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Landscape genetics of a North American songbird, the black-capped chickadee (Poecile atricapillus)

Adams, Rachael V.

Lethbridge, Alta. : University of Lethbridge, Dept. of Biological Sciences

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LANDSCAPE GENETICS OF A NORTH AMERICAN SONGBIRD, THE BLACK-CAPPED CHICKADEE (POECILE ATRICAPILLUS)

RACHAEL VANESSA ADAMS
BSc Zoology, University of Dundee (UK), 2009
MRes Crops for the Future, University of Dundee (UK), 2011

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfillment of the
Requirements for the Degree

[DOCTOR OF PHILOSOPHY]

Department of Biological Sciences
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

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PREPARATION OF THESIS

RACHAEL VANESSA ADAMS

Date of Defense: April 13, 2015

Dr. T. Burg   Associate Professor   Ph.D.
Supervisor

Dr. C. Goater  Associate Professor   Ph.D.
Thesis Examination Committee Member

Dr. H. Jiskoot  Associate Professor   Ph.D.
Thesis Examination Committee Member

Dr. S. Rood   Professor   Ph.D.
Internal Examiner

Dr. G. Spellman  Associate Professor   Ph.D.
External Examiner
Black Hills State University
Spearfish, South Dakota

Dr. J. Thomas   Professor   Ph.D.
Chair, Thesis Examination Committee
ABSTRACT

Understanding landscape influences on the spatial distribution of genetic variation in species is necessary for their successful conservation and preservation. This study investigated both rangewide and fine-scale patterns of population genetic structure of a small resident passerine to North America, the black-capped chickadee (*Poecile atricapillus*). Microsatellite data revealed high levels of genetic differentiation across their geographical range, particularly in the west resulting from a combination of historical (e.g., glaciers) and contemporary (e.g., mountains) barriers. Cryptic genetic structure was also observed at smaller spatial scales. Populations in British Columbia are genetically isolated owing to its highly complex landscape, with gene flow restricted to low elevation valleys with sufficient forest cover. In southern Alberta, not only is gene flow restricted to riparian corridors but it is also influenced by natural/anthropogenic breaks within these continuous linear features as well as ecological zonation, suggesting that chickadees are dependent on habitat quality for dispersal.
ACKNOWLEDGEMENTS

I was initially very apprehensive about moving to Lethbridge from my home in Scotland to pursue a PhD, but I am glad that I took the risk because quite frankly it has been an experience of a lifetime. Of course it was not going to be easy. Driving on the other side of the road and remembering to turn right on a red light was a puzzling start, but driving in Canada was necessary because everything is so spread out. For example, walking to the shop (sorry, store) to grab a pint of milk is not a quick five minute chore that I am used to, and pub crawls are challenging as you end up spending all your beer money on taxis (sorry, cabs) between pubs (sorry, bars). And do not even get me started on the weather! Yes, moving to Canada was a fun transition, and I will be sad to leave [the poutine and Tim Horton’s].

Throughout my PhD there have been both highs and lows, but I got there in the end and I have many people to thank for that. Foremost, I would like to thank my supervisor, Theresa Burg, first for giving me the opportunity to pursue a PhD in the first place, and second for putting up with me over the past 3+ years. Her patience, guidance and encouragement throughout this whole process has prepared me for a scientific career in the future and I will be forever grateful. I would also like to thank my committee members Cameron Goater and Hester Jiskoot for their valuable input and words of encouragement throughout the process; to Ken Otter and Steffi LaZerte for their collaboration with my BC study (Chapter 3), and finally to Stewart Rood for his expertise and interest in my riparian study (Chapter 4). Thanks also to past and present members of the Burg Lab for making each day enjoyable and more importantly, for listening to my constant labwork-related rants.
I am also very grateful to the Alberta Conservation Association for awarding me a substantial grant for carrying out my riparian study in Southern Alberta, and another important thanks to the Alberta Society for Professional Biologists for awarding me two scholarships during my PhD, one of which gave me the opportunity to go home and visit my family.

I was fortunate enough to have two elements to my PhD: labwork and fieldwork. Fieldwork gave me the opportunity to travel, teach new students and meet new people. I will always be grateful to all the members of Project Feederwatch who contributed their knowledge during fieldwork planning. I particularly want to thank Joanne Vinnedge and her family as well as Judy Kleger and Frank Lehmann (British Columbia), and Cynthia and Dave Wood (Idaho) for inviting us into their homes and for taking such an interest in my project. I would also like to acknowledge all of my field assistants; Alice Martin, Kari Gohdes, Colin Macfarlane, Emily Carpenter, Pamela Narváez, for being a part of my project and for experiencing every detail with me, and having to deal with my annoying early morning “wakey wakey” calls at 430 am, as well as my constant fear of being attacked by a bear.

I will always be grateful to everyone back home who supported and encouraged me to pursue this degree. To my parents, John and Vanessa Adams, for their kindness, love and support all throughout this process (and sending me gifts from home to maintain my sanity). To my brothers, Simon and Paul Adams, for constantly telling me how proud they are of me and lifting my spirits. To my trusted mentors Stephen Hubbard, Jane Wishart and Alan Barclay for their words of wisdom, reassurance and encouragement, and a BIG thanks to all my friends back home for staying in touch and believing in me. Of course, I cannot forget all the new friends that I have made while being here in
Lethbridge, of which there are too many to name so I shall list the nationalities: Canadian, English, American, French, Indian, Columbian, Philippine, German, Brazilian, Iranian, Mexican and last but not least, Zimbabwean. Thank you all for the memories and good times we have shared, for putting up with me and of course, for being a part of my Friday night pub tradition. You guys rock!

Finally I would like to personally thank my best friend, my partner in life and fiancé, Michael Wilbourn. Although he couldn’t physically be here (except for the odd holiday), he has been there for me every step of the way. He has been so supportive of my decision to pursue a PhD in Lethbridge and I am so grateful for that. I want to thank him for being so kind, generous, loving and caring, and for always being there for me when I needed him. More importantly, I want to thank him for listening, for making me laugh when I was sad, and for giving me the strength to complete my PhD. I can’t wait to see what the future holds for us both.
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LIST OF ABBREVIATIONS, ACRONYMS AND SYMBOLS

AFLP  Amplified Fragment Length Polymorphism
AIC  Akaike’s Information Criterion
AICc  corrected Akaike’s Information Criterion
AMOVA  analysis of Molecular Variance
AR  allelic richness
BAPS  Bayesian Analysis of Population Structure
bp  base pair
CA  California
CAR  conditional autocorrelation
COSEWIC  Committee on the Status of Endangered Wildlife in Canada
cpDNA  chloroplast DNA
DA  discriminant analysis
DAPC  Discriminant Analysis of Principal Components
DEM  digital elevation model
$D_{EST}$  Jost’s measure of genetic differentiation
DIC  deviance information criterion
DNA  deoxyribonucleic acid
dNTP  deoxyribonucleotide
ESRI  Environmental Systems Research Institute
FAO  Food and Agriculture Organisation of the United Nations
FDR  false discovery rate
FIS  inbreeding coefficient
$F_{ST}$  Wright’s fixation index
$F^{*}_{ST}$  standardised measure of genetic differentiation
GESTE  genetic structure inference based on genetic and environmental data.
GIS  Geographical Information System
$He$  expected heterozygosity
$Ho$  observed heterozygosity
HWE  Hardy-Weinberg equilibrium
HWY  highway
IAM  infinite alleles model
IBD  isolation by distance
IBDWS  isolation by distance web service
IBR  isolation by resistance
IUCN  International Union for Conservation of Nature
$K$  number of inferred genetic clusters
ka  thousand years ago
Km  kilometers
$KMAX$  maximum number of inferred genetic clusters
LAT (N)  latitude (North)
LCP  least cost path
LD  linkage disequilibrium
LGM  Last Glacial Maximum
LnPr (X|K)  estimated log probability of the data
LONG  longitude (West)
m  meters
McMC  Markov chain Monte Carlo
MgCl²  magnesium chloride
min  minutes
mtDNA  mitochondrial DNA
N  number of samples
Na  number of alleles
NSERC  Natural Sciences of Engineering Research Council of Canada
°C  degrees Celsius
P  P-value (significance)
PA  private alleles
PCA  Principal Component Analysis
PCoA  Principal Coordinate Analysis
PCR  polymerase chain reaction
Q  ancestry coefficient
r  partial correlation
R²  correlation coefficient
RFLP  Restriction Fragment Length Polymorphism
sec  seconds
SMM  stepwise mutation model
SMOGD  Software for the Measurement of Genetic Diversity
SSR  simple sequence repeat
TESS  Bayesian clustering using tessellations and Markov models for spatial population genetics
TPM  Two Phase Model
U  units
wᵢ  weighted AICc
µg  microgram
µl  microlitre
µM  micromolar
α  alpha
Δᵢ  AICc differences
ΔK  delta K
Ψ  interaction parameter

Populations

Chapter 2
AKA  Alaska Anchorage
AKF  Alaska Fairbanks
AKW  Alaska Wrangell
BCR  British Columbia Revelstoke
CAB  Central Alberta
CID  Central Idaho
CO  Colorado
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**Chapter 3**

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**Chapter 4**

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**Museums**

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CHAPTER 1: General Introduction

1.1 General Overview

Genetic variability of individuals determines a species’ evolutionary potential (Reed and Frankham, 2003; Frankham, 2010). Populations with low levels of genetic variation may be unable to adapt to changing environmental conditions, leaving them vulnerable to population declines, inbreeding and eventually extinction. One important source of genetic variation is gene flow (or migration), defined as the movement of genes from one population to another (Slatkin, 1987; Holderegger and Wagner, 2008). A migrant therefore must successfully interbreed for gene flow to occur. Successful dispersal of migrants can increase the effective population size (i.e., the number of breeding individuals in an idealised population (Wright, 1931)) through the influx of novel alleles, whereas smaller, isolated populations with little or no gene flow are more susceptible to the random effects of genetic drift (i.e., the random sampling of alleles within a population) and subsequent loss or fixation of alleles (Futuyma, 1998; Hyde, 2009). Gene flow can therefore have a positive effect on abundance and fitness by increasing variation within populations, impeding divergence between populations and countering local adaptation (i.e., the evolution of species to local environmental conditions).

The level of gene flow is dependent on the ability of individuals to disperse among populations (Anderson et al., 2010). There are both advantages and disadvantages to dispersal; the disperser can benefit from avoiding inbreeding, disease and predators, or they may struggle to find a suitable site or mate or may simply not survive the journey (Freeland et al., 2011). Even if an organism has the dispersal capability, movement can be impeded. For example, species that persist in highly fragmented landscapes often
occur in small disjunct populations (Ricketts, 2001). Understanding the degree to which
the landscape impedes or facilitates gene flow will ultimately help determine the long-
term viability of populations and/or species.

Traditionally, the “isolation by distance” model (IBD; Wright, 1943; Slatkin, 1993) has been used to study the effects of habitat on gene flow. IBD assumes that
individuals are more likely to disperse to nearby sites. As a result, the rate of gene flow is
expected to be inversely proportional to the geographic distance between sites (Freeland
et al., 2011). However, IBD fails to account for the arrangement of the landscape matrix
surrounding populations and their influence on dispersal. It assumes a homogeneous
environment where movement of organisms is dependent only on the physical distance
between habitat patches and symmetrical movement.

Recently, there has been a movement towards explicitly testing the effects of
landscape features and environmental variables on gene flow, because realistically,
populations often occur in heterogeneous landscapes where habitat patches are
surrounded by an intervening matrix of multiple features of varying quality (Cushman et
al., 2006). Dispersal among habitat patches is therefore dependent on the quality of the
matrix for the organism under study. Take a forest-dependent bird that wants to move
from patch A to patch B. There are two different routes to choose from; the shortest route
over a large patch of unsuitable habitat (e.g., grassland), or the longest route around the
grassland through a sheltered, forested corridor. Naturally, the bird will select the
forested corridor as this route increases its chances of survival. Therefore, the shortest
physical distance to movement is not necessarily the most likely route.

1.2 Landscape genetics
Many assumptions of classical population genetic approaches limit the ability of researchers to explicitly test the effects of different ecological factors when explaining patterns of population genetic structure, particularly when predicting gene flow in heterogeneous landscapes. For example, they assume that populations exist in discrete patches, landscapes are uniform and gene flow follows a simple IBD pattern (Holderegger and Wagner, 2008; Figure 1.1a).

The field ‘landscape genetics’ (Manel et al., 2003) developed as a new approach to address some of these limitations. Its emergence was facilitated by advances in landscape ecology, technological improvements in molecular methods and improvements in geographical information systems (GIS) (Storfer et al., 2007; Anderson et al., 2010; Sork and Waits, 2010; Manel and Holderegger, 2013). One important aspect of this growing field is the consideration that dispersal and subsequent gene flow of individuals, or populations, is largely dependent on the degree to which the landscape facilitates movement, otherwise known as landscape connectivity. Two components to landscape connectivity are structural connectivity (the physical characteristics of the landscape), and functional connectivity (the ability of organisms to move through the landscape) (Manel et al., 2003). Landscape genetics provides a means to test the influence of structural connectivity on functional connectivity by measuring the relationship between different environmental factors and gene flow at biologically meaningful scales (Cushman et al., 2006; Holderegger and Wagner, 2008; Figure 1b).

