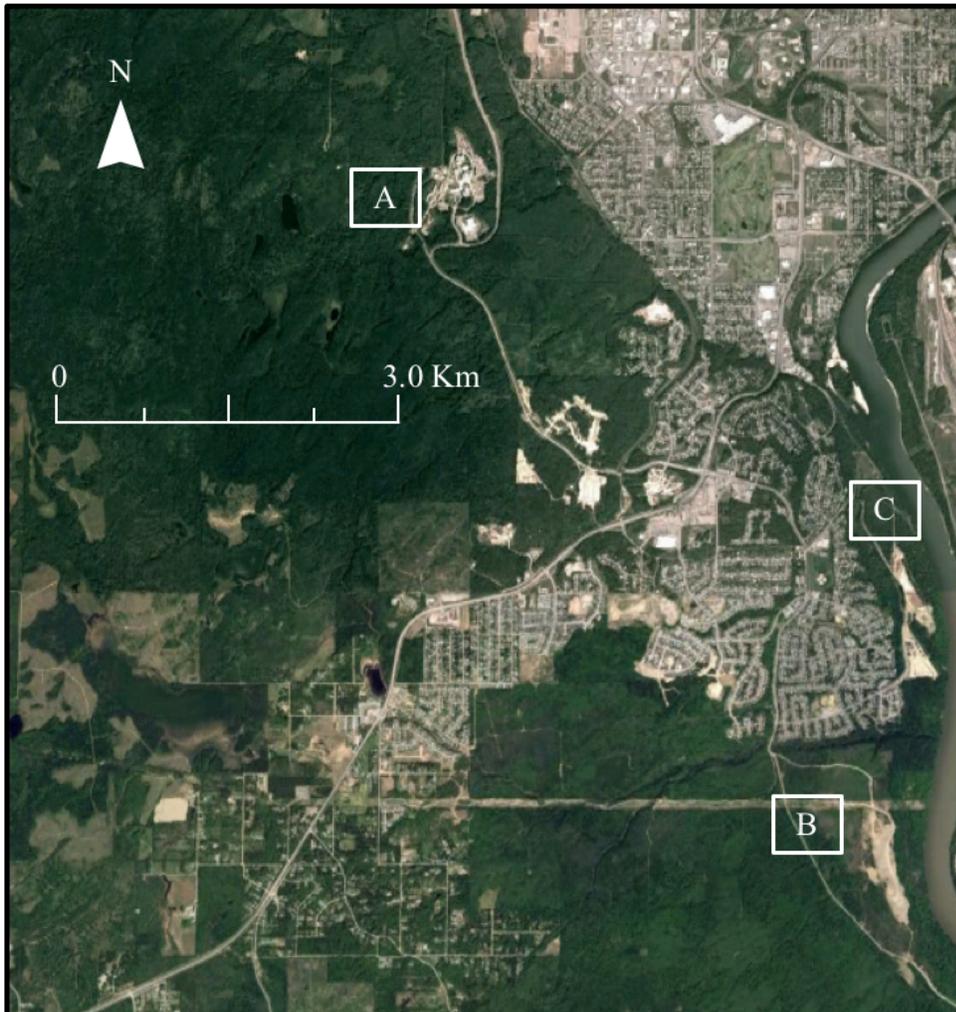


Figure 1.1 Locations of the three study areas near Prince George BC, including The University of Northern British Columbia Campus (A), a forest service road and major power transmission corridor (B), and newly developed road planned for residential construction (C).

**Chapter 2: Using Radio Frequency Identification (RFID) to Investigate the Gap-Crossing Decisions of Black-Capped Chickadees (*Poecile atricapillus*)**

## 2.1 Abstract

Gaps in forest habitat are well documented to negatively impact the movements of forest songbirds. However, much past research has utilized playback experiment designs, making it difficult to investigate long term movement patterns and identify factors that influence the movements of individuals. Here, we present a novel approach utilizing RFID to investigate gap-crossing decisions in black-capped chickadees. Using bird feeders outfitted with RFID readers, we were able to track the movement patterns of wintering black capped chickadees within forests and across gaps. We used logistic regression and an information theoretic approach to identify the factors that best predicted gap-crossing behaviours. There was evidence that gaps impeded movements of wintering black-capped chickadees, and that the best predictors of gap-crossing behaviours were site-specific factors. Birds were more likely to cross gaps with decreasing gap size and greater vegetation density over 1m high within the gap. We recommend that the primary way to increase connectivity for birds in fragmented habitats is to reduce the distance across gaps. Additionally, it may be beneficial increase shrubby or woody vegetation within the gap to a height of over 1m, as this also increases the likelihood of gap-crossing.

## 2.2 Introduction

Anthropogenic development and deforestation are causing increasing habitat fragmentation worldwide (Haddad et al. 2015). The result is a matrix of forest patches separated by deforested gaps that must be navigated by forest-dwelling animals. These gaps affect the movements and distribution of many taxa (e.g., Villard et al. 1999, Collinge 2000, Harris and Reed 2001, Bélisle and Desrochers 2002, Bakker and Van Vuren 2004, Riley et al. 2006, Janin et al. 2012, Duggan et al. 2012, Smith et al. 2013, Poessel et al. 2014), and can result in reduced connectivity between populations (Keller and Largiadèr 2003, Riley et al. 2006, Adams and Burg 2015) and decreased potential for juvenile dispersal (Beauchamp et al. 1997, With et al. 1997).

Gaps in forest habitat can impede movement between patches for many forest bird species (Desrochers and Hannon 1997, Harris and Reed 2001, Norris et al. 2002, Fraser and Stutchbury 2004). Generally, gap-crossing decisions are investigated using playbacks, a design that has become one of the standard methods for examining gap-crossing decisions in birds (Rodríguez et al. 2001, Harris and Reed 2001, Bélisle and Desrochers 2002, Tremblay and St. Clair 2009). Although playbacks are a practical and effective method for investigating gap-crossing behaviours, they are limited in a few ways. First, because birds generally use mobbing calls in the presence of predators (Curio et al. 1978), the use of mobbing calls during playback experiments may inflate the perception of predation risk. If birds perceive a greater predation risk when mobbing calls are played, they may be less willing to cross gaps than under other conditions. While there is evidence that mobbing call playbacks may influence risk-taking behaviour only at short distances from the playback speaker (i.e., <5m) (Desrochers et al. 2002), the degree to which this effect could be influencing bird movements in playback experiments remains unclear. Second, playback experiments often only describe short-term movement

patterns. In many cases playback trials last only several minutes (e.g., Desrochers and Hannon 1997, St Clair et al. 1998, Harris and Reed 2001, Bélisle and Desrochers 2002). Finally, because it is difficult to both identify and keep track of individuals during playbacks, it is difficult to use this type of study to determine what factors may be influencing individual bird movements and to investigate how gap-crossing propensities may vary between individuals.

Here, we use a novel approach with respect to the investigation of gap-crossing decisions in birds. We employed RFID as an alternative means to assess the permeability of habitat gaps, and to identify the individual factors that best predict avian gap-crossing decisions. By incorporating RFID readers into bird feeders (Bonter and Bridge 2011), we were be able to track the sequential movement patterns of wintering black-capped chickadees banded with PIT tags as they moved both within forests and across gaps. RFID is uniquely suited to address the limitations of playback studies, and to provide insight into the individual-specific factors that influence movement patterns. This approach enabled us to track the movements of individual birds over multiple days, and examine movement patterns over a longer time period than with playbacks. Importantly, the use of RFID feeders also allowed us to track birds across gaps without the use of mobbing calls which may influence gap-crossing decisions. Using RFID feeders to track bird movements, rather than using mobbing calls to entice birds to move, also allows us the ability to generalize our results to a broader range of scenarios, such as foraging or juvenile dispersal.

We predicted that birds would move more frequently between feeders that are on the same side of a gap compared to feeders placed on opposite sides of a gap. Furthermore, we predicted that that birds would also be less likely to travel between feeders on opposite sides of gaps as the size of the gap increased. We also predicted that smaller and younger birds would be

more likely to cross gaps, as these birds may have lower energetic reserves and/or less wintering experience than larger and older birds. Younger birds may therefore have greater incentive to cross habitat gaps, or less incentive to avoid them (Turcotte and Desrochers 2003, Zollner and Lima 2005).

## 2.3 Methods

### 2.3.1 RFID Feeders

We incorporated reader boards into the base of birdfeeders we constructed from a combination of PVC pipe and 3D printed parts. The RFID reader boards were built to the specifications outlined by Bonter and Bridge (2010) and were powered by eight C cell 1.5 V batteries. The scanning antenna in our system was located in the perch of the feeder, and detected tagged individuals that landed on the feeder. Our feeders logged data once per second if a tag was detected, and wrote these data to a text file stored on a 2GB SD card. The detection period for the feeder was 200 ms with a cycle time of 1000 ms. The detection frequency for both our feeders and PIT tags was 125 kHz. Data were only written if a tag was detected by the feeder.

PIT tags (IB Technology, Aylesbury UK) contained a microchip programed with a unique 10-digit identification code. These tags were mounted within leg bands and attached to the bird. Passive transponder tags do not have their own power source, and therefore can only be detected within the range of the antenna (approximately 2–3 cm).

### 2.3.2 Experimental Design

For each experiment (site), four RFID feeders were placed out simultaneously in a square arrangement centred on a linear habitat gap. Movements between feeders on the same side of a

gap did not require gap-crossing, while movement between feeders on opposite sides of a gap did require gap-crossing. By setting up feeders in this arrangement, we were able to compare the number of movements between feeders within the same forest patch and across gaps. Furthermore, because we tracked individual birds we were able to investigate factors that influenced each individual's movements (Table 2.1).

Habitat gaps were trails, roads, and power-line cuts that varied in width from 10–84m. For a given site, the distance between all feeders was equal, ranging from 90–150m depending on the size of the gap. A total of 15 sites were sampled across the 2015/2016 (n = 4) and 2016/2017 (n = 11) winters. Gap distances were measured using a Bushnell YardagePro Sport 600 laser rangefinder. At each site feeders were set up for 7 days. Only one set of 4 feeders was set up at each of the three study areas at a given time. Feeders were filled every 2–3 days (depending on usage) to ensure they were not empty at any time during the trial. Feeders were programmed to turn on one hour before sunrise and to turn off one hour after sunset to preserve battery power.