One of the first studies to use a landscape genetic approach was Piertney et al. (1998). They identified considerable genetic structuring among red grouse populations in Northeast Scotland. By explicitly evaluating landscape variables in the study area, they discovered an area of poor habitat quality associated with a river system that was
affecting dispersal capabilities in this species. Since its introduction, landscape genetics has been used to study gene flow in terrestrial mammals (e.g., roe-deer Capreolus capreolus (Coulon et al., 2006)); birds (e.g., red grouse Lagopus lagopus scoticus (Piertney et al., 1998)); aquatic animals (e.g., long-toed salamanders Ambystoma macrodactylum (Goldberg and Waits, 2010); plants (e.g., California valley oak Quercus lobata (Grivet et al., 2008)); and disease pathogens (e.g., black leaf streak pathogen Mycosphaerella fijiensis (Rieux et al., 2011)). Furthermore, landscape genetics can facilitate predictions of a population’s response to anthropogenic forces such as climate change, habitat destruction or human population growth (Sork and Waits, 2010) and identify specific barriers to gene flow not detectable by traditional methods. Landscape genetics can also offer the advantage of identifying features that facilitate gene flow such as habitat corridors, which are important in maintaining population connectivity (McRae, 2006). The identification of specific factors facilitating or barriers impeding dispersal and gene flow therefore has important implications for ecological, conservation, and evolutionary studies.

1.3 Factors influencing dispersal and gene flow

A species’ dispersal ability is influenced by impenetrable barriers within the landscape. The effect of barriers on gene flow can be similar across taxonomic groups or vary depending on the species and the type of environment in which they live (i.e., terrestrial vs. aquatic) (Storfer et al., 2010). For example, one study found that motorways facilitated dispersal in one ungulate species but restricted dispersal in another (Frantz et al., 2012), whereas rivers can promote dispersal in both Scottish Highland red deer Cervus elaphus (Perez-Espona et al., 2008) and coastal tailed frogs Ascaphus truei (Spear
and Storfer, 2008). Common dispersal barriers include large physical structures such as mountain ranges and large bodies of water, but can also include cryptic barriers such as climatic gradients, resource availability, intraspecific competition and behaviour.

1.3.1 Physical barriers

Physical barriers, sometimes termed “linear features” (Storfer et al., 2010) are distinct, easily recognizable structures. Mountain ranges are found across the globe from the Alps in Europe to the Himalayas in Asia and vary in terms of elevation, size and orientation. North America has a characteristically diverse landscape owing to a number of mountain ranges distributed in a north-south direction (i.e., the Rocky, Cascade, Appalachian, Sierra Nevada, and Coastal Mountains), so it is not surprising that mountains are frequently identified as barriers to gene flow in a variety of species (Sakaizumi et al., 1983; Stone et al., 2002; Barrowclough et al., 2004; Emel and Storfer, 2012) and play important roles in species diversification (Calsbeek et al., 2003).

Movement can also be restricted by large bodies of water (Piertney et al., 1998; Coulon et al., 2006; Mockford et al., 2007). The “riverine barrier hypothesis” was derived from the observation that many species’ ranges are bounded by rivers (Wallace, 1852). Numerous studies of gene flow and diversification of terrestrial vertebrates inhabiting the Amazon basin support this hypothesis (Gascon et al., 2000), particularly primates (Ayres and Clutton-Brock, 1992; Peres et al., 1996) and Neotropical birds (Hackett, 1993; Aleixo, 2004; 2006). Straits also appear to isolate populations from their mainland counterparts (Broders et al., 1999; Castella et al., 2000; Boys et al., 2005; Topp and Winker, 2008; Bull et al., 2010).
However, barriers are not always obvious as organisms may perceive their landscape at very different spatial scales (McRae and Beier, 2007). For example, small features such as variation in forest composition (Long et al., 2005) and climate (Fontaine et al., 2007; Yang et al., 2013) can influence patterns of gene flow. Habitat heterogeneity influences genetic differentiation in marine (e.g., ocean currents or circulation patterns (White et al., 2010)) and freshwater organisms (e.g., distribution of populations among drainages (Meeuwig et al., 2010)). This information would go unnoticed if studies had not focused on local genetic patterns.

Furthermore, physical barriers can be artificial, anthropogenic structures such as roads, cropland, urbanized areas and river dams to name a few. MacDougall-Shackleton et al. (2011) found that anthropogenically fragmented landscapes had a greater effect on genetic diversity of song sparrow (Melospiza melodia) populations than naturally fragmented landscapes. It is therefore, not surprising that artificial barriers have had a huge impact on dispersal movements in a number of taxa from mammals (Coulon et al., 2004; Epps et al., 2005) to birds (Johnson et al., 2003; Lindsay et al., 2008), plants (Young et al., 1996; Jump and Peñuelas, 2006; Vranckx et al., 2012), amphibians (reviewed in Cushman, 2006), and even invertebrates (Keller and Largiadèr, 2003; Keller et al., 2004). It is also important to consider previous conditions when explaining current patterns of genetic differentiation as oftentimes genetic signatures of past events can be maintained, particularly in organisms with limited or short dispersal distances (Hall and Beissinger, 2014). If these are not considered, this may lead to misinterpretations of the effects of anthropogenic disturbance (Jordan et al., 2009) or current demographic processes (Johansson et al., 2006) on the resulting genetic patterns.
1.3.2 Historical processes

Another field that examines contemporary distributions of species and the processes influencing their spatial genetic structure is phylogeography (Avise, 2000). Phylogeography investigates the historical processes influencing current patterns of genetic variation across large portions of species’ geographical ranges, whereas landscape genetics focuses on more recent and contemporary processes in distinct geographic regions (Wang, 2010). The scale (both spatial and temporal) is a key distinction between the fields.

Many studies examine the influence of the Pleistocene glaciations on phylogeographic patterns (Hewitt, 1996, 2004; Brunsfeld et al. 2001; Demboski et al., 2001; Lessa et al., 2003; Carstens & Knowles, 2007; Hofreiter & Stewart, 2009; Shafer et al., 2010). During the Quaternary period, severe climatic oscillations played a major role in shaping current landscapes (Avise, 2000; Hewitt, 2000; 2004). Changes such as the production of land bridges, from the combined effect of massive ice sheets and reduced sea levels, allowed large scale movement between previously isolated land masses. These changes altered species’ distributions through range expansions and contractions, which influenced the genetic variability of populations, and in some instances, resulted in the formation of new species (Pielou, 1991). Evidence from pollen cores suggests that northern temperate species’ ranges were restricted to regions mainly south of the ice sheets in locations known as ‘glacial refugia’ (Pielou, 1991; Hewitt, 2000). As the ice sheets retreated, northward expansion and colonisation into suitable habitat was a rapid process for some, but not all, temperate species, and the rate of colonization for each species was affected by factors such as dispersal capabilities, physical barriers, and habitat requirements (Hewitt, 1996). This information allows researchers to determine
the postglacial colonisation paths and the influence of barriers on the resulting genetic
structure of contemporary populations. These historical processes can leave imprints in
the observed genetic structure so when identifying barriers to gene flow, important
consideration of all possible influences is necessary to prevent errors in interpretation.

1.4 Molecular tools
There has been an enormous transition from using phenotypic data (e.g., morphology,
physiology and behaviour) to using molecular data to study genetic variation within and
among populations and/ or species (Sunnucks, 2000; Avise, 2004). Molecular markers
are defined as fragments of DNA with a known location in the genome. They allow us to
quantify genetic diversity, track the movements of individuals, measure inbreeding,
identify species from mixed samples, characterise new species and trace historical
patterns of dispersal (Avise, 2004). They also allow the quick detection and
characterization of genetic variation because of the growing ease with which molecular
data can be obtained from virtually any taxonomic group.

1.4.1 Marker choice
No single molecular marker is ideally suited to all evolutionary studies, so molecular
markers must be carefully selected to match the research question(s) as well as the
spatiotemporal scales. Some characteristics to consider include the mutation rate (do they
evolve fast enough to infer recent evolutionary histories?); the variability of the marker
(is the resolution fine enough to detect small genetic differences?); but also the genome
representativeness (are the markers distributed across the entire genome or within one
specific region?); and inheritance (are the markers uni-parental or bi-parentally inherited?) (Balkenhol et al., 2009; Wang, 2011).

Poor marker choice can lead to misinterpretations of the true genetic patterns. Problems can arise when single, uniparentally inherited markers (e.g., chloroplast (cp)/mitochondrial (mt) DNA) are used in studies of contemporary gene flow (Schlötterer, 2004; Wang, 2011). Firstly, some portions of these genomes evolve too slowly to be useful in inferring most recent and ongoing microevolutionary processes so choosing a highly variable marker is crucial. Secondly, using a molecular marker that is only inherited down the maternal line will only provide information about female dispersal. For example, Vandergast et al., (2007) used mtDNA sequence data from a single mtDNA gene (Cytochrome Oxidase-I) to infer the effects of recent and historical habitat fragmentation on genetic differentiation in the mahogany Jerusalem cricket (*Stenopelmatus mahogany*). Their choice of marker limited their results towards female dispersal and gene flow and did not account for male dispersal. In addition, as different genes in different genomic regions undergo different rates of recombination, genetic drift and selection, relying on one single locus could lead to sampling error (Selkoe and Toonen, 2006). In this case, using a combination of molecular markers from different genomes (e.g., nuclear and organelle) with different modes of inheritance (i.e., uni and bi-parental) would have improved the power of their study and would have provided a more complete picture of the overall pattern of genetic differentiation.

1.4.2 Microsatellites

Microsatellites (or simple sequence repeats (SSRs)) are a commonly used marker in population and landscape genetics studies (Jarne and Lagoda, 1996; Storfer et al., 2010).
Found throughout the nuclear genome, microsatellites are simple, short tandem repeats of between one and six nucleotides. Di- (e.g., AC), tri- (e.g., TAG) and tetra- (e.g., GATA) nucleotide repeats are the most commonly used markers (Jarne and Lagoda, 1996). The majority of microsatellite loci are selectively neutral and biparentally inherited. As a multi-locus marker, increasing the number of loci can increase statistical power (Landguth et al., 2012; Hall and Beissinger, 2014), but estimates of genetic differentiation using highly polymorphic loci must be interpreted with caution (Hedrick, 1999). They also have high mutation rates (due to polymerase slippage during DNA replication), so can generate high levels of allelic diversity, making them particularly useful for studying the effects of recent landscape change on patterns of genetic variation. There are two mutation-drift equilibrium models of microsatellite evolution which must be considered when making population genetic inferences: the classical stepwise mutation model (SMM; Ohta and Kimura, 1973) which states that one repeat is either gained or lost upon mutation (Figure 1.2a), and the infinite alleles model (IAM; Kimura and Crow, 1964) which states that any mutation will lead to a new allele (Figure 1.2b). DiRienzo et al. (1994) modified the SMM model into the two phase model (TPM) to more accurately explain microsatellite variation. This new model simply allowed for mutations of larger magnitude to occur, albeit at a lower frequency. It is important to note that microsatellites have lower lineage sorting rates so their use is limited to investigating current patterns of population genetic structure within a single species. Understanding structure would warrant some additional information and species’ histories which would require the use of additional molecular markers (e.g., mtDNA).

Despite being the marker of choice for many genetic studies, microsatellites do come with limitations. Firstly, primer development is costly and time consuming, but this
can be avoided if previously designed loci are readily available for the species of interest or, alternatively, closely related taxa. The innovation of next generation sequencing technologies is making the collection of loci much more feasible, but these technologies come with their own limitations especially when studying non-model organisms (McCormack et al., 2013). Selective neutrality of microsatellites is a common assumption and thus, their use has been restricted to testing neutral genetic diversity. However, it has long been recognized that microsatellites can be linked to loci under selection, or themselves be under selection (e.g., Huntington’s disease, fragile-X syndrome; Selkoe and Toonen, 2006), so neutrality of microsatellites should not always be presumed. High mutation rates can also result in homoplasy; the co-occurrence of alleles (including their size and sequence) resulting from convergence rather than decent and can lead to the underestimation of the degree of population divergence (Estoup et al, 1995; Jarne and Lagoda, 1996; Chambers and MacAvoy, 2000). Nevertheless, the high resolution generated by microsatellites makes them one of the most valuable molecular tools for estimating processes such as gene flow and functional connectivity within landscapes.

1.5 Statistical methods

Several approaches must be used to analyse the genetic diversity within a species, as this information will help us to understand and identify the evolutionary processes acting on populations (Excoffier and Heckel, 2006). However, different conclusions can arise when applying different analytical techniques (Balkenhol et al., 2009; Blair et al., 2012), so evaluating and comparing their efficacy and reliability is important. Whilst the list of programs available can be exhaustive (Storfer et al., 2010), the choice of methods
implemented is important to prevent errors in interpretation, and can depend on a number of factors such as the study question(s), the study organism(s), model assumptions, the type of genetic marker and the size of the dataset (i.e., the number of samples and number of loci).