### 2.3.3   Field Methods

At each site prior to setting up the RFID feeders, we banded 4–24 black-capped chickadees (Mean = 12 SD = 5) with PIT-tag mounted leg bands for a total of 192 individuals. For each site, birds were banded at two locations – one location on each side of the gap – located halfway between where the RFID feeders would subsequently be placed. We caught birds using standard passerine mist nets or Potter's traps. We then banded the birds with a single Canadian Wildlife Service aluminum band and a single 2.3 mm PIT tag.  We classified adult birds as either, hatch-year (HY) second-year (SY), after hatch-year or after-second-year (ASY) by assessing the

amount of white edging on their outer rectrices (Pyle 1997). For the purposes of analysis, birds were split into two age classes: birds in their second-year and younger, and birds older than second year, as the distinction between HY/SY and AHY/ASY birds is based on a calendar year and for our purposes not biologically relevant. We measured flattened wing chord length (mm), tail length (mm), tarsus length (mm), and weight (g) for each bird. We also calculated a weight-to-tarsus ratio, by regressing weight and tarsus and then using the residuals from that regression in our models. We used this measurement as a proxy of bird condition, with larger tarsus and lower weight indicating better body condition (Johnson et al. 1985). As black-capped chickadees are sexually monomorphic, and we were not capturing birds during the breeding season, all birds were sexed based on a combination of weight, wing, and tail measurements, and designated as either male, female, or unknown (Desrochers 1990).

### 2.3.4 Gap Vegetation

We classified gap vegetation for each site using digital photography to measure the density of shrubby vegetation within the gaps. Photos of a $1m^2$ board divided into a grid of 9 equal sized squares were taken at a distance of 5m. The amount of the board that was obstructed by the vegetation as a percentage was estimated to the nearest 5percent (i.e., greater the percent of the board that was obstructed, the denser the vegetation in the gap). One photo was taken at ground level, and another was taken at 1m height. Therefore, gap vegetation was represented from the ground to 1m height and from 1m to 2m height. Vegetation was sampled at half the distance across the gap, in direct line with both feeders on opposite sides of the gap. Vegetation was also sampled at one location in the centre of the gap, at each site.  We chose these points to sample vegetation as to be representative of the assumed path for birds between feeders. Vegetation

densities were then averaged for each site, and each site was then given this single value for its vegetation density score.

### 2.3.5 Weather Data

We obtained daily temperature data form the Environment Canada website (http://climate.weather.gc.ca/climate_data/daily_data_e.html?StationID=48370). Data on daily temperature included the maximum, minimum, and mean daily temperatures. These data were recorded at a weather station located at the Prince George International Airport (53°53' N, 122°40' W), roughly 6 km east from study area B and C, and roughly 9 km south-east from study area A (Figure 2.1). For 9 days during the study period daily temperature data were not available. For these 9 days the maximum, minimum, and mean daily temperatures were estimated by averaging the respective values for each variable from the day immediately before and after the missing value.

### 2.3.6 Data Analysis

We used R (R Development Core Team, 2008, 3.3.1) to organize the data, remove erroneous reads, and link the individual visits between feeders into movements using the R package feedr (v.0.9.0, LaZerte et al. 2017). A single read of a tagged individual, or multiple reads of the same individual with less than 3s between reads, was considered a single visit. Birds were considered to have made a movement between two feeders if they visited one feeder and then visited a different feeder at the same site at a later time on the same day. Only sequential visits between different feeders were considered moves. Movements that occurred over multiple days (e.g., present at one feeder in the evening and a different feeder the next morning) were not included in

analysis. We chose to exclude movements over multiple days because as the time between movements increases, it becomes more difficult to identify the factors that may have influenced that movement. Occasionally tags would be misread by the feeders, recording tag numbers that either did not exist or were never put on birds. We cross referenced all recorded tags in our data with our banding records and excluded any reads that did not match our records. For all analyses, only birds that made at least one movement between two feeders at a single site were included in the analysis. One site was excluded from analysis because birds only moved between two of the feeders in the grid, hindering our ability to make meaningful inferences about gap-crossing behaviours from these data. For all other sites at least 3 feeders recorded movements by birds between them.

### 2.3.7   Statistical Analysis

We used generalized linear models to investigate the movements and gap-crossing decisions of monitored birds.  First, we used a count model (negative binomial distribution, log link function) to investigate if gaps acted as barriers to bird movements. For this model, movements for each bird were summarized by type of movement (either across gap or within forest). Our dependant variable was the number of moves an individual bird made, and our independent variable was whether or not these movements were within contiguous forest or across gaps. Because many birds made zero movements of one type or the other, and because the count data were overdispersed, we used a negative binomial count model.

Second, we used logistic regression (binomial distribution, logit link function) to explore the factors that predicted gap crossing behaviour by black-capped chickadees. For these models, each individual bird movement was recorded as a single observation, with that movement either

being a non-gap crossing movement (0), or a gap-crossing movement (1). We used 14 variables to develop 18 models hypothesized to predict differences in gap-crossing behaviour among birds (Table 2.1). Model subsets were grouped by the type of variables included in the models: individual black-capped chickadee characteristics, study site characteristics/habitat, and a combination of variables from both subsets.

For the models predicting gap crossing behaviours, we used Akaike's Information Criterion with the correction for small sample size ($AIC_c$) to identify the most parsimonious model of the set (Anderson et al. 2000). For the most parsimonious model, we presented the non-standardized regression coefficients and the corresponding 95% confidence intervals. Confidence intervals that did not overlap 0 represented covariates with sufficient magnitude and precision to be considered statistically significant. We clustered data on bird ID to correct the variance for repeated sampling across time (Rogers 1994). We measured the fit of our top model by assessing the receiver operating characteristic (ROC), using a jackknife sampling method to produce independent predicted probabilities (Fielding and Bell 1997). We considered a model with an 'area under the curve' (AUC) score of 0.7 to 0.9 to be a good predictor and a model with a score of >0.9 as an excellent predictor of gap-crossing by monitored birds (Boyce et al. 2002). We used tolerance scores to check all variables for collinearity. All analyses were conducted with Stata 14 (StataCorp 2015).

## 2.4   Results

### 2.4.1   Count Model

A total of 2971 individual bird movements fit our criteria for analysis. Of the total movements, 2000 were between feeders on the same side of a habitat gap (no gap crossing), while 971 were

between feeders on opposite sides of a gap. Of the 192 birds banded, 130 made at least one

movement between two feeders that, again, fit our criteria for analysis. On average birds made

11.98 (SD = 18.07) movements between feeders on the same side of a gap, and 5.07 (SD = 6.35)

movements between feeders on opposite sides of a gap. The maximum number of movements a

single bird made between feeders was 110 and 32 for feeders on the same side and opposite sides

of the gap respectively.  Overall, birds made significantly fewer movements between feeders on

opposite sides of habitat gaps compared to movements between feeders on the same side of a gap

(Wald $\chi^2$ = 24.76 , $n$ = 334 , $P$<0.001; Table 2.2).


*2.4.2   Gap-Crossing Model Selection and Fit*

Of our proposed logistic regression models predicting gap-crossing behaviours, the

model with the lowest $AIC_c$ score belonged to the subset of models relating crossing behaviours

to a combination of study site and individual bird characteristics (Table 2.3). This model

included terms for gap distance, vegetation at 0–1m height, and vegetation at 1–2m height, zone

(study area), age, and sex, (Table 2.4). That model had good predictive performance (ROC =

0.74 SE = 0.001). However, only the variables gap distance and vegetation at 1–2m height had

confidence intervals that did not overlap 0 (Figure 2.2). Birds were 1.8 times less likely to cross

gaps as size increased from 10m to 40m, and 3.7 times less likely to cross as gap distance

increased to 70 m (Figure 2.3). Birds were also more likely to cross gaps as vegetation at 1–2m

height increased. For each 5% increase in vegetation density at 1–2m, crossing likelihood

increased by 1.7 times (Figure 2.4).

## 2.5   Discussion

Our results support previous findings that gaps in forest habitat impede the movements of forest songbirds (Desrochers and Hannon 1997, St Clair et al. 1998, Harris and Reed 2001, Bélisle et al. 2001, Develey and Stouffer 2001, Norris et al. 2002, Bélisle and Desrochers 2002, Creegan and Osborne 2005, Robertson and Radford 2009, Tremblay and St. Clair 2009, Adams and Burg 2015, ). As expected, gap distance played an important role in influencing gap-crossing decisions. Further, a key finding in our study was that the impact of gaps on bird movements can be partially mitigated by the presence of shrubby vegetation (1–2m) in the gap, which greatly increased the propensity of birds to cross even large openings. The most plausible explanation for why gaps impede movement for birds appears to be an increase in predation risk (Rodríguez et al. 2001, Tellería et al. 2001, Bélisle and Desrochers 2002), and vegetation in the gap likely decreases the birds' perception of risk exposure by allowing them to cross gaps via "stepping stones" of cover. Therefore, vegetation management could be an effective tool to decrease the effect of even large gaps acting as barriers to birds.

Some authors have suggested that the characteristics of individual birds are important when predicting how birds will move though fragmented habitats (Tellería et al. 2001, Bélisle and Desrochers 2002, Norris et al. 2002, Cox and Kesler 2012 ). We predicted that older birds, generally in better condition than younger birds, would be less likely to engage in a risky behaviour such as gap-crossing (Turcotte and Desrochers 2003, Zollner and Lima 2005). We designed our experiment to identify how differences among individual influence movements, however we found little evidence that individual variation influenced gap-crossing behaviours in black-capped chickadees. Because birds did not differ in their propensity to cross gaps based on age, sex, or size/condition, this suggests that increases in energetic costs of gap-crossing and/or

differences in wintering experience do not adequately explain the reluctance of forest birds to cross gaps. In contrast, other studies performed during the breeding season have found evidence suggesting male birds may be less adverse than females to gap-crossings potentially as they seek out EPCs (Norris et al. 2002, MacIntosh et al. 2011). This suggests that individual differences in gap-crossing may perhaps be seasonally dependent.