1.5.1 Genetic diversity and population structure

Genetic diversity, estimated using either allele or genotype frequencies, is an important feature of any population as it determines their ability to adapt and evolve to changing conditions and ultimately, their long-term survival. Initial testing for departures of allele frequencies from panmictic expectations (or Hardy-Weinberg Equilibrium; HWE) can provide an indication of whether or not other forces (e.g., genetic drift, mutation, migration, non-random mating, population size or natural selection) may be acting on a population. Descriptive measures can then help characterize genetic diversity of each population. These include measures of allelic richness, allelic diversity and observed heterozygosity (Beebee and Rowe, 2008; Freeland et al., 2011). For example, an observed heterozygote deficit is indicative that the population is not in HWE and thus may be susceptible to/ or undergoing inbreeding, natural selection or genetic drift.

One process that increases within population genetic diversity is gene flow. Estimating the level of gene flow or genetic structure of natural populations is a key component in population genetics studies and one popular approach is the calculation of genetic distances. \( F \)-statistics (Wright, 1951) are used to quantify population genetic differentiation between populations (Freeland et al., 2011), and the most common \( F \)-statistic calculated is the fixation index (or \( F_{ST} \)). \( F_{ST} \) assumes an island model (Wright, 1943); that all populations have equal rates of migration and gene flow is symmetrical.
(Freeland et al., 2011). Generally, if two populations have the same allele frequencies, they are not genetically differentiated and $F_{ST}$ will be zero, whereas if two populations are fixed for different alleles, they are genetically differentiated, and $F_{ST}$ will equal 1. There are a number of other related statistics, such as $G_{ST}$ and $D_{EST}$; developed as analogues of $F_{ST}$ to account for different properties of markers (Holsinger and Weir, 2009; Meirmans and Hedrick, 2011). Significance of $F_{ST}$ values is determined by a permutation procedure; where genotypes are shuffled among populations thousands of times with an $F_{ST}$ value calculated after each permutation. The resulting $P$-value is based on the number of times that these $F_{ST}$ values are equal or larger than the value calculated from the actual dataset (Freeland et al., 2011).

**1.5.2 Bayesian clustering algorithms**

Bayesian clustering algorithms are prominent computational tools for inferring genetic structure, but they do need to be implemented and interpreted with caution. For the most part, they assign individuals to genetic groups based on similarities in individual multi-locus genotypes and provide a good comparison to using predefined groupings. However, any model has a number of underlying assumptions, and any violation of assumptions may lead to qualitatively different conclusions. For example, many Bayesian methods attempt to infer genetic structure by minimizing Hardy-Weinberg and linkage disequilibrium within an inferred cluster (Safner et al., 2011). A crucial assumption is that individuals are not related as the inclusion of family members can severely bias results (Guinand et al., 2006; Anderson and Dunham, 2008).

Bayesian methods are based on the Markov chain Monte Carlo (McMC) simulation method which estimates the joint posterior distribution of a set of parameters.
without exploring the whole parameter space (Beaumont and Rannala, 2004: Epperson et al., 2010). The quality of results is influenced by a number of factors including the starting point, the length of starting chain (or burn in period) which removes the influence of the starting point, and modified parameter values between successive states (Epperson et al., 2010). Several consecutive runs need to be performed to ensure the chains have converged and that parameter space has been correctly explored (Excoffier and Heckel, 2006). Their performance also depends largely on the properties of the data (François and Durand, 2010). For example, empirical data sets often vary in sample size, number of loci and variability of loci which can all affect the ability of these programs to delineate groups. In addition, Bayesian methods can overestimate genetic structure if there is a strong IBD effect (Frantz et al., 2009) which can ultimately lead to errors when identifying conservation management units.

Nevertheless, they are attractive in their ability to incorporate background information into the model, in addition to the relative ease with which complex likelihood problems can be tackled by the use of computationally intensive McMC methods (Beaumont and Rannala, 2004). For example, recent advances in these tools have allowed users to incorporate individual geographic coordinates into their prior distributions. In these models, the probability of two individuals belonging to the same cluster is influenced by their geographical proximity. Thus, Bayesian methods have the advantage of characterizing spatially genetic groups and facilitating the detection of spatial boundaries and dispersal barriers in the landscape (Guillot et al., 2005; Chen et al., 2007; Corander et al., 2008). Since Bayesian clustering programs are increasingly used to estimate the number of genetic clusters within a given data set, their performance is often evaluated and compared with empirical and simulated data to confirm their
robustness (Schwartz and McKelvey, 2009; François and Durand, 2010; Landguth et al., 2010; Safner et al., 2011).

1.5.3 Multivariate and distance-based analyses

Multivariate analyses have been used for decades to extract various types of information from genetic marker data (Jombart et al., 2009). A number of advantages have set them apart from classical approaches (e.g., Bayesian clustering approaches) owing to their popular use in genetics studies. Multivariate methods are exploratory, meaning they do not rely on specific assumptions of the data such as specific population genetics models (e.g., Hardy-Weinberg and linkage equilibrium) and are used to simply summarize the level of genetic variability within the data. They also require less computing power and thus can provide a result within minutes, in comparison to hours or even days and, more importantly, can handle extremely large datasets (Patterson et al., 2006). Two approaches that are ideal in detecting population structure are the principal component analysis (PCA) and principal coordinate analysis (PCoA); these ordination methods decompose multilocus genetic data into two dimensional scatter plots which represent spatial genetic structure. PCoA (Gower, 1966), implemented in this thesis, summarizes matrices of genetic distance (or $F_{ST}$) between populations, allowing the users to explore the visual similarities in the data within a distance matrix. PCoA is often compared to individual Bayesian methods to confirm the level of population genetic structure.

One approach to help explain species-environment relationships (Legendre and Fortin, 1989) is the ‘Mantel test’ which was first proposed in 1967 and first applied in population genetics by Sokal (1979). The test relates pairwise measures of genetic differentiation to geographic distance measures to identify the landscape and/or
environmental characteristics that facilitate or impede gene flow (Storfer et al., 2010). It explicitly tests the correlation between two distance matrices; the two most commonly assessed are genetic vs. geographical distance (or IBD), but can be applied to any spatial distance measure to evaluate the relationships between geographical/ environmental distances and genetic divergence (Lozier et al., 2013; Diniz-Filho et al., 2013). Mantel tests have, however, been criticized for their low power and high rates of type I error (Legendre and Fortin, 2010), but despite this, and provided they are applied and interpreted correctly, they are still the most popular and frequently used method today (Cushman et al., 2013).

1.5.4 Landscape genetic tools

1.5.4.1 Geographical Information Systems

To understand the processes governing evolutionary patterns requires the consideration of environmental variation (e.g., temperature, precipitation and elevation). A Geographic Information System (GIS) is a tool that allows researchers to explicitly incorporate, visualize, analyse and interpret environmental data to understand patterns and trends (Chang, 2009). Spatially distributed data and spatial interpolation are used to generate digital images of environmental variables resulting in a GIS map or layer. However, caution must be taken when using GIS information as errors in the data sources could produce misleading conclusions (Kosak et al., 2008). Outdated data, data from different sources, and classification errors are just a few examples which could impact results. For example, errors can occur in climatic data layers if weather stations are not widely distributed across the study area or if extreme topographic heterogeneity dominates the region (Hutchison, 1989).
Although evolutionary studies were slow on the uptake of GIS due to the need for interdisciplinary collaboration (Etherington, 2011), it has since been widely recognized as a popular tool in phylogeography and landscape genetic studies when assessing patterns of gene flow, population structure and species distributions (Knowles et al., 2007; Holderegger and Wagner, 2008; Kozak et al., 2008; Chan et al., 2011). For example, GIS-based data such as habitat cover and topography can now be used to determine if environmental variables can better explain genetic distances between populations than simple linear geographical distances. GIS data can also be used to visualize the amount of genetic diversity across landscapes (Vandergast et al., 2011) and model species distributions using past, present and future environmental conditions (Guisan and Zimmermann, 2000; Carstens and Richards, 2007; Brown and Anderson, 2014).

1.5.4.2 Dispersal route analysis

Spatial information on landscape and environmental characteristics can be used to create resistance surfaces, which are raster-based maps built in a GIS framework that can then be used to model permeability of habitat types to dispersal (Spear et al., 2010). Briefly, each grid cell on a resistance surface map is assigned a cost value indicating whether that specific habitat limits (assigned a high value) or facilitates (assigned a low value) dispersal. Inferring resistance costs for each factor does, however, require some prior knowledge of the study organism, such as habitat suitability from presence/absence data or movement data from monitoring or tracking studies, or expert opinion (Shirk et al., 2010; Zeller et al., 2012). Resistance distances among populations (or sampling sites) can then be assigned for each habitat type or a combination of resistance surfaces and their influence tested against genetic distances.
Two methods are commonly used to measure resistance distances. The least cost path (LCP) model calculates the rectilinear path of least resistance between two locations with the total cost of the path representing the least-cost distance (Spear et al., 2010). However, this method assumes organisms make informed decisions of their movements and does not include effects of other species, and therefore may not represent the true dispersal route. The second and more frequently used method is the isolation by resistance (IBR) model implemented in CIRCUITSCAPE v4.0 (McRae, 2006) which calculates all possible pathways of least resistance across the landscape using electrical circuit theory. The IBR model better represents gene flow across heterogeneous landscapes as it incorporates factors other than geographical distance. A number of studies have shown that this method consistently outperforms standard models of gene flow such as IBD and LCP (McRae et al., 2008; Shirk et al., 2010; Unfried et al., 2013) and can provide novel and possibly unexpected insights into the processes influencing genetic differentiation. For example, Keller and Holderegger (2013) found that while short distance dispersal of damselflies was restricted to stream corridors, long distance dispersal occurred over larger agricultural landscapes. Gene flow studies using IBR models have generated other surprising patterns. For example, Peterman and Semlitsch (2013) found that the western slimy salamander (Plethodon albagula) were more abundant in moist, cool landscapes where the rate of water loss was the lowest. From this, Peterman et al. (2014) predicted that gene flow would be best predicted by a resistance surface representing the rate of water loss across the landscape. In fact, while this resistance surface was well supported, it affected gene flow contrary to their predictions, where genetic resistance actually decreased with increasing water loss, meaning that salamander abundance is a poor predictor of genetic differentiation.
another study, Spear et al. (2005) predicted that gene flow in the tiger blotched salamander (*Ambystoma tigrinum melanostictum*) would be impeded by open shrub habitat because previous studies found that amphibians tend to avoid open habitats due to the risk of predation and desiccation. Again, the contrary was found where gene connectivity was actually facilitated by these open shrub areas. These findings illustrate the need to incorporate additional ecological factors in studies of gene flow as they can provide novel insight when investigating the processes driving population genetic structure.

**1.6 Study species**

**1.6.1 Paridae**

The Paridae is a diverse songbird family composed of small, morphologically similar, gregarious birds found across both the Northern and Southern Hemisphere, commonly referred to as “tits” in the Old World and “chickadees” or “titmice” in the New World. They occupy a great diversity of habitats, particularly vegetated areas in temperate regions and are known for being cavity nesters and caching food items (Sherry, 1989; Gill et al., 2005). Approximately 56 species have been recognized to date and, after including subspecies, a complete phylogeny of all 67 in-group taxa worldwide was recently completed by Johansson et al. (2013).

North American parids consist of seven chickadee (genus *Poecile*) and five titmice (genus *Baeolophus*) species. Monophyly of the chickadees is strongly supported (Gill et al., 2005; Johansson et al., 2013) and the seven species are often grouped in accordance with the colour of their cap: the “brown-capped” group including the boreal (*P. hudsonicus*), chestnut-backed (*P. rufescens*) and the Siberian (*P. cinctus*) chickadee and
the “black-capped” group including black-capped (*P. atricapillus*), mountain (*P. gambelii*), Carolina (*P. carolinensis*) and Mexican (*P. sclateri*) chickadee. The range distributions of chickadees vary depending on the species, with some being more restricted than others. For example, *P. rufescens* are limited to the Pacific Coast whereas *P. hudsonicus* are more widely distributed from coast to coast. Although some ranges overlap, chickadees are for the most part ecologically segregated by habitat requirements (Campbell et al., 1997).

### 1.6.2 Black-capped chickadee

The black-capped chickadee (*Poecile atricapillus*, L. 1766), of which there are nine subspecies, is a small songbird common to North America with a widespread distribution across most of Canada and the upper two thirds of the United States (Figure 1.3). They are mid-high latitude, resident birds with only juveniles engaging in long distance dispersal post fledging (Smith, 1991). As they are non-migratory, there is the potential for restricted gene flow especially in heterogeneous landscapes. Although geographically widespread, they exhibit habitat preference towards low elevation deciduous woodlands near the forest edge, but have been observed in mixed woodlands, open woods, parks and disturbed areas (Smith, 1991). While they are generalist feeders, they are known to cache food prior to the winter (Smith, 1990). This behaviour illustrates the dependency of chickadees on local environmental conditions, and that any form of habitat loss or alteration could be detrimental to the retrieval of cached food items and ultimately, their survival.

Although the black-capped chickadee has been extensively studied in the literature, little is known about the way certain landscape structures or environmental
variables affect dispersal and gene flow. Previous research has focused primarily on hybridization effects between the black-capped chickadee and Carolina chickadee, *P. carolinensis* (Curry, 2005; Reudink *et al*., 2007), in addition to reproductive success (Fort and Otter, 2004); vocalisations (Guillette *et al*., 2010); mate preference (Bronson *et al*., 2003); extra-pair paternity (Otter *et al*., 1998); and winter survival (Cooper and Swainson, 1994), amongst others. Interestingly, Roth II and Pravosudov (2009) and Roth II *et al.* (2012) discovered that spatial memory and learning capabilities improved with increasing latitude (and climate severity) in the black-capped chickadee; two important factors in food caching animals when accurate retrieval is crucial for winter survival. As such, there is the potential for specific landscape and environmental variables to play an important role in the genetic diversity of this species.

While many landscape genetic studies have focused on species with limited distributions (Levy *et al*., 2013; Castillo *et al*., 2014), ground dwelling organisms with limited dispersal abilities (Funk *et al*., 2005; Cushman *et al*., 2006; Hagerty *et al*., 2011; Dileo *et al*., 2013; Soare *et al*., 2014), species of conservation concern (Segelbacher *et al*., 2010; Quemere *et al*., 2010) or a combination of the above, few studies have attempted to investigate gene flow in a common and stable species with high dispersal potential. Birds are often assumed to be great dispersers because of their flight capabilities, however, not all birds are long distance migrants and breaks in the landscape can greatly affect genetic diversity. For example, the house sparrow (*Passer domesticus*) has an extensive range encompassing most of the world. Despite being extremely common, they are a sedentary species and consequently, studies have found that large water bodies restrict gene flow in the species and lead to differentiation (Kekkonen *et al*., 2011). More importantly, on a smaller geographical scale, populations have suffered severe declines in areas
experiencing agricultural intensification and urbanization (Vangestel et al., 2012). Thus, as another sedentary and widespread species, isolated black-capped chickadee populations may also be under threat of reduced genetic diversity from localized environmental change at very small spatial scales.

1.7 Thesis aims and approaches

The aim of this study is to use a landscape genetics approach to investigate the spatial distribution of genetic variation in the black-capped chickadee and the identification of landscape and other environmental features impeding or facilitating dispersal and subsequent gene flow, which may not be detectable by traditional methods. Both large and small geographical scales were evaluated to investigate patterns of genetic structure as spatial scale can greatly affect inferences (Cushman and Landguth, 2010).

I used high resolution microsatellite genetic markers to test fine-scale ecological questions particularly recent gene flow (Sunnucks, 2000; Avise, 2004; Selkoe and Toonen, 2006). As previous studies have focused mostly on historical patterns of gene flow in the black-capped chickadee (Gill et al., 1993; Hindley, 2013) or attempted to explain contemporary genetic structure but with a limited sampling regime given their distribution (Pravosudov et al., 2012), this study will provide a more complete picture of the chickadee’s current evolutionary status.

Altogether, this information will give us a better understanding of how black-capped chickadees interact with their environment and bridge the gap in our knowledge of this species’ ecology to facilitate predictions of how populations may respond to future environmental change. More importantly, this information is not limited to birds, as
restricted dispersal seen here applies to other organisms that share similar characteristics (i.e., habitat requirements) and life histories.

1.8 Predictions

1.8.1 Range wide genetic structure

The black-capped chickadee has a widespread distribution and their range coincides with a number of large physical barriers (Figure 1.3). I predict that populations situated on either side of mountain ranges (e.g., the Rocky, Cascade and the Alaskan Mountains) will be genetically differentiated. However, the Rocky Mountain Range has been found to restrict dispersal in some species (Milot et al., 2000; Lovette et al., 2004; Burg et al., 2005; Peters et al., 2005), but not in others (Colbeck et al., 2008; Pierson et al., 2010; Lait and Burg, 2013; van Els et al., 2014). Island populations also show patterns of genetic isolation from their mainland counterparts (Frankham, 1997). Since the black-capped chickadee population on Newfoundland (an eastern island separated from the continent by a large water barrier) was found to be genetically distinct in previous studies (Gill et al., 1993; Hindley et al., 2013), it is likely that it will also show patterns of genetic divergence in this study. Newfoundland includes a subspecies of the black-capped chickadee (P. a. bartletti; American Ornithologists’ Union, 1957) suggestive of continued isolation. Furthermore, Newfoundland is home to a number of genetically distinct populations of mammals (Broders et al., 1999; McGowan et al., 1999, Kyle and Strobeck, 2003, Laurence et al., 2011), plants (Boys et al., 2005) and birds (Zink and Dittmann, 1993; Zink, 1994; Holder et al., 1999; Lait and Burg, 2013); so isolation of populations on this island is not uncommon.
1.8.2 Small scale genetic structure

Assessing population genetic structure at a microgeographical scale has greatly improved connectivity questions and can allow us to expand our understanding of the evolutionary processes within spatially complex environments (Balkenhol et al., 2009). In this thesis, population structure was assessed in two very different geographical regions; in British Columbia (a highly diverse landscape consisting of 14 biogeoclimatic zones) and southern Alberta (a relatively simple landscape within the Great Plains composed of primarily prairie grassland interspersed with riparian associated forested corridors).

Both natural and anthropogenic forces influence British Columbia’s landscape. Mountain ranges scattered throughout the province create climatic gradients with subsequent changes to terrain and forest composition. Heterogeneity within the landscape matrix may impede dispersal and gene flow among populations. In addition, habitat fragmentation occurs through forestry practices, particularly in the central plateau region, as well as through habitat loss by natural processes such as forest fires and insect outbreaks. Loss of habitat has already impacted biodiversity in this region (Blackburn et al., 2003; Wahbe et al., 2005; Munõz-Fuentes et al., 2009) and has the potential of impacting many more (Wind, 1999), including the black-capped chickadee.

In Alberta, the situation is somewhat different. Prairie grassland dominates the landscape with treed areas limited to the Rocky Mountain foothills, riparian zones and urban areas. The perceived risk of crossing large expanses of unsuitable habitat to reach new favourable sites may limit gene flow in this region and as a result, it is likely that population differentiation will be prevalent between rivers systems in this forest species. Within river systems, development (e.g., dams) and natural breaks in riparian forest may also restrict dispersal, suggesting that gene flow will be reduced between populations on
either side of these barriers. Unsuitable habitat is a significant barrier to gene flow (McRae and Beier, 2007). For example, dry grassland reduces gene flow among salamanders (Rittenhouse and Semlitsch, 2006) and American puma populations (McRae et al., 2005), savanna habitats fragment lemur populations (Radespiel et al., 2008) and high elevation forest cover reduces habitat connectivity in alpine butterflies (Keyghobadi et al., 2005). These provide additional evidence that unsuitable habitat and other barriers in Alberta may limit chickadee connectivity. Additionally, one study conducted in the mid-western USA found that the abundance of avian species (including black-capped chickadees) was much higher in hybrid poplar spp. plantations than rowcrop or small-grain fields, and that birds were more attracted to the plantations in agricultural landscapes than forested regions (Christian et al., 1997). This information suggests that hybrid poplar zones which are prevalent in certain riparian systems in Alberta could also influence chickadee movements.

1.9 Thesis Overview

The thesis has been assembled into five chapters. This first chapter provided a general background of the importance of using a combination of advanced genetic, landscape and statistical tools to identify the key processes influencing the genetic structure of populations across heterogeneous landscapes, and the effects this can have on the evolutionary process. The following three data chapters utilise microsatellite markers to infer genetic patterns, and are presented in paper format. Chapter 2 examines the overall population genetic structure of the black-capped chickadee across its entire geographical range and determines whether obvious physical barriers (e.g., mountains, large water bodies and areas of unsuitable habitat) act to restrict dispersal and gene flow in this
species. Chapter 3 builds on an unexpected microgeographic genetic structure in British Columbia identified in Chapter 2 where no obvious physical structures could explain the patterns of differentiation. Here, a transect-based sampling approach was adopted to help identify barriers in a diverse landscape. Chapter 4 investigates population structure within a more homogeneous landscape in southern Alberta, also on a microgeographical scale. Both Chapters 3 and 4 describe similar methods to Chapter 2, but also employ a landscape genetic tool (CIRCUITSCAPE v4.0; McRae, 2006) to determine the paths of least resistance to dispersal and to identify the landscape features influencing gene flow in the black-capped chickadee. The final chapter summarises the main results found in all three data chapters. I describe how the types of environment and geographical scales can have different effects on the genetic structure of populations and how using a landscape genetic approach can further our knowledge of species x environment interactions to help facilitate predictions of gene flow to further landscape change. Future research that can build upon the current findings is also suggested.
1.10 References


Figure 1.1. Two representations of the same landscape used to assess structural connectivity in a) classical population genetics and b) landscape genetics studies (modified from Holderegger and Wagner, 2008). In classical population genetics, the movement of individuals between populations and the rate of gene flow is expected to depend on the physical distance between them (i.e., IBD). Landscape genetics, however, takes into consideration the nature of the intervening habitat matrix between populations. In this case, the matrix is composed of patches of varying quality (grassland, urban and arable land), barriers (road) or transitions from one physical state to another (forest converted to road which subsequently fragments one habitat patch) which could all have a different effect on dispersal and genetic differentiation.
Figure 1.2. Simplified diagrams of two mutation models representing microsatellite marker evolution (modified from Walsh, 2001). The Stepwise Mutation Model (a) where each mutation results in an addition (+) or deletion (-) of a single repeat (AC) and the infinite alleles model (b) where every mutation leads to a new allele (represented by a coloured circle).
Figure 1.3. Map representing the range distribution (shaded green) of the black-capped chickadee (inset) modified from Smith (1991). Included in the map are putative physical barriers to gene flow. From west to east, black dashed lines represent the Coastal (top left), Cascades (middle left) and Sierra Nevada (bottom left) Mountains then the Rocky Mountains and Appalachian Mountains. The blue solid line represents the Strait of Belle Isle and Cabot Strait isolating Newfoundland.

Map projection: Lambert Conformal Conic (long: -160°W to -40°W; lat 30°N to 80°N).
CHAPTER 2

Influence of ecological and geological features on rangewide patterns of genetic structure in a widespread passerine.

Running title: Rangewide genetic structure of chickadees

R. V. Adams ¹,² T. M. Burg ¹

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¹University of Lethbridge, Department of Biological Sciences, 4401 University Drive, Lethbridge, AB, T1K 3M4, Canada.
²Corresponding author: rachael.adams@uleth.ca
2.1 Abstract

Geological and ecological features restrict dispersal and gene flow, leading to isolated populations. Dispersal barriers can be obvious physical structures in the landscape; however microgeographic differences can also lead to genetic isolation. Our study examined dispersal barriers at both macro- and micro-geographical scales in the black-capped chickadee, a resident North American songbird. Although birds have high dispersal potential, evidence suggests dispersal is restricted by barriers. The chickadee’s range encompasses a number of physiological features which may impede movement and lead to divergence. Analyses of 913 individuals from 34 sampling sites across the entire range using 11 microsatellite loci revealed as many as 13 genetic clusters. Populations in the east were largely panmictic whereas populations in the western portion of the range showed significant genetic structure which often coincided with large mountain ranges, such as the Cascade and Rocky Mountains as well as areas of unsuitable habitat. Unlike populations in the central and southern Rockies, populations on either side of the northern Rockies were not genetically distinct. Furthermore, Northeast Oregon represents a forested island within the Great Basin; genetically isolated from all other populations. Substructuring at the microgeographical scale was also evident within the Fraser Plateau of central British Columbia, and in the southeast Rockies where no obvious physical barriers are present, suggesting additional factors may be impeding dispersal and gene flow. Dispersal barriers are therefore not restricted to large physical structures, though mountain ranges and large water bodies do play a large role in structuring populations in this study.

Keywords: black-capped chickadee, elevation, population connectivity, microsatellites, population structure, dispersal barriers
2.2 Introduction

Dispersal is the ecological process where individuals move from one population to another to reproduce. This process facilitates gene flow and is essential for the persistence of populations and species. However, ecological and geological features can affect the ability of individuals to move across landscapes and those that restrict dispersal are termed a “barrier”. Barriers therefore play a key role in the genetic structuring of populations by influencing important evolutionary processes such as gene flow and adaptation.

Over the last decade, landscape genetics has contributed to our understanding of how contemporary landscapes influence the spatial distribution of genetic variation in a variety of organisms (Manel and Holderegger, 2013). Topographical features (Smissen et al., 2013), unsuitable habitat (Piertney et al., 1998), and anthropogenic disturbance to the landscape (Young et al., 1996) have all been identified as factors strongly influencing population genetic structure in previous studies. Examining the effects of landscape features and environmental variables on current genetic patterns will provide us with a better understanding of how species interact with their environment. Not only does landscape genetics allow us to assess the environmental contributors of population structuring, it also compliments phylogeographic studies allowing researchers to tease apart the effects of historical and contemporary processes on gene flow in complex landscapes.

During the Quaternary period, severe climatic oscillations played a major role in shaping current landscapes and a number of genetic studies have documented the effects of climatic fluctuations on species distributions since the Last Glacial Maximum (LGM), approximately 26.5 ka to 19 to 20 thousand years ago (Hewitt, 1996, 2004; Carstens and
Knowles, 2007; Clark et al., 2009). While these historical processes may have contributed to how species are distributed today, many physical structures influenced the dispersal routes of new colonisers, some of which still exist in contemporary landscapes and continue to restrict movement. For example, mountain ranges provide an elevational limit to dispersal and large bodies of water may be perceived as too risky or energetically costly to cross. Barriers can also be climate related (e.g., large arid regions) or occur at microgeographic scales (e.g., habitat fragmentation). So, although historical processes are important to consider when assessing the genetic integrity of populations, contemporary processes ultimately impact the spatial distribution of genetic variation seen today.