## 2.6 Literature Cited

Adams, R. V., and T. M. Burg (2015). Gene flow of a forest-dependent bird across a fragmented landscape. PLoS ONE 10:e0140938.

Anderson, D. R., K. P. Burnham, and W. L. Thompson (2000). Null hypothesis testing: problems, prevalence, and an alternative. The Journal of Wildlife Management 64:912–923.

Bakker, V. J., and D. H. Van Vuren (2004). Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. Conservation Biology 18:689–697.

Beauchamp, G., M. Belisle, and L.-A. Giraldeau (1997). Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. Journal of Animal Ecology 66:671–682.

Bélisle, M., and A. Desrochers (2002). Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17:219–231.

Bélisle, M., A. Desrochers, and M.-J. Fortin (2001). Influence of forest cover on the movements of forest birds: A homing experiment. Ecology 82:1893–1904.

Bonter, D. N., and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. Journal of Field Ornithology 82:1–10.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow (2002). Evaluating resource selection functions. Ecological Modelling 157:281–300.

Collinge, S. K. (2000). Effects of grassland fragmentation on insect species loss, colonization, and movement patterns. Ecology 81:2211–2226.

Cox, A. S., and D. C. Kesler (2012). Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. Behavioral Ecology 23:1068–1077.

Creegan, H. P., and P. E. Osborne (2005). Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. Journal of Applied Ecology 42:678–687.

Curio, E., U. Ernst, and W. Vieth (1978). The Adaptive Significance of Avian Mobbing. Zeitschrift für Tierpsychologie 48:184–202.

Desrochers, A. (1989). Sex, dominance, and microhabitat use in wintering black-capped chickadees: A field experiment. Ecology 70:636–645.

Desrochers, A. (1990). Sex determination of black-capped chickadees with a discriminant analysis. Journal of Field Ornithology 61:79–84.

Desrochers, A., M. Bélisle, and J. Bourque (2002). Do mobbing calls affect the perception of predation risk by forest birds? Animal Behaviour 64:709–714.

Desrochers, A., and M.-J. Fortin (2000). Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. Oikos 91:376–384.

Desrochers, A., and S. J. Hannon (1997). Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204–1210.

Develey, P. F., and P. C. Stouffer (2001). Effects of roads on movements by understory birds in mixed-species flocks in central Amazonian Brazil. Conservation Biology 15:1416–1422.

Duggan, J. M., E. J. Heske, and R. L. Schooley (2012). Gap-crossing decisions by adult Franklin's ground squirrels in agricultural landscapes. Journal of Mammalogy 93:1231–1239.

Fielding, A. H., and J. F. Bell (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Foote, Jennifer R., Daniel J. Mennill, Laurene M. Ratcliffe and Susan M. Smith.(2010). Black-capped chickadee (*Poecile atricapillus*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna-org.prxy.lib.unbc.ca/Species-Account/bna/species/bkcchi

Fraser, G. S., and B. J. M. Stutchbury (2004). Area-sensitive forest birds move extensively among forest patches. Biological Conservation 118:377–387.

Groom, J. D. (2009). Patch colonization dynamics in Carolina Chickadees (*Poecile carolinensis*) in a fragmented landscape: A manipulative study. The Auk 123:1149–1160.

Haddad, N. M. (1999). Corridor use predicted from behaviors at habitat boundaries. The American Naturalist 153:215–227.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, et al. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

Harris, R. J., and J. M. Reed (2001). Territorial movements of black-throated blue warblers in a landscape fragmented by forestry. The Auk 118:544–549.

Janin, A., J.-P. Léna, and P. Joly (2012). Habitat fragmentation affects movement behavior of migrating juvenile common toads. Behavioral Ecology and Sociobiology 66:1351–1356.

Johnson, D. H., G. L. Krapu, K. J. Reinecke, and D. G. Jorde (1985). An evaluation of condition indices for birds. The Journal of Wildlife Management 49:569–575.

Keller, I., and C. R. Largiadèr (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London B: Biological Sciences 270:417–423.

LaZerte, S. E., M. W. Reudink, K. A. Otter, J. Kusack, J. M. Bailey, A. Woolverton, M. Paetkau, A. de Jong, and D. J. Hill (2017). feedr and animalnexus.ca: A paired R package and user-friendly Web application for transforming and visualizing animal movement data from static stations. Ecology and Evolution 00:1-13.

MacIntosh, T., B. J. M. Stutchbury, and M. L. Evans (2011). Gap-crossing by wood thrushes (*Hylocichla mustelina*) in a fragmented landscape. Canadian Journal of Zoology 89:1091–1097.

Norris, D. R., B. J. M. Stutchbury, and F. Thompson III (2002). Sexual differences in gap-crossing ability of a forest songbird in a fragmented landscape revealed through radiotracking. The Auk 119:528–532.

Poessel, S. A., C. L. Burdett, E. E. Boydston, L. M. Lyren, R. S. Alonso, R. N. Fisher, and K. R. Crooks (2014). Roads influence movement and home ranges of a fragmentation-sensitive carnivore, the bobcat, in an urban landscape. Biological Conservation 180:224–232.

Ricketts, T. H. (2001). The matrix matters: effective isolation in fragmented landscapes. The American Naturalist 158:87–99.

Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne (2006). A southern California freeway is a physical and social barrier to gene flow in carnivores: Physical and Social Barrier To Gene Flow. Molecular Ecology 15:1733–1741.

Robertson, O. J., and J. Q. Radford (2009). Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecology 34:435–446.

Rodríguez, A., H. Andrén, and G. Jansson (2001). Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95:383–396.

Rogers, W. (1994). Regression standard errors in clustered samples. Stata Technical Bulletin 3.

Smith, M. J., G. J. Forbes, and M. G. Betts (2013). Landscape configuration influences gap-crossing decisions of northern flying squirrel (*Glaucomys sabrinus*). Biological Conservation 168:176–183.

StataCorp (2015) Stata Statistical Software: Release 14. StataCorp., College Station, Texas, USA.

St. Clair, C. C., M. Bélisle, A. Desrochers, and S. Hannon (1998). Winter responses of forest birds to habitat corridors and gaps. Conservation Ecology 2:13.

St-Louis, V., J. D. Forester, D. Pelletier, M. Bélisle, A. Desrochers, B. Rayfield, M. A. Wulder, and J. A. Cardille (2014). Circuit theory emphasizes the importance of edge-crossing decisions in dispersal-scale movements of a forest passerine. Landscape Ecology 29:831–841.

Tellería, J. L., E. Virgós, R. Carbonell, J. Pérez-Tris, and T. Santos (2001). Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. Oikos:253–264.

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.

Turcotte, Y., and A. Desrochers (2003). Landscape-dependent response to predation risk by forest birds. Oikos 100:614–618.

Villard, M. A., M. K. Trzcinski, and G. Merriam (1999). Fragmentation effects on forest birds: Relative influence of woodland cover and configuration on landscape occupancy. Conservation Biology 13:774–783.

With, K. A., R. H. Gardner, and M. G. Turner (1997). Landscape connectivity and population distributions in heterogeneous environments. Oikos:151–169.

Zollner, P. A., and S. L. Lima (2005). Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108:219–230.

## 2.7 Tables

Table 2.1 Description of independent variables and coding used to predict gap-crossing behaviours of black-capped chickadees. Variables are split into 2 categories, bird demographics and site characteristics, and used to create the three model subsets. Combination models consisted of variables from both categories.

| Model  Subsets and Variable | Description |
| --- | --- |
| Bird Demographics | |
| Age | Bird age class (0 = SY, 1 = ASY) |
| Sex | Male, Female, or Unknown |
| Weight to Tarsus Ratio | Ratio of bird weight to tarsus length, used as proxy for condition; larger ratio indicates better condition. |
| Site | |
| Gap Distance | Average width for the gap for a given site. |
| Vegetation (0m) | Vegetation density for a gap at 0–1 m height. |
| Vegetation (1m) | Vegetation density for a gap at 1–2 m height. |
| Traffic Presence | Whether or not there was vehicle traffic in the gap (i.e., roads had traffic while trails and powerlines did not.) |
| Study Area | Indicates study area A, B , or C (See Figure 1.1) |
| Elapsed Movement Time | Amount of time elapsed between detections at two feeders or movement time. |
| Min. Daily Temperature | Minimum temperature for the day a movement occurred on. |
| Max Daily Temperature | Maximum temperature for the day a movement occurred on. |
| Mean Daily Temperature | Mean temperature for the day a movement occurred on. |
| Date | Modified ordinal date as number of days since October 1. |
| Day of Experiment | Day number of experiment (e.g., First day of experiment = 1, last day of experiment = 7). |

Table 2.2 Results of the negative binomial count model comparing the number of movements by black-capped chickadees between feeders separated by a gap to those in continuous forest (Wald $\chi^2 = 24.76$, $n = 334$, $P<0.001$).

|  |  |  |  |  |  | 95% Ci | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Model | Variable | Coefficient | Std. Err. | $z$ | $P$ | Lower | Upper |
| Gap-crossing count model | Move type (gap or continuous movement) | $-0.74$ | 0.15 | $-4.98$ | <0.001 | $-1.04$ | $-0.45$ |

Table 2.3 Proposed candidate models, number of parameters (*K*), log-likelihoods (LL), Akaike's

Information Criterion (AIC$_c$) Scores, and AIC$_c$ differences from the top model (bold) used to

quantify gap-crossing decisions by monitored black-capped chickadees.