The black-capped chickadee (*Poecile atricapillus*) is a small, generalist songbird common throughout North America (Figure 2.1). They are an ideal model for understanding how landscape features influence dispersal and gene flow as their current distribution encompasses a wide and diverse geographic region. Although geographically widespread, they are year round residents with localised distributions. Only juveniles engage in limited dispersal (approximately 1.1 km; Brennan and Morrison, 1991) creating the potential for restricted gene flow. Due to their generalist nature, suitable habitat is not limited but they do exhibit preference for different types of woodland varying from deciduous and coniferous woodland to forested wetlands, favourable riparian communities, deciduous shrubs and even urban, suburban and disturbed areas (Smith, 1993). As cavity nesters, they are however, dependent on trees or snags with advanced decay, particularly of those found in mature forest. They also show a varied diet, feeding on mixed berries, seeds and insects in winter months, switching to a completely insectivorous diet in the breeding season (Runde and Capen, 1987; Smith, 1993). Thus,
habitat quality is important for reproductive and foraging success of this species (Fort and Otter, 2004). While black-capped chickadee behaviour is extensively studied in North America, little is known about the roles barriers play in structuring populations. Previous research focused primarily on hybridization between the black-capped chickadee and other chickadees, (e.g., *P. carolinensis* (Davidson *et al.*, 2013); *P. hudsonicus* (Lait *et al.*, 2012) and *P. gambeli* (Grava *et al.*, 2012), vocalisations (Guillette *et al.*, 2010) and winter survival (Cooper and Swanson 1994)). Geographical variation in song, plumage and morphology (Roth and Pravosudov, 2009; Smith, 1993) in addition to differences in hippocampal gene expression profiles (Pravosudov *et al.*, 2013) are suggestive of divergence among populations. Moreover, previous studies using high resolution genetic data (Gill *et al.*, 1993; Pravosudov *et al.*, 2012; Hindley, 2013) have all identified genetically distinct populations of the black-capped chickadee over a large geographical range. Hindley’s (2013) study showed the most comprehensive sampling design, but was limited by the use of a single maternally inherited locus (mitochondrial DNA control region). By creating a picture of the overall genetic structure of the black-capped chickadee across a wide range of environments, this current study can help provide additional insights into other ecological patterns found in this species. For example, do patterns in song and morphology reflect differences in genetic patterns and therefore different selective pressures?

The aims of this study are to investigate how contemporary landscapes have shaped the spatial patterns of genetic variation and population structuring of the black-capped chickadee and to identify potential barriers to dispersal providing additional insights into their ecological and evolutionary potential using microsatellite markers. Birds can be used as mobile indicators of habitat quality, so as a common, widely
distributed songbird that responds relatively quickly to environmental change (e.g., in insect outbreaks (Gray, 1989)) the black-capped chickadee is an ideal model organism for investigating population structure and gene flow in contemporary landscapes at both large and small geographical scales.

In this study, we aim to answer the following questions:

1. Do mountain ranges and large bodies of water restrict gene flow across the black-capped chickadee’s range? Mountain ranges have been found to restrict dispersal in a number of organisms (e.g., the downy woodpecker *Picoides pubescens* (Pulgarín-R and Burg, 2012); the hairy woodpecker *Picoides villosus* (Graham and Burg, 2012) and the tundra vole *Micotus oeconomus* (Galbreath and Cook, 2004)) producing in some cases a clear east/ west divide corresponding to the Rocky and/or Cascade Mountains. We predict significant genetic differences among samples collected on either side of mountain ranges. The most prominent ranges include the Rocky Mountains, the Alaskan Mountain range and the Cascade Mountains. Black-capped chickadees are notably absent from Vancouver Island, Haida Gwaii (also known as the Queen Charlotte Islands) and the Alexander Archipelago, suggesting large expanses of water are also significant dispersal barriers. The island of Newfoundland is separated from continental populations by the Strait of Belle Isle and Cabot Strait and mtDNA studies show restricted maternal gene flow between Newfoundland and the mainland in black-capped chickadees (Gill et al., 1993; Hindley, 2013). As such, we predict populations on Newfoundland will be genetically distinct from those on the mainland.
2. Are fine scale genetic differences present within the black-capped chickadee populations? We predict finer scale differences in population structure will be found (in comparison to previous mtDNA and amplified fragment length polymorphism (AFLP) studies) using high resolution microsatellite markers as the result of ecological differences across the species’ range. Restricted gene flow can result from recent modifications to the landscape creating small-scale barriers (e.g., change in habitat composition). Habitat loss and associated fragmentation can reduce connectivity and create small, isolated populations leading to increased genetic differentiation (Young et al., 1996).

2.3 Methods

2.3.1 Sampling and DNA extraction

Adult birds were captured using mist nets and call playback over six breeding seasons (2007-2012). Blood samples (< 100 µl from the brachial vein) and/or feather samples were collected from across the species’ range (Figure 2.1, Appendix 1.1). Suspected family groups and juveniles were removed from the data. Sampling sites were confined to a 40 km radius where possible and a total of 913 individuals from 34 populations were sampled across North America. Each bird was banded with a numbered metal band to prevent re-sampling. All blood samples were stored in (~1 ml) 95% ethanol and, on return to the laboratory, stored at -80°C. Additionally, museum tissue samples (toe pads and skin) were obtained to supplement field sampling (see Acknowledgements). Museum samples were collected within the last thirty years with the oldest sample obtained in
1983. DNA was extracted from blood ethanol mix (10 μl), tissue (~1 μg) or feather samples using a modified Chelex protocol (Walsh et al., 1991).

2.3.2 DNA amplification and microsatellite genotyping

A subset of individuals was initially screened with 54 passerine microsatellite loci. In total, 29 microsatellite loci yielded PCR products, of which eighteen loci were monomorphic (Aar1 (Hannson et al., 2000), Ase48, Ase56 (Richardson et al., 2000), CE150, CE152, CE207, CETC215, CM014, CM026 (Poláková et al., 2007), CtA105 (Tarvin, 2006), Gfo6 (Petren, 1998), Hofi20, Hofi24, Hofi5 (Hawley, 2005), Lox1 (Piertney et al., 1998), NPAS2 (Steinmeyer et al., 2009), Pca2 (Dawson et al., 2000) and VeCr02 (Stenzler et al., 2004)), and eleven were polymorphic (Appendix 1.2).

DNA was amplified in 10 μl reactions containing MgCl₂ (Appendix 1.2), 0.2 mM dNTPs, 1 μM each primer pair (forward and reverse) and 0.5 U Taq DNA polymerase. All forward primers were synthesised with an M13 sequence on the 5’ end to allow for incorporation of a fluorescently labelled M13 primer (0.05 μM; Burg et al., 2005) during DNA amplification. One percent formamide was added to reactions involving PAT MP 2-14. Among eleven markers, six could be multiplexed in three sets of two markers each (PAT MP 2-14/Titgata39, Escu6/Titgata02 and Ppi2/Cuµ28). For multiplex reactions involving loci Escu6 and Titgata02, PCR conditions for Titgata02 were used.

We used a two-step annealing protocol: one cycle of 94°C for 2 min, 50°C for 45 sec and 72°C for 1 min, followed by 7 cycles of 94°C for 1 min, 50°C for 30 sec and 72°C for 45 sec, followed by 25 cycles of 94°C for 30 sec, 52°C for 30 sec and 72°C for 45 sec, followed by a final extension step of 72°C for 5 min. For two loci (PAT MP 2-43 and Titgata02), the second step was increased from 25 to 31 cycles. Subsequently, products
were denatured and run on a 6% polyacrylamide gel on a LI-COR 4300 DNA Analyser (LI-COR Inc., Lincoln, NE, USA) and manually scored using Saga Lite Electrophoresis Software ((LI-COR Inc., Lincoln, NE, USA). For each gel, three positive controls of known size were included to maintain consistent allele sizing, and all gels were scored by a second person to reduce the possibility of scoring error.

2.3.3 Genetic Diversity

Standard statistical analyses were performed on all individuals unless otherwise indicated. MICRO-CHECKER v2.2.3 was used to detect any errors within the data such as input errors, allelic dropout, stutter or null alleles (van Oosterhout et al., 2004). Allelic richness was calculated in FSTAT v2.9.2.3 (Goudet, 2001) after removing under sampled populations (\( N \leq 5 \)). Tests for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were performed in GENEPOP v4.0.10 (Raymond and Rousset, 1995) using default Markov chain parameters (100 batches, 1000 iterations and 1000 dememorisation steps). Levels of significance were adjusted for multiple statistical tests within populations using a modified False Discovery Rate (FDR) correction method (Benjamini and Yekutieli, 2001). Finally, to determine the levels of population genetic diversity, both observed and expected heterozygosities were calculated in GenAlEx v6.5 (Peakall and Smouse, 2012).

2.3.4 Genetic clustering analyses

Several Bayesian clustering methods are currently available to infer the spatial structure of genetic data (Latch et al., 2006). Genetic structure was therefore assessed using three approaches (one non spatial and two spatial): STRUCTURE v2.3.4 (Pritchard et al.,
2000), BAPS v5.4 (Bayesian Analysis of Population Structure; Corander et al., 2008) and TESS v2.3 (Chen et al., 2007).

As assignments are based on individual multilocus genotypes rather than population allele frequencies, we included samples from all 34 populations as small population sizes will not bias assignment results. All three programs use a Bayesian clustering approach which assigns individuals to clusters by maximising HWE and minimising LD. They differ in their underlying model and assumptions (reviewed in François & Durand, 2010) and some include the type of algorithm used and how the true number of clusters (K) is determined. For example, STRUCTURE and TESS use a Markov chain Monte Carlo (McMC) simulation and complex hierarchical Bayesian modelling whereas BAPS models genetic structure using a combination of analytical and stochastic methods which is computationally more efficient, particularly for large datasets (Corander et al., 2008). Ultimately, STRUCTURE uses a non spatial prior distribution; relying purely on the genetic data whereas BAPS and TESS explicitly incorporate spatial information (i.e., geographic coordinates) from genotyped individuals to infer genetic clusters. All three programs work well when genetic differentiation among clusters is low ($F_{ST} \leq 0.05$; Latch et al., 2006).

STRUCTURE was run using the admixture model, correlated allele frequencies (Falush et al., 2003), lamda fixed at 1 and locations as priors (locpriors). Ten independent runs for each value of K (1-10) were conducted to determine the optimal K. Runs were performed using 50,000 burn in periods followed by 100,000 McMC repetitions. The results from replicate runs were averaged using STRUCTURE HARVESTER v0.6.6 (Earl and vonHoldt, 2012). Both delta K ($\Delta K$; Evanno et al., 2005), LnPr(X|K) and Bayes Factor (Pritchard et al., 2000) were used to determine K.
Following the initial run, subsets of the data (i.e., individuals which formed a single cluster from the initial runs) were re-run to establish if further structure was present using the same parameters and five runs for each value of $K$. Individuals that showed mixed ancestry to two clusters ($Q < 60\%$) were rerun together with a subset of individuals from each of the two groups to confirm assignment.

BAPS was run with the option ‘clustering of individuals’ followed by ‘cluster of groups of individuals’, both for $K_{\text{MAX}} = 34$. BAPS searches for all values of $K$ up to the value given for $K_{\text{MAX}}$ and gives a final $K$ for the maximum log (marginal likelihood). The ‘spatial clustering of groups’ option was then used on all individuals and their corresponding group geographic coordinates (weighted mid-point values for each population projected in DIVA GIS v7.5 (Hijmans et al., 2012)). This option has been shown to increase the power to detect underlying population structure and allows the user to visually investigate population structure using Voronoi tessellations.

Using the number of clusters inferred from STRUCTURE, TESS was run using 100,000 sweeps and 50,000 burn-in sweeps for $K_{\text{MAX}}$ (2-13) to identify which $K$ produced the highest likelihoods. The CAR (conditional autocorrelation) admixture model based on the Delaunay tessellation was used and a deviance information criterion (DIC), a measure of model fit, is computed for each run. We conducted ten replicates for each value of $K_{\text{MAX}}$ with an interaction parameter ($\Psi$; the degree to which the geographical information influences individual assignment) of 0.6 as described in Chen et al., (2007). To determine the true number of clusters, we retained 20% of the lowest DIC to identify which $K$ produced the highest likelihood ($K_{\text{MAX}}$) and lowest DIC. We also averaged DIC over all ten runs for each value of $K_{\text{MAX}}$ as often the optimum cluster is the value that coincides with the plateau of the DIC curve.
2.3.5 Population Structure

All populations with a small sample size ($N \leq 5$) were removed from population level analyses (CoOR $N = 2$; NC $N = 5$ and LAB $N = 5$) unless otherwise indicated. Pairwise $F_{ST}$ values were calculated in ARLEQUIN v3.5 (Excoffier and Lischer, 2010) to investigate the degree of genetic differentiation among the predefined populations (significance determined by 1023 permutations). As the theoretical maximum of 1 for $F_{ST}$ is only valid when there are two alleles, $F'_{ST}$ standardised by the maximum value it can obtain were also calculated in GenAlEx v6.5 (Peakall and Smouse, 2012).