| Model | *K* | LL | AIC$_c$ | AIC DIFF |
|---|---|---|---|---|
| Bird Characteristics | | | | |
| Age, WT ratio, Sex | 5 | − 1646.55 | 3297.12 | 491.52 |
| WT ratio, Age | 3 | − 1648.89 | 3299.79 | 494.19 |
| WT ratio, Sex | 4 | − 1658.03 | 3319.08 | 513.48 |
| Age | 2 | − 1659.25 | 3319.51 | 513.91 |
| Sex, Age | 4 | − 1658.62 | 3320.26 | 514.66 |
| Sex | 3 | − 1671.67 | 3345.36 | 539.76 |
| | | | | |
| Site/Habitat Characteristics | | | | |
| Gap dist, Veg(0m), Veg(1m), Study area | 6 | − 1416.02 | 2837.07 | 31.47 |
| Gap dist,Veg(0m), Veg(1m) | 4 | − 1445.79 | 2894.59 | 89.00 |
| Gap dist,Veg(0m), Veg(1m), Traffic | 5 | − 1445.77 | 2895.56 | 89.96 |
| Veg(0m),Veg(1m), Traffic | 4 | − 1488.25 | 2979.51 | 173.91 |
| Gap dist, Max temp, Min temp, Mean temp | 5 | − 1495.75 | 2995.52 | 189.92 |
| Gap distance | 2 | − 1528.77 | 3058.55 | 252.95 |
| Max temp, Min temp, Mean temp, Date, Exp day | 5 | − 1583.39 | 3170.80 | 365.21 |
| | | | | |
| Site/Habitat + Bird Characteristics | | | | |
| **Gap dist, Veg(0m), Veg(1m), Study area, Age, Sex** | **9** | **− 1398.77** | **2805.60** | **0.00** |
| Gap dist, Veg(0m), Veg(1m), Age, Sex | 7 | − 1418.79 | 2843.62 | 38.02 |
| Gap dist, Vege(0m), Veg(1m), Age | 5 | − 1435.21 | 2874.44 | 68.84 |
| Gap dist, Age, Sex | 5 | − 1502.15 | 3008.33 | 202.73 |
| Gap dist, Age | 3 | − 1516.80 | 3035.61 | 230.01 |

Table 2.4 Coefficients of the top ranked logistic regression model predicting gap-crossing behaviours in black-capped chickadees. (ROC = 0.741 SE = 0.001). Positive coefficients indicate greater likelihood of gap crossing, while negative coefficients indicate reduced likelihood of gap crossing.

| Variable | Coefficient | Robust Std Err | $z$ | $P$ | 95% CI Lower | Upper |
|---|---|---|---|---|---|---|
| Gap Distance | − 0.06 | 0.01 | − 4.43 | <0.001 | −0.09 | −0.04 |
| Vegetation 0-1m | 0.01 | 0.03 | 0.31 | 0.76 | −0.05 | 0.06 |
| Vegetation 1-2m | 1.00 | 0.19 | 5.37 | <0.001 | 0.64 | 1.37 |
| Study area | | | | | | |
| B | − 0.80 | 0.43 | −1.85 | 0.07 | −0.09 | 1.30 |
| C | − 0.82 | 0.45 | − 1.8 | 0.07 | −1.71 | 0.07 |
| Age (ASY) | 0.61 | 0.35 | 1.71 | 0.09 | −0.09 | 1.30 |
| Sex | | | | | | |
| Male | − 0.34 | 0.44 | − 0.78 | 0.44 | −1.21 | 0.52 |
| Unknown | 0.08 | 0.39 | 0.21 | 0.84 | −0.68 | 0.84 |

## 2.8 Figures
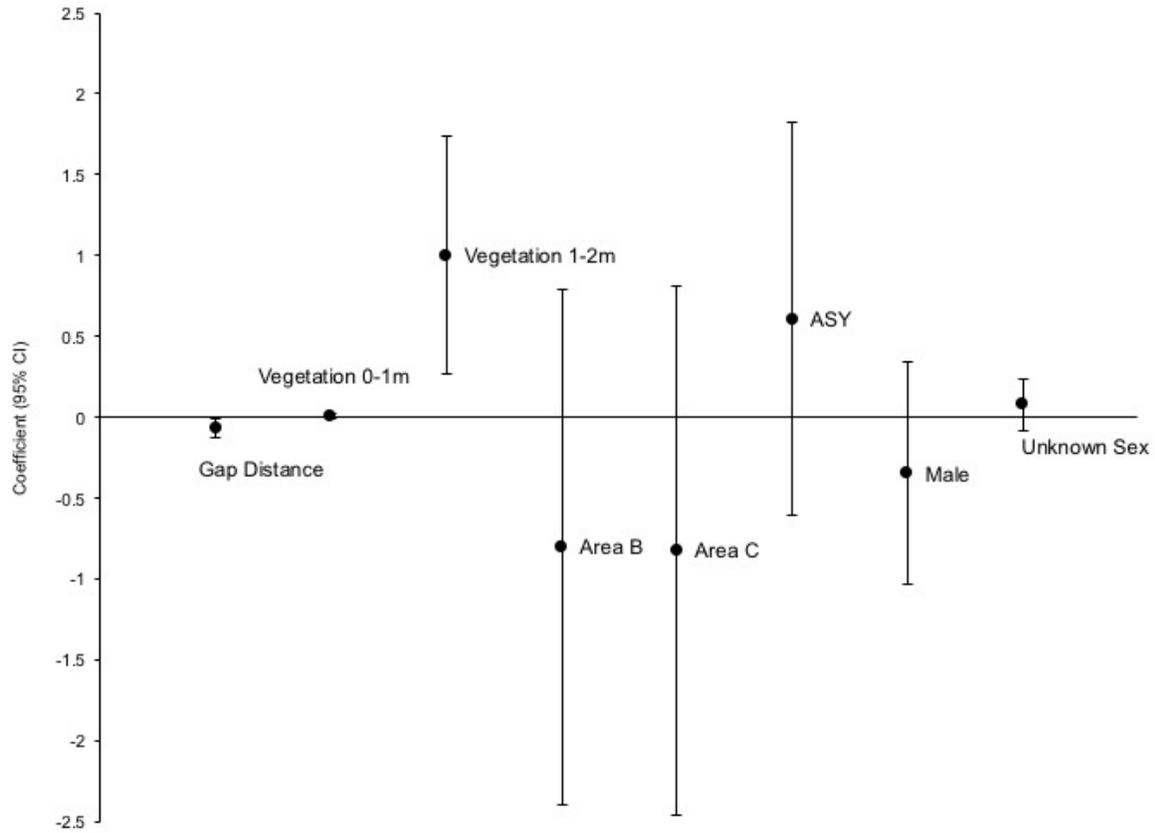


Figure 2.1 Coefficients and 95% confidence intervals from the top ranked logistic regression model explaining gap-crossing behaviours in black-capped chickadees. Positive coefficients represent an increase in gap-crossing likelihood while negative coefficients represent a decrease in likelihood.
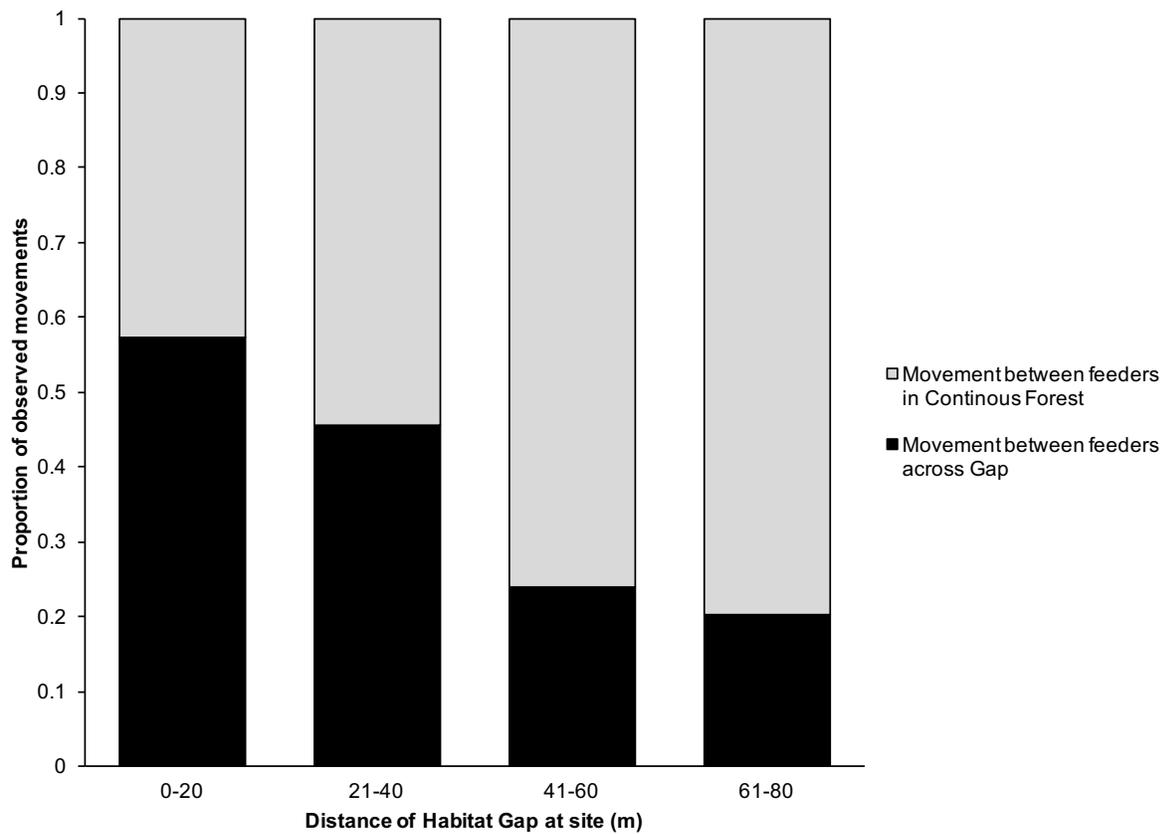
Figure 2.2 Proportion of movements of black-capped chickadees between feeders for a given

distance range. Black area represents the proportion of total movements between feeders that did

involve a gap crossing, gray area represents movements that did not involve a gap crossing.
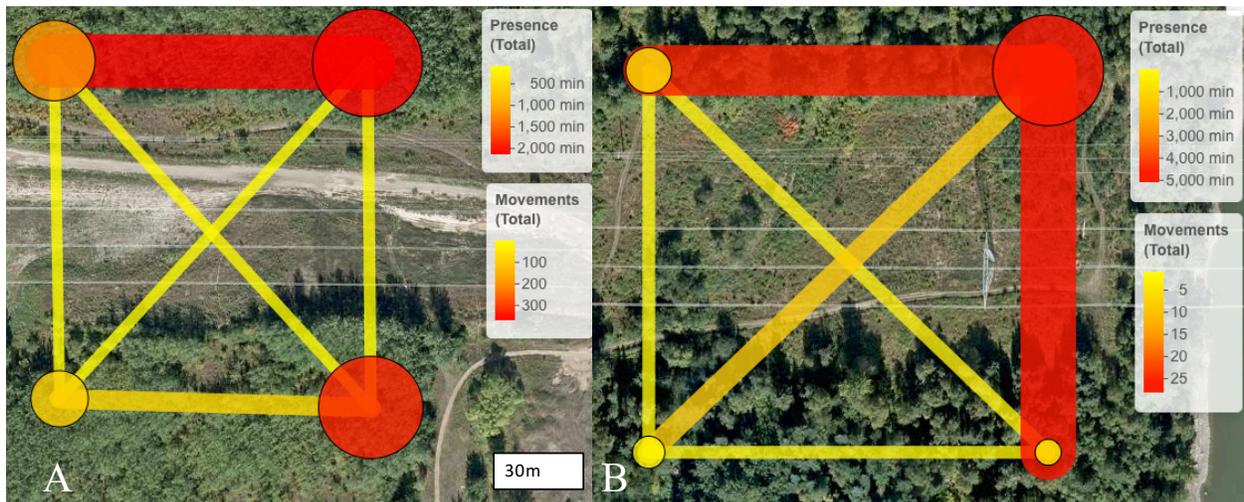
Figure 2.3 Two RFID feeder grids both centered on the same linear power line cut, separated by approximately 0.55 Km. Both sites have a gap distance of 68m, and would therefore be expected to present a substantial barrier to bird movements. However, because site B had greater density of intervening vegetation within the gap, a much larger proportion of the total moves at site B consisted of gap crossings compared to site A. Size of circles around feeder locations indicate usage for that feeder, with greater usage being indicated by a larger circle. Path usage is indicated by line width, again with thicker lines indicating greater path usage.

**Chapter 3: Comparing Gap-crossing Responses in Black-capped Chickadees (*Poecile atricapillus*) Induced by Playback to a Novel RFID Method**

### 3.1 Abstract

Gaps in forest habitat can limit the movements of many animals, including songbirds. Here, we report the results of a playback experiment investigating the gap-crossing decisions of black-capped chickadees (*Poecile atricapillus*). We wanted to evaluate the results of our RFID method against a well established protocol, specifically to investigate if mobbing calls bias playback studies by making birds less likely to cross gaps. We also investigated changes in gap-crossing behaviour before and after the food supplementation that was part of our RFID experiments described in Chapter 2. We used mixed effects logistic regression to analyze the responses of birds to our playbacks. We found that gaps had a significant negative impact on the movements of black-capped chickadees during our playback experiments. We also found that food supplementation appears to decrease the likelihood of birds responding to playbacks across gaps. We hypothesize that birds may be engaging in a trade off between foraging efficiency and predation risk, with increased food availability resulting in a decrease in propensity to take risks.

**3.2   Introduction**

The ability to move across the landscape is an integral part of an organism's ability to disperse (With et al. 1997) and for populations to maintain genetic connectivity (Keller and Largiadèr 2003). It is therefore essential that we have a thorough understanding of how individuals will react when faced with habitat barriers. Gaps in continuous forest cover, often created by anthropogenic disturbances, can limit connectivity not only for ground dwelling organisms (Bakker and Van Vuren 2004), but also for more free-moving taxa such as birds (Desrochers and Hannon 1997a, Haddad 1999, Desrochers and Fortin 2000, Harris and Reed 2001, Bélisle et al. 2001, Bélisle and Desrochers 2002).  However, there are practical challenges in studying the movement of forest songbirds across gaps.

Playback experiments are one of the most widely employed methods to study the impacts of gaps on bird movements (Desrochers and Hannon 1997a, St Clair et al. 1998, Rodríguez et al. 2001, Harris and Reed 2001, Bélisle and Desrochers 2002, St. Clair 2003, Tremblay and St. Clair 2009). While this method can be practical and efficient, it is difficult to track and identify differences in movement behaviour among individuals during these experiments. These experiments also represent short-term responses, with trials typically lasting only several minutes (St Clair et al. 1998, Tremblay and St. Clair 2009). Therefore, playbacks may not be representative of gap-crossing behaviours over longer time periods. Playback studies also require the use of a song or mobbing call to entice birds to move. In the case of mobbing calls this may be problematic. Mobbing calls are typically used as an intraspecific alert to the presence of predators (Evans et al. 1993). Birds hearing the mobbing call playbacks may infer the presence of an aerial predator in the area.  Because one of the main factors thought to influence gap-crossing behaviour is predation risk (Zollner and Lima 2005), the use of mobbing calls may

reduce the willingness of birds to cross gaps. This may result in playback studies over-estimating the impacts of gaps on forest songbirds. Although Desrochers et al. (2002) concluded that the use of mobbing calls likely do not influence bird's perception of predation, they did demonstrate that chickadees behaved more cautiously in the presence of mobbing calls.

One means of determining whether playback studies suffer from these potential biases is to conduct a playback in concert with other independent methods for investigating gap-crossing decisions in birds. Here, we present the results of a playback study, performed at the same sites as the RFID tracking method described in Chapter 2. Our primary objective was to compare the results from both methods. We wanted to know if using mobbing calls biases the results of playback studies by making birds less likely to cross gaps. Also, we wanted to evaluate the results of our RFID method against a well established protocol. We conducted playbacks both before and after the RFID feeders sampling period. As our RFID method involved the use of birdfeeders to detect tagged individuals, our secondary objective was to investigate if food supplementation influenced the gap-crossing decisions of birds.


**3.3    Methods**

*3.3.1    Field Methods*

We adapted our playback protocol from Tremblay and St. Clair (2009) so our results would be comparable to similar playback experiments (St. Clair 2003, Tremblay and St. Clair 2009).  We conducted 23 playbacks at 12 different sites. At each site we conducted one playback trial before any birds were banded and before feeders were placed at that location. At the end of the 7-day RFID sampling period, we then conducted a second playback trial at each location. At each site we conducted two types of playbacks: 1) playbacks where the origin and destination locations

were on opposite sides of a gap (gap trials), and 2) playbacks where the origin and destinations were not separated by a gap (forest trials) (Figure 3.1). The playback distances at each site were the same for the gap and forest trials. Playback and gap distances ranged from 17 to 80 m. Gap distances were measured using a Bushnell YardagePro Sport 600 laser rangefinder. We alternated between which trial type (gap or forest) was performed first at each site to control for possible habituation to the mobbing call.

### 3.3.2   Playback protocol

Each playback trial was conducted by two observers, one positioned at the playback origin and the other at the playback destination. Each observer had a speaker (Logitech X100) connected to an iPod Touch that was used to broadcast the mobbing call. The speaker was located roughly 1.5m above the ground and positioned so that the speaker was pointing in the direction of the other observer. Volume was standardized across all trials (Approximately 80 decibels at 1m, measured with a GoldLine SPL120 sound pressure meter). These volume settings were chosen as they were similar to those of natural calling, and were also sufficiently loud enough to be audible to the second observer at all distances sampled.

We began each playback with a 30-second primer of black-capped chickadee mobbing calls at the origin location followed by one minute of silence. Next, we began playing the same mobbing call at the origin location for up to a maximum of six minutes, or until no new birds had arrived for one minute. If no birds responded after the first two minutes of the 6-minute playback, we stopped the playback for two minutes, then restarted the trial. This protocol was repeated until either the entire 6-minute playback had elapsed with no birds responding (in which case the trials were aborted until the next day – see below), or birds responded to the mobbing

call. For a playback trial at the origin location to proceed to testing at the destination location, at least one bird had to have been attracted to within 10m of the origin speaker and indicate some form of responsiveness (calls, approach) to the mobbing call. Once these conditions had been met, the observer at the origin turned their speaker off, and moved to a location half-way between the origin and destination speakers to observe and record birds moving from the initial location to the destination speaker. Simultaneously, the observer at the destination began their mobbing call playback. The destination mobbing call was played for 6 minutes continuously, and the conditions for a bird to be considered to have responded to the destination call were the same as those used at the origin location. After the first playback type (gap or forest trial) was completed, the reciprocal trial was conducted immediately (typically within 1–2 minutes). If only one or neither of the gap or forest playback trials was successful in attracting birds to the origin location, the playback was postponed then attempted again the following day. We recorded the number of birds at the initial location and the number of individuals that moved to the destination, and used this proportion as the dependent variable in our models.

### 3.3.3 Statistical Analysis

We performed all statistical analyses using STATA 14 (StataCorp 2015). We based our analysis on that of Tremblay and St. Clair (2009). To analyze the responses of birds to our playbacks, we constructed mixed-effects logistic regression models with binomial distributions and logit link functions. We used the number of birds at the destination (i.e., number of bird that moved in response to playback) as our dependent variable with the number of birds at the initial location (i.e., total number of bird involved in playback) as a binomial denominator (Papke and Woodridge 1996). The dependent variable in all of our models was therefore the proportion of

birds involved in the playback that moved in response to the playback call at the destination, hereafter, referred to as the response proportion. A response proportion of 1 indicates that all birds from the initial location moved to the destination, and a response proportion of 0 indicates that no birds from the initial location moved to the destination. All of our models included a random intercept for site to account for the two types of trials (gap trials and forest trials) being performed at the same sites.

To ask whether performing a gap playback trial or a forest playback trial first at a site impacted the responsiveness of birds to playbacks overall (i.e., forest and gap trial playbacks together), we used the response proportion as the dependent variable and the trial type that was performed first at that site as a categorical predictor variable (forest trial = 0, gap trial = 1). Using similar analyses, we also asked whether the type of playback trial conduced first impacted the responsiveness of birds to forest and gap trial playbacks separately.