Since traditional $F_{ST}$ is often criticised by its dependency on within-population diversity, sample sizes, and its use with highly variable molecular markers such as microsatellites (Meirmans and Hedrick, 2011), we also calculated an alternative diversity measure, $D_{EST}$ (Jost, 2008), using the software SMOGD v1.2.5 (Crawford, 2010). The overall value of $D_{EST}$ is calculated as the harmonic mean across loci for each pairwise population comparison and is suggested to be more accurate for identifying population structure. Measures from both $D_{EST}$ and $F_{ST}$ were compared to determine the true level of genetic differentiation. We also assessed the level of concordance between the two estimates by plotting linearised $D_{EST}$ values ($D_{EST} / (1 - D_{EST})$) against linearised $F_{ST}$ values ($F_{ST} / (1 - F_{ST})$) using a Mantel test in GenAlEx v6.5. Significance was determined using 9999 permutations. To further assess population structure, a hierarchical analysis of molecular variance (AMOVA) was carried out in ARLEQUIN v3.5 on the various groupings produced from both STRUCTURE and BAPS.

2.3.6 Effects of barriers on population structure
Isolation by distance (IBD) was tested using a Mantel test in GenAlEx v6.5 using linearised $F_{ST}$ values. Significance was determined using 9999 permutations and geographic distances (km) were calculated using the GEOGRAPHIC DISTANCE MATRIX GENERATOR v1.2.3. (http://biodiversityinformatics.amnh.org/open_source/gdmg/). Straight line distances are not always accurate as barriers can affect dispersal routes and for that reason, we also tested shortest distance through suitable habitat. For example, distance through forest was calculated for populations located on or around the Great Plains (CO, SD, UT, MT, SAB1, SAB2, LETH, CAB, SK, MB, MI, IL and MO).

BARRIER v2.2 uses a geometry approach to compute barriers on a Delaunay triangulation (Manni et al., 2004). Monmonier’s algorithm identifies areas where genetic differences between pairs of populations are the largest. Using a genetic distance matrix ($F_{ST}$), BARRIER identifies the location and direction of barriers to provide a visual representation of how the landscape influences dispersal in comparison to IBD. We computed the first ten genetic boundaries using an $F_{ST}$ distance matrix for all populations (excluding sites with ≤ 5 samples: CoOR, NC and LAB).

Finally, we used GIS landscape genetics toolbox (Vandergast et al., 2011) to visualise the distribution of genetic diversity across geographical space. The toolbox is run within the Geographical Information System software package ArcGIS® v.9 (ESRI, Redlands, CA) and utilises the population pairwise genetic distances ($F_{ST}$) to produce a genetic divergence raster surface (or heat map). This will help evaluate our hypothesised barriers to movement by plotting values on a map.

2.3.7 Landscape genetics
A landscape genetic approach was used to assess the influence of environmental factors on genetic differentiation in the black-capped chickadee. We used GESTE v2.0 (Foll and Gaggiotti, 2006), a hierarchical Bayesian method which estimates population-specific $F_{ST}$ values and links them to environmental variables using a generalized linear model. It evaluates likelihoods of models that include all the factors, their combinations and a constant (which excludes all variables). Posterior probabilities are used to identify the factor(s) that influence genetic structure. Using a reversible jump McMC method and default parameters, we conducted 10 pilot runs with a burn-in of 50,000 iterations to obtain convergence and a chain length of $2.5 \times 10^5$, separated by a thinning interval of 20. A total of six factors were considered, including three environmental variables (annual average temperature, precipitation and elevation) and three related to distance (latitude, longitude and distance to unsuitable habitat). We tested a number of scenarios to determine the models with the highest probabilities. Certain factors were also tested under different environmental scenarios to more closely examine their influence on genetic structuring (as conducted in Wellenreuther et al., 2011). Three environmental scenarios were assessed; spatial, climatic, and geographic. In the spatial scenario, we tested latitude and longitude, for the climatic scenario we tested annual average temperature and precipitation, and with the geographic scenario we tested elevation and distance to unsuitable habitat. As only two factors are being assessed in these specific scenarios, we added a factor interaction as suggested by Foll and Gaggiotti (2006), and kept all other parameters at their default setting.

2.4 Results

2.4.1 Genetic diversity
In total, 913 individuals from 34 populations were successfully genotyped for eleven variable microsatellite loci with the overall number of alleles per locus ranging from five to 46 (Appendix 1.2). Observed heterozygosity ranged from 0.52 (PG) to 0.73 (CoOR) across all loci and expected heterozygosity ranged from 0.39 (NC) to 0.73 (LAB and MI; Table 2.1). Allelic richness (which accounts for uneven sample size) ranged from 5.26 (AKA) to 8.00 (ON) (Table 2.1). Nineteen of the 34 populations contained private alleles (Table 2.1): 16 populations contained one or two private alleles whereas NSNB had the highest (ten), PG had five and Ft.St.J had four private alleles. Evidence of null alleles and homozygote excess was found for locus Pman45. Exclusion of this locus did not change the results and so was included in the final analyses.

Disequilibrium and departures from HWE were detected following corrections for multiple comparisons. Significant LD was detected between Titgata02 and Cuµ28 and between Escu6 and Pman71 within ID ($P \leq 0.001$; $\leq 0.001$ respectively); between Escu6 and Titgata02 and Escu6 and Ppi2 within SAB1 ($P \leq 0.001$; $\leq 0.001$ respectively); between Titgata39 and Titgata02 within SK ($P \leq 0.001$) and between Titgata02 and Ppi2 within UT ($P \leq 0.001$). LD was not consistent across populations and genotypes showed no association suggesting that LD detected here could be a result of a type 1 error. Significant deviations from HWE were evident for fourteen population/loci comparisons: Ft.St.J at locus PAT MP 2-43; AKA, MI, Ft.St.J, SOR, NSNB and WV at locus Pman45; SAB2 and MB at locus Ppi2 and PG deviated at PAT MP 2-14, Titgata39, Titgata02, Escu6 and PAT MP 2-43. We checked the data for populations that deviated from HWE at two or more loci for the presence of family groups which could explain deviations from Hardy Weinberg expectations. While a number of individuals were caught at the same location on the same day in PG and NSNB, no evidence of family groups was found.
Hierarchical STRUCTURE estimated thirteen clusters (Figures 2.2, 2.3 and Appendix 1.3). The initial run of all of the samples resulted in $K = 3$, using mean log likelihood ($\text{Pr}(X|K) = -34930$) and $\Delta K$, and consisted of: the three Alaskan populations (AKA, AKF, AKW), the Fraser Plateau populations (PG and Ft.St.J), and all other populations (‘main’; Figure 2.2a). The two latter clusters showed evidence of further structure. The Fraser Plateau group subdivided into two groups, PG and Ft.St.J ($\text{Pr}(X|K) = -3034$; Figure 2.2b). The ‘main’ cluster produced three clusters: western, central and eastern ($\text{Pr}(X|K) = -28689$; Figure 2.2c). Nine of the populations showed evidence of mixed ancestry (NWBC, BCR, LETH, MB, CID, MT, IL, LAB and NC). Each of these populations was run with individuals from the two clusters to which they had high Q values. NWBC, BCR, LETH and MB clustered with the western cluster, MT with the central cluster and the remaining three populations with the eastern cluster (results not shown). These nine populations were then grouped accordingly for additional analyses. Further runs were performed on the western, central and eastern clusters using a hierarchical approach. Subsequent runs of the western group (Figures 2.2d – g) resulted in a total of five clusters: Canadian Pacific-Prairies (NBC, all AB populations, SK and MB; $\text{Pr}(X|K) = -14136$), Pacific (WA, SOR, CoOR; $\text{Pr}(X|K) = -8710$), Northwest Rockies (NWBC and BCR; $\text{Pr}(X|K) = -6614$); Idaho (CID and ID) in the Intermountain West and finally NEOR $\text{Pr}(X|K) = -2383$). The central group subdivided into three clusters: eastern Rockies (MT, SD and UT; $\text{Pr}(X|K) = -4041$), CO and NM ($\text{Pr}(X|K) = -1096$; Figures 2.2h and i). The eastern cluster was further subdivided into two clusters: NL and eastern
mainland (Pr(X|K) = -10073; Figure 2.2j). All runs were supported by a Bayes Factor of 1 and ΔK.

The two spatial methods were unable to identify finer differences detected in STRUCTURE despite incorporating individual spatial information. BAPS estimated five distinct clusters (Figure 2.3) in comparison to STRUCTURE’s thirteen. Concordant with groups identified by STRUCTURE, BAPS identified both AK and the Fraser Plateau as being two genetically distinct units in addition to the southern Rockies populations (CO and NM), and Oregon (CoOR and SOR); while the remaining populations formed the fifth cluster. For TESS analyses, the mean DIC plot did not plateau (Appendix 1.4). The mean DIC for $K_{\text{MAX}}$ of 12 disrupted the curve indicating that the program may have failed to converge. Nevertheless, after comparing runs for various assumed $K$ (2-13), $K_{\text{MAX}}$ was estimated from the highest likelihood and lowest DIC run to be thirteen (average log likelihood: -33818; DIC: 68793.3). The effective number of clusters with this parameter was four (Appendix 1.5), detecting the same three groupings as the initial run of STRUCTURE (Figure 2.2a) and an additional cluster representing Newfoundland which was not detected by BAPS.

2.4.3 Population Structure

Pairwise $F_{ST}$ values ranged from -0.014 to 0.148 (Appendix 1.6) and 318 of the 465 values were significant after corrections for multiple tests. Of the 87 non-significant pairwise $F_{ST}$ values, 27 were between adjacent sampling sites. Population wide $F'_{ST}$ was 0.231 (Appendix 1.7). Significant population structure was detected by $D_{\text{EST}}$ which ranged from 0.030 to 0.316 (Appendix 1.6). Pairwise $D_{\text{EST}}$ and $F_{ST}$ values shared a significant, positive correlation ($R^2 = 0.496; P \leq 0.001$).
Using a hierarchical AMOVA, the highest among group variance (5.75%) was produced using three groups (AK, Fraser Plateau and all remaining populations). Among group variance decreased once the “remaining populations” were split into western, central and eastern groups, but as these regions were split further into their respective groups identified in the hierarchical STRUCTURE runs, among group variance steadily increased. Once NEOR was split from the Intermountain West group, the amount of variance increased to 4.06% and a final run of all thirteen groups from STRUCTURE resulted in 4.12%. Meanwhile, when populations were analysed according to BAPS ($K = 5$) and TESS ($K = 4$) groupings, among group variance was 5.25% and 5.08% respectively.

### 2.4.4 Effects of barriers on population structure

The test for isolation by distance (IBD) among all black-capped chickadee populations using straight line distances was not significant ($R^2 = 0.010; P = 0.16$). However, we did find significant IBD within some clusters identified by STRUCTURE. IBD was significant for the eastern mainland group when NL was included ($R^2 = 0.358; P = 0.01$), but not when NL was removed ($R^2 = 0.003; P = 0.24$). For other populations separated by large geographical barriers (i.e., unsuitable habitat), we found a significant effect of IBD using the shortest distance through suitable habitat. For example, when testing populations located around the Great Plains, using the shortest distance through forested habitat resulted in a significant IBD pattern ($R^2 = 0.137; P = 0.01$).

BARRIER identified nine discontinuities. Boundaries detected to the ninth order were considered the most strongly supported for the level of population structure observed in the data, and were overlaid onto a map for visual interpretation (Figure 2.3).
Boundaries detected after the ninth order did not conform to differences observed in previous analyses (e.g., pairwise $F_{ST}$ and $D_{EST}$) and so were removed. Overall, populations where barriers exist were significantly different from all other populations ($P \leq 0.008$). Eight of the linear barriers identified were concordant with STRUCTURE results where populations on either side of the barrier belong to different clusters. The ninth barrier which encircles PG and Ft.St.J was confirmed by STRUCTURE, BAPS and TESS, however, BARRIER failed to identify a genetic discontinuity between these two populations as found in STRUCTURE.

The heat map produced from the GIS toolbox species divergence analysis supports the presence of multiple barriers particularly in the western portion of the range (Figure 4). It shows isolation of Alaska, Pacific, Fraser Plateau and NEOR groups and moderate isolation of Newfoundland. CO and NM are isolated from UT to the west and MO in the east. $F_{ST}$ values to MT are modest to low across prairies and “around” the Great Plains.

2.4.5 Landscape Genetics

Landscape genetics analyses in GESTE revealed a number of environmental variables influencing genetic structure in the black-capped chickadee. When all factors were run together, GESTE struggled to find the model with the highest probability (results not shown). For all single factor runs, the model including the constant produced the highest posterior probability (Table 2.2a). However, some single factor runs produced higher probability models than the environmental scenarios with two factors. For example, the highest constant/factor model involved distance to unsuitable habitat (0.481) followed closely by annual mean temperature (0.479). Interestingly, the influence of longitude
(east-west) was slightly higher than latitude (north-south) on the genetic differentiation (0.472 and 0.469 respectively).