Because we wanted to investigate the how supplemental feeding may influence playback responses, we tested if responses differed before and after food supplementation. To test this, we used the response proportion as the dependent variable and whether the trial was performed pre-feeding or post-feeding as a categorical predictor variable (pre-feeding = 0, post-feeding = 1). To test if this effect may only be present during gap or forest trials we then partitioned the data into gap trials and forest trials, and again tested response proportion as the dependent variable and whether the trial was performed pre-feeding or post-feeding as a categorical predictor variable (pre-feeding = 0, post-feeding = 1) on both datasets.

To ask whether gaps in forest habitat negatively impacted bird movements, we used the response proportion as the dependent variable, the trial type as a categorical predictor variable (forest trial = 0, gap trial = 1), and the playback distance as a continuous predictor variable. We

looked at the interaction between playback type and distance because we suspected the effect of distance on response proportion may only be evident during gap trials. In this model, we used the response proportion as the dependent variable, trial type and playback distance as predictor variable, and included a trial type x playback distance interaction term. To further investigate significant interactions between trial type and playback distance, we used the response proportion as the dependent variable and playback distance as a continuous predictor variable, for both gap trials and forest trials separately.

## 3.4    Results

Likelihood of birds to respond to a playback was not influenced by which trial (gap or forest) was performed first (Table 3.1), therefore we did not analyze playbacks separately based on which trial at each site was performed first or include it as a random effect in our models. Birds were significantly less likely to respond to playbacks during the post-feeding playback trials compared to the pre-feeding playback trials (Table 3.2). This was true when all trials were analyzed together (Wald $\chi^2 = 17.90$ , $n = 46$, $P < 0.001$), and when gap trials (Wald $\chi^2 = 9.10$ , $n = 23$ , $P < 0.01$) and forest trials (Wald $\chi^2 = 11.50$ , $n = 23$ , $P < 0.001$) were analyzed separately.  Therefore, all subsequent analysis is separated into pre-feeding and post-feeding.

For the pre-feeding trials, increased playback distance did not influence the proportion of birds that responded to the playback (Table 3.3). However, birds were significantly less likely to respond to gap-trial playbacks compared to forest-trial playbacks (Table 3.3). We found no significant interaction between playback distance and trial type. We therefore dropped the non-significant interaction to derive our final model for the pre-feeding trials (Wald $\chi^2 = 10.79$ , $n = 24$ , $P < 0.01$; Table 3.3).

When analyzing the post-feeding trials, birds were also significantly less likely to respond to gap-trial playbacks compared to the forest trials (Table 3.4). We again found no significant effect of distance on response probability during the post feeding trials (Table 3.4). When we looked at the interaction between distance and gap type we found a significant positive effect (Wald $\chi^2 = 11.83$, $n = 22$, $P < 0.01$; Table 3.4). This interaction suggests that, birds were more likely to respond to gap-trial playbacks as distance increased. However, when we investigated this interaction further playback distance had no significant effect on response probability in the post-feeding gap trials (Wald $\chi^2 = 2.08$, $n = 11$, $P = 0.15$; Table 3.5) or in the post-feeding forest trials (Wald $\chi^2 = 2.25$, $n = 11$, $P = 0.13$; Table 3.5).

## 3.5   Discussion

Black-capped chickadees were significantly less likely to respond to playbacks across gaps compared to within forest, indicating that gaps act as barriers to movement. This finding is also in agreement with results from our RFID experiments at the same sites, which also demonstrated that these gaps act as barriers to movements during foraging. Our results provide further evidence that using mobbing calls during playback experiments does not seem to bias bird gap-crossing decisions by influencing their perception of predation (Desrochers et al. 2002).

Perhaps the most interesting result of our study was the decrease in response probability between our pre-feeding and post-feeding playback trials. Because our pre-feeding and post-feeding trials were separated by at least 7 days, habituation to playbacks is unlikely to explain the reduction in response probability. One possibility is that food supplementation may have diminished the risk taking propensity of birds in the area. Turcotte and Desrochers (2003) demonstrated that birds in forest fragments that were supplemented with food did not venture as

44

far beyond forest edges compared to those in unsupplemented fragments. They concluded that decreased energy stress, due to greater food resource abundance, resulted in a decrease in risk-taking behaviour, suggesting a trade-off between foraging efficiency and predation risk (Lima and Dill 1990, Walther and Gosler 2001). Because mobbing is a risky behaviour (Sordahl 1990), birds may have been less likely to respond to mobbing calls in our playback experiment when food was supplemented. Interestingly, we did not find any decrease in gap-crossing likelihood during the duration of our RFID experiments. Birds were no less likely to cross gaps on the final day of our 7-day RFID sampling period experiment than on the first. However, as we were constrained by a relativity small sample size for our playback experiments, more work is needed to investigate how food availability may influence the movements and behaviour of forest songbirds in fragmented habitats.

When we analyzed the post-feeding playback trials alone we found that birds were more likely to respond to gap-trial playbacks as gap distance increased. This unexpected result was present for our post-feeding playback trials only. However, this result appears to be due to a few outlier responses where birds responded to our playbacks at higher rates than would be expected at large gap distances, rather than an overall trend of increasing responses with increased gap distance (Figure 3.2).

Our playback results run somewhat contrary to our RFID results and to other playback studies, in that increased gap distance did not impose a greater impediment to movement (Desrochers and Hannon 1997, Rodríguez et al. 2001, Harris and Reed 2001, Bélisle and Desrochers 2002, Tremblay and St. Clair 2009). Because gaps at our study site ranged only in distance from 17 to 80 m, we were limited to playbacks of these distances compared to similar playback studies in which distances were as great as 160 m (i.e., Desrochers and Hannon 1997).

Had we been able to sample larger gap distances, differences in response probability may have been more pronounced. In contrast to our playbacks however, we did observe a negative relationship between increased gap-distance and gap-crossing probability using our RFID method. Considering the range of gap-distances for both experiments were comparable, these results suggest that RFID data allowed for a more nuanced analysis of bird movements. We were able to observe a much greater number of individual movements using RFID ($n = 2971$) than a playback approach ($n = 47$), this likely gave us greater statistical power to uncover subtle differences in gap-crossing behaviours.

Playbacks can be an effective method for investigating how habitat features influence bird movements, and have a variety of benefits when compared to using RFID. Playbacks are inexpensive, and are easily repeatable across a variety of different habitat features. However, playbacks are limited in their ability to compare gap-crossing behaviours of individual birds. Additionally, because playback observations last only several minutes, repeated sampling is required to make observations about how movement patterns may change over time. In contrast, RFID is well suited to track the movements of individual birds, making it an excellent tool to investigate how individual factors may influence movement decisions. RFID also lends itself to investigating long-term movement patterns, as RFID readers can be left in the field to passively collect data without the need for researchers to be present. However, this technique does suffer from increased set up, cost, and sampling time, in addition to requiring the investigator to band a substantial number of birds with PIT tags. Ultimately, the decision to use either technique will be dictated by the research question of interest, and the time and resources available to the investigator.

## 3.6    Literature Cited

Bakker, V. J., and D. H. Van Vuren (2004). Gap-Crossing Decisions by the Red Squirrel, a Forest-Dependent Small Mammal. Conservation Biology 18:689–697.

Beauchamp, G., M. Belisle, and L.-A. Giraldeau (1997). Influence of Conspecific Attraction on the Spatial Distribution of Learning Foragers in a Patchy Habitat. Journal of Animal Ecology 66:671–682.

Bélisle, M., and A. Desrochers (2002). Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17:219–231.

Bélisle, M., A. Desrochers, and M.-J. Fortin (2001). Influence of Forest Cover on the Movements of Forest Birds: A Homing Experiment. Ecology 82:1893–1904.

Betts, M. G., A. S. Hadley, and P. J. Doran (2005). Avian Mobbing Response is Restricted by Territory Boundaries: Experimental Evidence from Two Species of Forest Warblers. Ethology 111:821–835.

Bonter, D. N., and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. Journal of Field Ornithology 82:1–10.

Desrochers, A., M. Bélisle, and J. Bourque (2002). Do mobbing calls affect the perception of predation risk by forest birds? Animal Behaviour 64:709–714.

Desrochers, A., and M.-J. Fortin (2000). Understanding avian responses to forest boundaries: a case study with chickadee winter flocks. Oikos 91:376–384.

Desrochers, A., and S. J. Hannon (1997a). Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204–1210.

Desrochers, A., and S. J. Hannon (1997b). Gap Crossing Decisions by Forest Songbirds during the Post-Fledging Period. Conservation Biology 11:1204–1210.

Evans, C. S., L. Evans, and P. Marler (1993). On the meaning of alarm calls: functional reference in an avian vocal system. Animal Behaviour 46:23–38.

Haddad, N. M. (1999). Corridor Use Predicted from Behaviors at Habitat Boundaries. The American Naturalist 153:215–227.

Harris, R. J., and J. M. Reed (2001). Territorial Movements of Black-throated Blue Warblers in a Landscape Fragmented by Forestry. The Auk 118:544–549.

Keller, I., and C. R. Largiadèr (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London B: Biological Sciences 270:417–423.

Lima, S. L., and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Papke, L. E., and J. M. Wooldridge (1996). Econometric methods for fractional response variables with an application to 401(k) plan participation rates. Journal of Applied Econometrics 11:619–632.

Rodríguez, A., H. Andrén, and G. Jansson (2001). Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95:383–396.

Sordahl, T. A. (1990). The Risks of Avian Mobbing and Distraction Behavior: An Anecdotal Review. The Wilson Bulletin 102:349–352.

StataCorp (2015) Stata Statistical Software: Release 14. StataCorp., College Station, Texas, USA.

St. Clair, C. C. (2003). Comparative Permeability of Roads, Rivers, and Meadows to Songbirds in Banff National Park. Conservation Biology 17:1151–1160.

St. Clair, C. C., M. Bélisle, A. Desrochers, and S. Hannon (1998). Winter responses of forest birds to habitat corridors and gaps. Conservation Ecology 2:13.

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.

Turcotte, Y., and A. Desrochers (2003). Landscape-dependent response to predation risk by forest birds. Oikos 100:614–618.

Walther, B., and A. Gosler (2001). The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: Parus). Oecologia 129:312–320.

With, K. A., R. H. Gardner, and M. G. Turner (1997). Landscape connectivity and population distributions in heterogeneous environments. Oikos:151–169.

Zollner, P. A., and S. L. Lima (2005). Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108:219–230.

## 3.7 Tables

Table 3.1 Coefficients of the logistic regression models investigating if black-capped chickadee responses to playback experiments are effected by which trial type (gap or forest) is performed first. Positive coefficients represent and increased likelihood of playback response while negative coefficients represent decreased likelihood of response. Separate models were used to investigate the effect of trial order on all trials combined (Wald $\chi^2 = 0.03$ , $n = 46$, $P = 0.86$), gap trials (Wald $\chi^2 = 0.50$, $n = 23$, $P = 0.48$ ), and forest trials  (Wald $\chi^2 = 0.24$ , $n = 23$, $P = 0.62$).

| Model | Variables | Coefficient | n | Std. Err. | $z$ | 95 % CI Lower | Upper | *P* value |
|---|---|---|---|---|---|---|---|---|
| **All trials** | | | | | | | | |
| | First playback type | − 0.08 | 46 | 0.45 | −0.17 | − 0.97 | 0.81 | 0.86 |
| **Gap trials** | | | | | | | | |
| | First playback type | 0.46 | 23 | 0.64 | 0.71 | − 0.81 | 1.72 | 0.48 |
| **Forest trials** | | | | | | | | |
| | First playback type | − 0.37 | 23 | 0.76 | −0.49 | − 1.85 | 1.11 | 0.62 |

Table 3.2 Coefficients of the logistic regression models investigating if black-capped chickadee responses to playback experiments are effected by supplemental feeding. Positive coefficients represent and increased likelihood of playback response while negative coefficients represent decreased likelihood of response. Separate models were used to investigate the effect of supplementation on all trials combined (Wald $\chi^2$ = 17.90 , $n$ = 46, $P$ < 0.001), gap trials (Wald $\chi^2$ = 9.10 , $n$ = 23 , $P$ < 0.01), and forest trials (Wald $\chi^2$ = 11.50 , $n$ = 23 , $P$ < 0.001).

| Model | Variables | Coefficient | n | Std. Err. | z | 95 % CI Lower | Upper | P value |
|---|---|---|---|---|---|---|---|---|
| **All trials** | | | | | | | | |
| | Pre vs Post | − 1.52 | 46 | 0.36 | − 4.23 | − 2.22 | − 0.81 | < 0.001 |
| **Gap trials only** | | | | | | | | |
| | Pre vs Post | − 2.56 | 23 | 0.76 | − 3.39 | − 4.04 | − 1.08 | < 0.001 |
| **Forest trials only** | | | | | | | | |
| | Pre vs Post | − 1.99 | 23 | 0.66 | − 3.02 | − 3.29 | − 0.70 | < 0.01 |

Table 3.3 Coefficients of the logistic regression models investigating if gaps act as barriers to black-capped chickadee movements and the influence of playback distance on playback responses for the pre-feeding trials. Positive coefficients represent and increased likelihood of playback response while negative coefficients represent decreased likelihood of response (Wald $\chi^2 = 10.79$, $n = 24$, $P < 0.01$).

| Variable | Coefficient | Std. Err. | $z$ | 95 % CI Lower | 95 % CI Upper | $P$ value |
|---|---|---|---|---|---|---|
| Distance | − 0.001 | 0.02 | − 0.04 | − 0.04 | 0.04 | 0.97 |
| Trial type (Gap /Forest ) | − 2.13 | 0.65 | − 3.28 | − 3.41 | − 0.86 | < 0.01 |

Table 3.4 Coefficients of the logistic regression models investigating if gaps act as barriers to black-capped chickadee movements and the influence of playback distance on playback responses for the post-feeding trials. Positive coefficients represent and increased likelihood of playback response while negative coefficients represent decreased likelihood of response (Wald $\chi^2 = 11.83$, $n = 22$, $P < 0.01$).

| Variable | Coefficient | Std. Err. | $z$ | 95 % CI | | $P$ value |
| | | | | Lower | Upper | |
|---|---|---|---|---|---|---|
| Distance | $-0.03$ | 0.02 | $-1.56$ | $-0.06$ | 0.01 | 0.12 |
| Trial type (Gap /Forest ) | $-5.65$ | 1.86 | $-3.04$ | $-9.30$ | $-2.00$ | $<0.01$ |
| DistanceXTrial type | 0.08 | 0.03 | 2.35 | 0.01 | 0.14 | 0.02 |

Table 3.5 Coefficients of the logistic regression models investigating the significant positive interaction between trial type and playback distance for the post-feeding playbacks. Data was split into gap (Wald $\chi^2$ = 2.08 , $n$ = 11 , $P$ = 0.15) and forest trials (Wald $\chi^2$ = 2.25 , $n$ = 11 , $P$ = 0.13) and tested separately. Response probability was the dependent variable in the models and distance as a continuous predictor. Positive coefficients represent and increased likelihood of playback response while negative coefficients represent decreased likelihood of response.

| | Variables | Coefficient | n | Std. Err. | $z$ | 95 % CI | | $P$ value |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | | | Lower | Upper | |
| **Gap trials** | | | | | | | | |
| | Distance | 0.05 | 11 | 0.03 | 1.50 | − 0.01 | 0.11 | 0.13 |
| **Forest trials** | | | | | | | | |
| | Distance | − 0.03 | 11 | 0.02 | − 1.44 | − 0.07 | 0.01 | 0.15 |

## 3.8 Figures



Figure 3.1. Example experimental setup for our playback trials for both the forest trials(a) and the gap trials (b). Origin speakers represented by (1) and destination speakers represented by (2), with bird path represented by dotted lines.
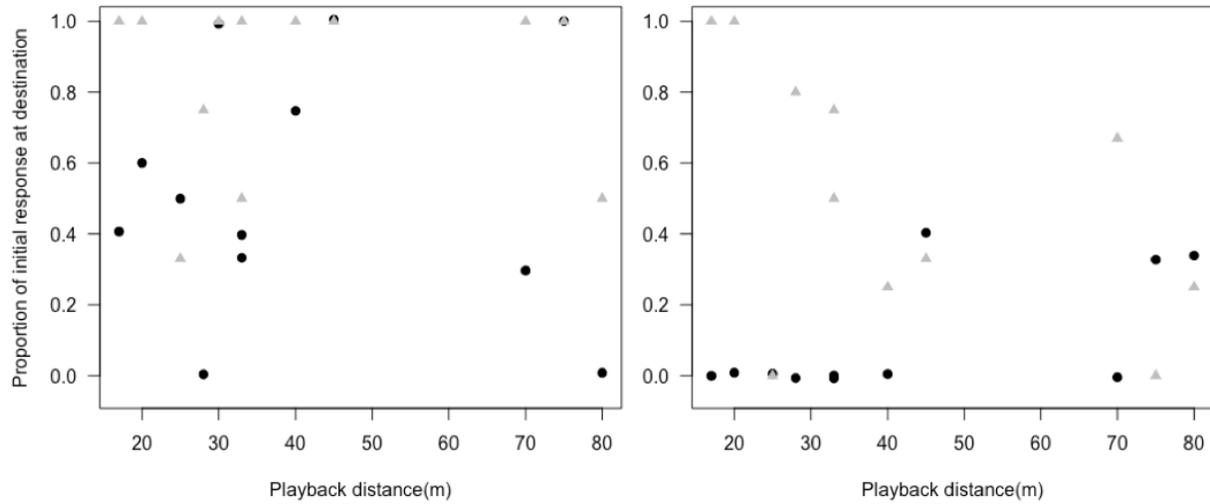
Figure 3.2. Proportion of responses to destination playbacks across all playback distances for gap (circles) and forest (triangles) trials both pre-feeding (left), post-feeding (right). Post-feeding trails had much lower responses overall compared to pre-feeding trials, however in the post-feeding trials a few responses at large distances likely skewed our results to show a positive interaction between gap-trial playback responses and increased gap-distance.

**Chapter 4: Conclusion**

The primary goal of this project was to gain a better understanding of the behavioral decisions made by individual black-capped chickadees when moving through fragmented habitats. My results provide strong evidence that linear gaps constrain the movements of black-capped chickadees. Further, that larger gaps impede the movements of chickadees to a greater degree than smaller gaps. Greater vegetation within the gap appears to facilitate movements compared to those with little or no vegetation. Interestingly, this was only true for vegetation over 1m in height. Vegetation over 1m in height likely increases movements across gaps for chickadees as they are generally arboreal foragers (Foote et al. 2010), and vegetation above 1m is more natural for them to move though compared to lower lying vegetation. However, this may suggest that the effective height for vegetation in facilitating movements across gaps may be dependent on a species life history or foraging strategy. For instance, while only vegetation at a height greater than 1m facilitated movements for chickadees, vegetation below this height may still be effective for facilitating the movements of understory birds (Castellón and Sieving 2006).

A secondary goal of this project was to compare the results of my RFID experiments with the results of playbacks conducted at the same sites. Given that the results from both my RFID and playback experiments were in agreement to the extent that gaps negatively impacted bird movements, I believe this demonstrates that either method is appropriate to use to investigate the gap-crossing decisions of black-capped chickadees. One of the limitations of playback studies is the difficulty in investigating behavioural differences among individuals. However, individual variation in age, sex, or condition, did not appear to influence gap-crossing behaviours in my RFID experiments. Therefore, this limitation of playbacks may not be of consequence if

differences between individual black-capped chickadees do not predict differences in gap-crossing behaviour.

Inhabiting fragmented habitats can be energetically costly to forest songbirds. Gaps can increase the cost of movement by increasing the time it takes to move though the landscape (Bélisle et al. 2001), and by decreasing a bird's abilities to forage (Huhta et al. 1998) and disperse efficiently (Lens and Dhondt 1994, Desrochers and Hannon 1997, Zollner and Lima 2005, Cox and Kesler 2012). Due to constraints on individual movements, habitat fragmentation could increase the cost of behaviours thought to be adaptive, such as extra pair copulations (EPCs) (Norris and Stutchbury 2001), possibly resulting in decreased frequency of such behaviours. Although any one of these factors alone does not necessarily make fragmented habitats entirely inhospitable for birds, their cumulative effects have clear negative impacts on the fitness of birds. On a global scale, the negative impacts of forest fragmentation are possibly contributing to the overall trend in decreasing songbird populations world wide (Hoffmann et al. 2010). With increasing development in the form of agriculture, urbanization, and resource extraction further impacting natural landscapes, understanding and predicting how birds will react to these changes is essential.