Of all three environmental scenarios (Table 2.2b), the model with the highest posterior probability was the spatial scenario which included latitude, longitude and their interaction term (0.678), suggesting geographic location is an important determinant in the genetic structuring of populations. In the climatic and geographic scenarios, no factors were strongly correlated with pairwise $F_{ST}$ values as the models including only the constant outperformed the rest (climate: 0.216; geographic: 0.214). Despite this, the model with the second highest posterior probability in the climate scenario included precipitation (0.204); this factor also displayed the highest sum of probabilities (0.388). In the geographic scenario, the model with the second highest posterior probability included elevation (0.197) and again had the highest sum of probabilities (0.384).

2.5 Discussion

Microsatellite analyses revealed significant population structuring across the black-capped chickadee’s range. Using clustering programs as many as thirteen groups were found supporting the idea of restricted gene flow. The main groups found in this study are: Alaska, Fraser Plateau (which split into Ft.St.J and PG), eastern Rockies, eastern mainland, Newfoundland, Canadian Pacific-Prairies, Pacific, NW Rockies, southern Rockies (which split into CO and NM), Intermountain West, and finally NEOR. The level of genetic structure is much greater in the west, and may reflect the complex landscape of western North America.

2.5.1 Bayesian analyses comparisons
All Bayesian analyses (STRUCTURE, BAPS and TESS) estimated similar genetic clusters. BAPS failed to separate Newfoundland, or identify substructure in western North America including the differences within the Fraser Plateau and southern Rockies. Although BAPS is computationally more efficient and incorporates the spatial distribution of populations, it struggled to identify key signatures of fine scale genetic structure. Comparatively, most studies have reported the overestimation of genetic clusters using BAPS (Aspi et al., 2006; Latch et al., 2006) or congruence with STRUCTURE (Canestrelli et al., 2008) rather than the underestimation as found in this study.

Although TESS and STRUCTURE often detect a similar number of genetic clusters (Francois and Durand, 2010), in this study TESS failed to identify the key signatures of genetic differentiation in black-capped chickadees. It did detect the same three genetic clusters (AK, Fraser Plateau and main) as the initial STRUCTURE run when all individuals were included, as well as a fourth cluster involving Newfoundland. This information suggests that when using Bayesian clustering methods to evaluate the spatial genetic structure of organisms, a comparison is essential to detect different levels of population structure and to continue beyond one single run as additional structure can be hidden by noisy data.

2.5.2 Macrogeographic dispersal barriers

A number of prominent landscape features correspond with genetic clusters of black-capped chickadees across North America, including both mountain ranges, particularly in the west, unsuitable habitat in the centre and large water bodies in the east.
In Alaska a series of three tall mountain ranges (Chugach, Wrangell and Alaska), effectively isolate the three Alaskan black-capped chickadee populations from the rest of their range. Our data support the genetic isolation of the Alaskan populations and confirms previous findings by Pravosudov et al. (2012) and Hindley (2013). Black-capped chickadees in Alaska have larger hippocampus volumes with a subsequent increase in spatial memory and learning capabilities reflecting selective pressures to retrieve cached food items in severe winter climates (Roth and Pravosudov, 2009; Roth et al., 2012). These differences combined with morphological differences support restricted gene flow between Alaska and adjacent populations. Mountains also restrict dispersal in other parts of the chickadee’s range. For example, the Pacific group (WA, CoOR and SOR) and Intermountain West (NEOR, CID and ID), separated by the Cascade Mountains, are genetically distinct (Figures 2.3 and 2.4). This pattern is repeated for a number of other populations on either side of the Rocky and Blue Mountains.

Contrary to our earlier prediction, not all mountains are effective dispersal barriers. Populations separated by the northern Rocky Mountains (with the exception of NWBC and BCR) show no evidence of significant population differentiation in either STRUCTURE or $F_{ST}$ and $D_{EST}$ comparisons (Figures 2.2 and 2.3; Appendix 1.6). In contrast, populations on either side of the central and southern Rockies are genetically distinct from each other. This was unexpected as the highest tree line elevation; a factor likely to facilitate effective dispersal of forest birds through mountainous valleys and across ranges, actually occurs in the southern Rockies. So although tree line elevation is higher in the American Rockies (3000 m in the eastern Rockies (WY) to 3500 m in the southern Rockies (CO)) than the Canadian Rockies (2400 m) (Körner, 1998), it is possible that lower elevation, treed mountain valleys in the northern Rockies (the lowest
elevation being approximately 950 m in comparison to 1500 m in the south) may facilitate dispersal between populations. Overall, mountain topography (particularly elevation) is an effective dispersal barrier to black-capped chickadees and limiting gene flow in the south and has impacted dispersal in a number of organisms such as thin horn sheep (*Ovis dalli*; Worley *et al.*, 2004). However, mountain ranges are highly heterogeneous environments and low elevation valleys can also increase population connectivity (Pérez-Espona *et al.*, 2008; Hagerty *et al.*, 2010).

Differentiation within the central and southern Rockies cannot solely be explained by contemporary barriers. Historical processes also contributed to the genetic structuring in these regions as similar phylogeographic and genetic patterns in north western North America are found in a number of organisms (Avise, 2000). Specifically the genetic patterns found in our study are concordant with other plant and animal species (Lee & Adams, 1989; Nielson *et al.*, 2001; Hindley, 2013). Several hypotheses (i.e., biotic distributions, ancient vicariance, dispersal, refugia) have been proposed to explain the genetic concordance observed among diverse taxa (Brunsfeld *et al.*, 2001; Carstens *et al.*, 2005).

Mountain ranges in western North America have undergone a complex history of geological and environmental fluctuations combined with successive glacial-interglacial cycles which have subsequently influenced ecosystems within and around them. The genetic divergence of coastal (WA, CoOR and SOR) and interior (ID, CID) populations of black-capped chickadees for both mtDNA and nuclear DNA, may have been influenced by features formed by “ancient vicariance” events such as the uplift of the Cascades combined with the Columbia basin rain shadow; limiting dispersal between these groups (Brunsfeld *et al.*, 2001). The “multiple refugia” hypothesis also helps
explain the level of genetic differentiation within the Rocky Mountains (Brunsfeld et al., 2001; Shafer et al., 2010). The Bitterroot crest (located along the northcentral Idaho/Montana border) restricts forest connectivity between the eastern and western slopes, and major river canyons have fragmented forest communities throughout the range. In our study, populations in central/southern Rockies are isolated from each other (e.g., CID and ID are differentiated from MT and UT) and from northern populations such as SAB and BCR. This east-west and north-south split is consistent with other studies (Good and Sullivan, 2001) and supports the idea of multiple valley refugia during the Pleistocene.

Black-capped chickadees on Newfoundland are genetically distinct from all continental populations suggesting that large water bodies restrict dispersal. Pairwise $F_{ST}$ and $D_{EST}$ values involving NL were all significant (with the exception of MB ($N = 11$)) and relatively high ($F_{ST}$ and $D_{EST} = 0.013$ and $0.039$ (MB) to $0.108$ and $0.221$ (PG) respectively, Appendix 1.6). The Strait of Belle Isle and Cabot Strait have separated Newfoundland from the mainland for approximately 12,000 years (Pielou, 1991). Distances to the mainland are relatively short (18 km to Labrador and 110 km to Nova Scotia); however, oceanic conditions are often harsh. MtDNA data support the presence of genetically distinct groups and show no evidence of maternal gene flow between Newfoundland and continental populations (Gill et al., 1993; Hindley, 2013). Large expanses of water are effective barriers to dispersal in a number of other species. Genetically distinct Newfoundland populations have been found in mammals (pine martin *Martes americana* (McGowan et al., 1999); plants (red pine *Pinus resinosa* (Boys et al., 2005)) and other chickadees (boreal chickadee (*Poecile hudsonicus*; Lait and Burg, 2013) suggesting that long term isolation of Newfoundland while not common, is not restricted to black-capped chickadees.
Geographical distance does influence population structuring when distances are measured through suitable habitat. The presence of other dispersal barriers, such as mountains, limits the ability to detect IBD at the rangewide scale using simple straight line distance (McRae 2006). In the central portion of the black-capped chickadee range lies the Great Plains; a broad expanse of flat land, covered in prairie grassland. As a forest dependent songbird, habitat in this region is unsuitable for dispersal due to lack of trees, necessary for movement. In order for chickadees to move from one side of the Great Plains to the other, they would be required to travel around (through suitable habitat), rather than straight across the unforested landscape. When pairs of populations associated with this region were tested, the effect of geographic distance is clear. Pairwise $F_{ST}$ and $D_{EST}$ values are high, and significant, for populations on either side of the Great Plains (Figure 2.4; Appendix 1.6). Black-capped chickadee dispersal is therefore limited by geographic distances that are influenced by suitable habitat which explains why populations to the east of the Great Plains are genetically dissimilar from those to the west.

2.5.3 Population differentiation within continuous habitat

We found additional population structure that cannot be explained by mountain or water barriers. In the southern Rockies, substructuring between CO and NM may reflect large areas of unsuitable habitat in the form of open desert and grassland. A similar pattern was found for the American puma (*Puma concolor*) across the southwestern US (McRae *et al.*, 2005). Similarly, the unexpected genetic discontinuity of SD and SK, from MB and MO (Figure 2.3) identified by BARRIER corresponds to the large areas of prairie grasslands (i.e., the Great Plains). While black-capped chickadees are present in the
forests surrounding the grasslands, the large geographical distance required to travel in
order to circumscribe the unforested area may be impeding movement. Sacks et al.
(2004) found that gaps in habitat corresponded to genetically distinct populations in
coyotes (*Canus latrans*). Chestnut-backed chickadees show a similar pattern whereby
discontinuities in suitable habitat result in genetically isolated populations (Burg et al.,
2006). Animals perceive the landscape at different spatial scales and what appears to be a
relatively small break in continuous habitat (e.g., 18 km from Newfoundland to Labrador
or < 10 km between suitable coyote habitat) is perceived by the individual as a large
enough risk that dispersal is restricted (Holderegger and Wagner, 2008).

Another population isolated by unsuitable habitat, and mountains, is NEOR which
is a genetically isolated island. Within northeast Oregon, the Blue Mountains stretch
from southeast Washington towards the Snake River along the Oregon-Idaho border and
are associated with the Columbia River Plateau, a flood basalt range located between the
Cascade and Rocky mountain ranges. Although mountain ranges may be involved in
genetic differentiation, it is possible that the high elevation plateau represents a forested
island within the Great Basin; a distinctive natural desert region of western North
America bordered by the Sierra Nevada on the west, the Wasatch Mountains (UT) on the
east, the Columbia Plateau to the north and the Mojave Desert (CA) to the south. With its
rugged north-south mountain ranges and deep intervening valleys, combined with the
absence of forested communities in lower elevations, the Great Basin isolates NEOR
from nearby populations in Oregon, Idaho and all other populations.

The genetic isolation and differentiation of two central British Columbia
populations in the Fraser Plateau was unexpected. The closest sampling site to these two
populations is ~188 km away (NBC) and habitat within the region is continuous.
Additionally, the further genetic differentiation of PG and Ft.St.J within the Fraser Plateau, supported by a number of analyses, was surprising given the small geographical distance between these populations (straight line distance ~120 km). It is possible that a recent change to the habitat composition due to forestry both between and encircling these two populations could be impeding movement. Logging in this area and the relative size and abundance of cut blocks may be restricting dispersal and gene flow. Approximately 1 – 18% of the total cut block area is retained, however, a recent biodiversity assessment in British Columbia stated that it would take over 140 years to recruit appropriate habitat and over 200 years to recruit specific old growth stand structure elements such as large trees and snags (Ministry of Forests, Land and Natural Resource Operations, 2012); the latter being suitable breeding habitat for the black-capped chickadee. Alternatively, the outbreak of the mountain pine beetle (Dendroctonus ponderosae) in British Columbia since the 1950s has led to a huge infestation and devastation of black-capped chickadee habitat (Axelson et al., 2009). At least 4.2 million hectares of mature and old lodgepole pine (Pinus contorta) stands have been infested (Proulx & Kariz, 2005) resulting in huge clearcut operations to recover the infested timber. Although, black-capped chickadees are niche generalists, they are forest-dependent and so this infestation combined with the removal of infected trees has an indirect effect on breeding and dispersal. A large number of private alleles present in both PG and Ft.St.J suggest that additional factors may also explain structuring in this region. For example, a high proportion of private alleles may suggest hybridisation with other chickadees through the introgression of species specific alleles, but a more advanced landscape genetics approach at a smaller geographical scale is necessary to determine the cause of population structuring in this region.

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2.5.4 Landscape genetics analyses

GESTE confirms the influence of latitude and longitude and their interaction on population structuring providing additional support to previous analyses. While all other factors showed no significant influence on genetic differentiation among black-capped chickadee populations, we cannot rule them out as many exhibited similar posterior probabilities. Populations in this study experience a wide range of different climates (Peel et al., 2007). For example, populations located at high elevation and high latitudes experience harsher polar climates in comparison to coastal populations within temperate climates (with increased precipitation) and those in the south which experience dry arid climates. Climatic differences result in changes to vegetation, including trees. The complex biogeography may allow black-capped chickadees to adapt to their local environment. In addition, populations located close to unsuitable habitat or barriers have fewer dispersal opportunities (Burg et al., 2005). In this study, many groups (e.g., the Alaska and Pacific groups) are highly isolated suggesting that interplay between gene flow and local adaptation could explain genetic structure among populations but this is beyond the scope of this study. Further research into adaptive traits and/or loci within this species will allow for a more meaningful interpretation.