Habitat fragmentation may also impact the evolution of birds over time. Habitat fragmentation is well documented to limit gene flow between populations (Keller and Largiadèr 2003, Riley et al. 2006, Adams and Burg 2015). Limited gene flow generally results in decreased genetic diversity within populations. Because genetic diversity is essential for adaptation, habitat fragmentation may have negative impacts on the ability of black-capped chickadees to respond in an adaptive way to increasingly fragmented environments in the future. Furthermore, reduced genetic diversity can also make populations more susceptible to the spread of pathogens and

infection (O'Brien and Evermann 1988). This may be problematic even for abundant, generalist species, such as the black-capped chickadee, as human influences are likely to further change the landscape and climate at a rate that will be difficult for many species to adapt to.

My research helps to expand our knowledge of the individual gap-crossing decisions made by black-capped chickadees. Furthermore, my findings demonstrate the efficacy of past work using playbacks, and helps to further the use of novel applications of RFID technology in ornithology. My research also demonstrates, the large potential for RFID to be used in tracking the movements of songbirds, and the potential integration of RFID with other techniques or equipment beyond birdfeeders. Beyond black-capped chickadees, my research may also help to predict how other winter resident birds (e.g., mountain chickadees, nuthatches, woodpeckers, and some owl species) may also be impacted by habitat fragmentation.

### 4.1.1    *Future directions*

RFID technology provides the ability to track movements of songbirds, and to investigate factors that influence the movements of individual birds. Although it has been posited that individual characteristics may play a role in gap crossing decisions I did  not find this to be the case (Tellería et al. 2001, Bélisle and Desrochers 2002, Norris et al. 2002, Cox and Kesler 2012 ). During winter, black-capped chickadees move through the landscape as flocks of variable size that are comprised of individuals of differing age, sex, dominance rank, and/or body condition (Foote et al. 2010). Forest fragmentation has been shown to influence flock structure and behaviour in the related blue tit (*Parus caeruleus*) (Tellería et al. 2001). Therefore, flock dynamics and structure may be of greater importance in influencing black-capped chickadee movements through fragmented habitats during the winter compared to individual

characteristics. I suggest that future studies examining the gap-crossing behaviours of black-capped chickadees do so at the scale of flocks, and investigate how flock structure and dynamics influence behaviour of birds as they move through fragmented landscapes. Furthermore, as chickadee winter flocks often interact with other species, such as nuthatches, future work should also investigate how interspecific interactions influence flock behaviour, dominance, and movement.

Although there is research investigating gap-crossing decisions of forest songbirds during both the breeding (e.g., Norris et al. 2002, MacIntosh et al. 2011) and non-breeding seasons (e.g., St Clair et al. 1998, Tellería et al. 2001), there is still a substantial amount of uncertainty as to how individual differences in gap-crossing behaviours translate into breeding success, if at all. Examining how individuals respond to habitat fragmentation, and how these responses are related to the fitness of an individual is essential for a complete understanding of how habitat fragmentation influences the ecology and evolution of a species. Furthermore, it is important to understand how associations between responses to habitat fragmentation and breeding success vary among species. While it may not be practical to study how every species responds to habitat fragmentation, especially in terms of breeding success, it may be useful to study how differing life histories or feeding guilds respond, therefore allowing for inferences from model species to other species of concern.

Given that my research demonstrated the importance of vegetation within the gap as influencing gap-crossing behaviour, future work should further investigate how vegetation within gaps influences bird movements. To do so, I recommend that investigators use a similar RFID experimental design as myself, but rather than choose specific sites based on the amount of vegetation, I suggest that researchers deliberately manipulate the landscape. Performing this kind

of experiment would give researchers greater control over the amount and kind of vegetation within the gap, and also what kind of vegetation best promotes bird movements. Although altering vegetation within the gap will likely change gap-crossing propensity of forest song birds, it remains unknown if doing so will impact birds immediately or if there will be some temporal lag between the time the vegetation is manipulated and changes in the gap-crossing behaviour of birds. By studying bird movements before and after creation and manipulation of a gap researchers can investigate the effectiveness of different mitigation strategies. Such information is important for understanding the impacts of future and current developments, and implementing the most practical, efficient, and effective management strategies.

There appears to be good evidence that the reluctance of birds to cross gaps stems from an increase in predation risk (Rodríguez et al. 2001, Tellería et al. 2001, Turcotte and Desrochers 2003, Zollner and Lima 2005). This risk likely comes mostly from aerial predators such as hawks, falcons, and small owls. One way to further test this hypothesis would be to look at how time of day influences gap-crossing behaviours. If songbirds are most concerned about limiting their predation risk from aerial predator such as owls, we would expect them to be less likely to cross gaps during dusk and dawn, as this is when predation risk from owls is highest (Rodríguez et al. 2001, Zollner and Lima 2005).

### 4.1.2   Implications for Conservation and Management

The primary way to increase connectivity for birds in fragmented habitats is to reduce the distance across gaps. Ideally gaps would be limited in size to roughly less than 30m, as this appears to be the threshold distance at which the likelihood of crossing greatly declines (Desrochers 1989, St Clair et al. 1998, Harris and Reed 2001, Bélisle and Desrochers 2002,

Tremblay and St. Clair 2009). Mitigation could be achieved in a number of ways, one possibility being to design habitat gaps with sections of trees/shrubs retained as stepping stones, effectively reducing the perceived gap distance to birds and thus increasing connectivity. Another way to mitigate the effects of large gaps would be to leave narrower sections of the gap at regular spacing (e.g. every 1km) along the length of the gap.  This second approach could be best applied to long linear gaps – such as pipeline or power line corridors – to provide regular crossing points. However, I acknowledge that these solutions may not be practical in many instances. In such cases it appears that it may also be beneficial to place or allow shrubby or woody vegetation within the gap to grow back to a height of over 1m (Rodríguez et al. 2001).

## Literature Cited

Adams, R. V., and T. M. Burg (2015). Gene flow of a forest-dependent bird across a fragmented landscape. PLoS ONE 10:e0140938.

Bélisle, M., and A. Desrochers (2002). Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landscape Ecology 17:219–231.

Bélisle, M., A. Desrochers, and M.-J. Fortin (2001). Influence of forest cover on the movements of forest birds: A homing experiment. Ecology 82:1893–1904.

Castellón, T. D., and K. E. Sieving (2006). An experimental test of matrix permeability and corridor use by an endemic understory bird. conservation biology 20:135–145.

Cox, A. S., and D. C. Kesler (2012). Prospecting behavior and the influence of forest cover on natal dispersal in a resident bird. Behavioral Ecology 23:1068–1077.

Desrochers, A. (1989). Sex, dominance, and microhabitat use in wintering black-capped chickadees: A field experiment. Ecology 70:636–645.

Desrochers, A., and S. J. Hannon (1997). Gap crossing decisions by forest songbirds during the post-fledging period. Conservation Biology 11:1204–1210.

Foote, Jennifer R., Daniel J. Mennill, Laurene M. Ratcliffe and Susan M. Smith.(2010).Black-capped chickadee (*Poecile atricapillus*), The Birds of North America (P. G. Rodewald,

Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna-org.prxy.lib.unbc.ca/Species-Account/bna/species/bkcchi

Harris, R. J., and J. M. Reed (2001). Territorial movements of black-throated blue warblers in a landscape fragmented by forestry. The Auk 118:544–549.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Boehm, T. M. Brooks, S. H. M. Butchart, K. E. Carpenter, J. Chanson, B. Collen, N. A. Cox, W. R. T. Darwall, et al. (2010). The impact of conservation on the status of the world's vertebrates. Science 330:1503–1509.

Huhta, E., J. Jokimakp, and P. Rahko (1998). Distribution and reproductive success of the Pied Flycatcher (*Ficedula hypoleuca)* in relation to forest patch size and vegetation characteristics; the effect of scale. Ibis 140:214–222.

Keller, I., and C. R. Largiadèr (2003). Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London B: Biological Sciences 270:417–423.

Lens, L., and A. A. Dhondt (1994). Effects of habitat fragmentation on the timing of Crested Tit (*Parus cristatus)* natal dispersal. Ibis 136:147–152.

MacIntosh, T., B. J. M. Stutchbury, and M. L. Evans (2011). Gap-crossing by Wood Thrushes (*Hylocichla mustelina*) in a fragmented landscape. Canadian Journal of Zoology 89:1091–1097.

Norris, D. R., and B. J. M. Stutchbury (2001). Extraterritorial movements of a forest songbird in a fragmented landscape. Conservation Biology 15:729–736.

Norris, D. R., B. J. M. Stutchbury, and F. Thompson III (2002). Sexual differences in gap-crossing ability of a forest songbird in a fragmented landscape revealed through radiotracking. The Auk 119:528–532.

O'Brien, S. J., and J. F. Evermann (1988). Interactive influence of infectious disease and genetic diversity in natural populations. Trends in Ecology & Evolution 3:254–259.

Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne (2006). A southern California freeway is a physical and social barrier to gene flow in carnivores: physical and social barrier to gene flow. Molecular Ecology 15:1733–1741.

Rodríguez, A., H. Andrén, and G. Jansson (2001). Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95:383–396.

St Clair, C. C., M. Bélisle, A. Desrochers, and S. Hannon (1998). Winter responses of forest birds to habitat corridors and gaps. Conservation Ecology 2:13.

Tellería, J. L., E. Virgós, R. Carbonell, J. Pérez-Tris, and T. Santos (2001). Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. Oikos:253–264.

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.

Turcotte, Y., and A. Desrochers (2003). Landscape-dependent response to predation risk by forest birds. Oikos 100:614–618.

Zollner, P. A., and S. L. Lima (2005). Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108:219–230.