2.5.5 Nuclear versus mitochondrial DNA patterns

Using mtDNA restriction fragment length polymorphism data (RFLP), Gill et al. (1993) first explored population differentiation in the black-capped chickadee. Two groups were found with individuals from Newfoundland being genetically distinct from all continental populations (results not shown). More recently, Hindley (2013) identified five groups
with mtDNA sequence data; Newfoundland as well as additional structuring of the continental group (Pacific, Alaska, SE Rockies and main Northeast group; Appendix 1.8). A number of these groupings using mtDNA are identical to those in our study, although our microsatellite data identified finer scale differences. Pravosudov et al. (2012) identified four groupings with nuclear AFLP data collected from only ten populations, some of which were used in this study (AK, BC, WA, MT and CO; Appendix 1.8). Alaska and Washington were both distinct from other populations; BC and MT formed a cluster and there was an eastern group. Differences such as BC (PG) clustering with MT, and CO with the eastern populations (MN, KS, IA and ME) in their study are not unexpected. Our groupings match some of those identified using the alternative nuclear marker. Although AFLPs show similar levels of differentiation, microsatellites often show higher levels of within-population diversity due to their codominant, multiallelic nature (Marriette et al., 2001) which may have contributed to the higher levels of genetic structure found in our study. In addition, our study included an additional 24 populations. Overall, two identical groups were identified by all recent datasets: Alaska and Pacific. Our microsatellite data also support the presence of a genetically distinct group on Newfoundland as identified by both Hindley (2013) and Gill et al. (1993) suggesting that Newfoundland may have acted as a refugium during the LGM as previously claimed.

2.6 Conclusions

Higher levels of genetic differentiation were found in black-capped chickadee populations across North America using microsatellite markers in comparison to previous studies (e.g., mtDNA, AFLPs and RFLPs), illustrating the sensitivity of microsatellites to detect fine scale genetic structure. Population differentiation was more prominent in the western
portion of the black-capped chickadee range and coincided with a number of landscape features such as mountain ranges and habitat discontinuities. Continued isolation may influence evolutionary processes (gene flow, adaptation) in future generations, particularly in a constantly changing environment. This pattern may also be reflected in other resident organisms. Further study is necessary to detect the locations of genetic breaks among subgroups at the microgeographical scale, particularly within the Fraser Plateau, to help identify the corresponding landscape structures or features restricting dispersal and gene flow among these neighbouring populations.

2.7 Acknowledgements

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2.8 References


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Table 2.1. For each sampling site, the location (latitude (lat) and longitude (long)), sample size (N) and site abbreviation (site) are shown. Microsatellite summary statistics for each population and all loci include: number of private alleles (PA), observed (Ho) and expected (He) heterozygosities and allelic richness (AR).

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Table 2.2. Six environmental variables were tested in GESTE v2.0 to determine their influence on population genetic structure of the black-capped chickadee. Posterior probabilities of models for runs which included (a) one individual factor and (b) factors under three different environmental scenarios are provided. For each environmental scenario we provide the sum of posterior probabilities of models including a given factor (i) and the posterior probability of the five models considered for each scenario (ii). Bold values indicate the factor with highest score.

a)  

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Geographic Scenario  

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Figure 2.1. Map illustrating the current geographical distribution of the black-capped chickadee (*Poecile atricapillus*) across North America with sampling locations (See Table 2.1 for abbreviations) projected in ArcGIS® v.10.
Figure 2.2. Inferred population structure of the black-capped chickadee (*Poecile atricapillus*) from eleven microsatellite loci using STRUCTURE v2.3.4 (Pritchard *et al.*, 2000) for (a) \(K = 3\); all individuals from 34 populations, (b) \(K = 2\); Fraser Plateau (Ft.St.J and PG), (c) \(K = 3\) after removing structured populations from the first run (d) \(K = 2\); for all western populations which resulted in (e) \(K = 2\); Canadian Pacific-Prairies (CAB, LETH, SAB1, SAB2, MB, SK, NBC) and Pacific (WA, SOR, CoOR), (f) \(K = 2\); NW Rockies (NWBC, BCR) and Intermountain West (CID, ID and NEOR) with further substructuring of NEOR (g). The central and southern Rocky Mountain regions resulted in (h) Eastern Rockies (MT, SD and UT) and (i) substructuring of NM and CO and finally, the eastern populations resulted in (j) \(K = 2\); Eastern mainland (IL, MI, MO, ON, NSNB, LAB, NC, WV) and Newfoundland (NL). Each vertical line represents one individual and the colour(s) of each line represents the proportion of assignment of that individual to each genetic cluster.
Figure 2.3. Distribution map illustrating coloured population assignment as inferred from STRUCTURE v2.3.4 for all black-capped chickadee individuals based on eleven microsatellite loci. Also included are the five genetic clusters found using BAPS v5.4 (solid circles; the fifth cluster includes the remaining 25 populations), and the four clusters found using TESS v2.3 (triangles; the fourth cluster includes the remaining 28 populations). Dashed lines and circles represent barriers or genetic boundaries as identified in the program BARRIER v 2.2. On the main figure elevation is indicated with grey shading (darker shades of grey indicate higher elevation) and the inset shows forest cover (dark green = closed forest; mid green = open/fragmented forest; light green = other vegetation types; FAO, 2001).
Figure 2.4. A heat map of pairwise $F_{ST}$ values for eleven microsatellite loci in the black-capped chickadee. Red indicates high $F_{ST}$ values and blue, low $F_{ST}$ values. Each sampling site is represented by a black dot (see Figure 2.1 for location names).
CHAPTER 3

Influence of landscape features on the microgeographic genetic structure of a resident songbird.

R. V. Adams $^{1,2}$, S. LaZerte$^3$, K. A. Otter$^3$, T. M. Burg$^1$

Prepared as manuscript for submission

$^1$University of Lethbridge, Department of Biological Sciences, 4401 University Drive, Lethbridge, AB, T1K 3M4, Canada.

$^2$Corresponding author: rachael.adams@uleth.ca

$^3$University of Northern British Columbia, Department of Ecosystem Science and Management, 3333 University Way, Prince George, BC, V2N 4Z9, Canada.
3.1 Abstract
The spatial arrangement of the landscape matrix influences dispersal and gene flow among populations. In this study, we evaluated the effects of landscape heterogeneity on the genetic structure of a common resident songbird, the black-capped chickadee (*Poecile atricapillus*), at a regional scale. Previous work revealed significant population genetic differentiation in British Columbia which could not be explained by physical barriers. We therefore investigated the relationship of landscape variability and the effects of additional environmental factors on gene flow. A total of 399 individuals from 15 populations were genotyped for fourteen microsatellite loci and analyses revealed significant population structuring. A comparison of two Bayesian clustering analyses (STRUCTURE and GENELAND) revealed as many as nine genetic clusters, compared with four in the previous study, with isolation in the north, the central plateau, the south and southeast. Although GESTE analyses failed to identify any factors strongly influencing genetic differentiation, Mantel and partial Mantel tests combined with Akaike’s information criterion scores revealed a significant effect of land cover and elevation on genetic differentiation. It appears that gene flow in black-capped chickadees is highly dependent on low elevation valleys with sufficient forest cover, and combined with climatic variability, could lead to local adaptation in certain areas. This study demonstrates the importance of incorporating additional landscape features when understanding patterns of gene flow.

Keywords: black-capped chickadee, gene flow, landscape genetics, microsatellites, population genetic structure, Circuitscape, barriers
3.2 Introduction
Dispersal and gene flow are crucial for maintaining population connectivity and species persistence, whilst preventing population differentiation and species divergence. However, landscapes are rarely a uniform matrix of essential elements facilitating the constant flow of individuals and genes among populations and maintaining genetic mixing. Heterogeneous and patchy landscapes can reduce population connectivity by restricting dispersal and can create discrete, isolated groups (Baguette and Van Dyck, 2007). To overcome this complexity, landscape genetics (Manel et al., 2003) offers new approaches to explicitly test the influence of landscape elements on genetic structure to identify barriers corresponding to structured populations (Holderegger and Wagner, 2008; Sork and Waits, 2010; Manel and Holderegger, 2013).

Large physical structures (e.g., mountain ranges, large water bodies and unsuitable habitat) appear to be obvious barriers to dispersal and subsequent gene flow, however, their influence may vary within and between species which can make the identification of specific factors mediating connectivity challenging (With et al., 1997). Using a landscape genetics approach, Frantz et al. (2012) found that motorways influenced genetic structuring in red deer (Cervus elaphus), but not wild boars (Sus scrofa). Furthermore, the effects of landscape features may vary across a species range, as was discovered in the ornate dragon lizard (Ctenophorus ornatus), where land clearing was associated with genetic differentiation in one area, but not another (Levy et al., 2012). Smaller, less conspicuous structures or environmental variables, such as microclimate, may also influence gene flow. For example, gene flow in wolverines (Gulo gulo) is facilitated by areas of persistent spring snow cover (Schwartz et al., 2009), whereas in the blue tailed damselfly (Ischnura elegans), levels of local precipitation corresponded to restricted gene flow (Wellenreuther et al.,
Landscape genetics allows the effects of multiple factors on current patterns of genetic structure to be examined across different spatial scales and across species with varying dispersal capabilities, allowing us to gain a better and improved understanding of how organisms interact with their environment, and how they may respond to future environmental change.

Habitat fragmentation from natural and human-mediated processes can impact the spatial distribution of genetic variation at large and small geographical scales. In North America, glacial history combined with complex physiography in the west has severely altered and fragmented the landscape, influencing individual dispersal, population dynamics and distributions of a number of species (Avise, 2000; Hewitt, 1996). Contemporary factors can also reduce population connectivity through removal of suitable habitat. For example, a natural outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) has spread over 18 million ha of forest in western North America and is estimated to have killed 710 million cubic meters of timber. Habitat degradation is further escalated through clear cut operations to recover the infested timber (Ministry of Forests, Land and Natural Resource Operations, 2012). Removal of forests impacts wildlife communities, including cavity-nesters (Martin et al., 2006), by altering food availability, light and moisture, and indirectly by altering habitat suitability and species composition. Exploitation of resources and agricultural conversion can also threaten biodiversity. For instance, the northern spotted owl (*Strix occidentalis caurina*) whose restricted range in the Pacific North West combined with removal of its associated dense, late successional forest habitat has left the species federally threatened (COSEWIC, 2008; Blackburn et al., 2003; Yezerinac and Moola, 2006), with disease and displacement by conspecifics acting secondarily (Kelly et al., 2003).
We conducted a fine-scale landscape genetic assessment of a common resident songbird, the black-capped chickadee, in British Columbia (BC). British Columbia’s complex climatic and vegetation history following the Last Glacial Maximum (26.5 – 19 thousand years ago) combined with major regional transitions resulting from broad-scale climatic gradients (i.e., moisture, temperature and topography) have contributed to its rich and heterogeneous landscape (Gavin and Hu, 2013; Figure 1a). British Columbia contains six ecozones and 14 biogeoclimatic zones (Meidinger and Pojar, 1991) created by mountain ranges which influence habitat-determining factors such as precipitation and topography. For example, a major longitudinal moisture gradient formed by the Coastal Mountains is characterised by dominant maritime moist conifer forest in the west, transitioning to sagebrush steppe, mixed conifer and pine forest in the east, whereas in the interior, a latitudinal gradient formed by increasing summer moisture is characterised by desert steppe in the south transitioning to subboreal and boreal spruce forest in the north.

Our previous study identified population genetic structuring in central British Columbia, but assessing gene flow on a range wide scale meant that smaller geographical barriers were less noticeable due to the sampling regime (Adams and Burg, 2015). In this study, we carried out a transect-based sampling approach to identify where the genetic breaks occur and to evaluate the processes driving differentiation. Fine-scale sampling allowed a more detailed examination of the landscape patterns and processes influencing population genetic structuring. In addition, a larger number of microsatellite markers were used to better capture the spatial distribution of genetic variation of this generalist species (Runde et al., 1987; Selkoe and Toonen, 2006). The study area comprises a number of different habitats and environmental conditions, so studying genetic variability in a species with limited
dispersal potential will allow us to understand how habitat heterogeneity affects the ecology and evolution of populations. We hypothesise: 1) fine scale population genetic differentiation will be evident in the black-capped chickadee; 2) dispersal and gene flow are influenced by landscape features and environmental variables and 3) habitat fragmentation isolates populations in central and southern British Columbia.

3.3 Methods

3.3.1 Study Species

The black-capped chickadee (*Poecile atricapillus*) is a resident songbird, common throughout most of North America with a range that covers a large and complex geographical area. Black-capped chickadees are an important study species because they are generalists meaning they are able to thrive in a variety of different environmental conditions, but they do have a preference for mixed deciduous and coniferous woodland (Smith, 1993). Despite this, some life history characteristics of this species means that habitat quality is important for their evolutionary success. As cavity nesters, they are dependent on advanced decaying trees or snags in mature forests for breeding and winter survival. Their diet requirements also vary depending on the season with preference for mixed berries, seeds and insects in the winter in comparison to a completely insectivorous diet during the breeding season (Runde *et al.*, 1987). Although they have been observed in disturbed areas, studies have found that low quality habitats can negatively affect the reproduction (Fort *et al.*, 2004a), territoriality (Fort *et al.*, 2004b), song output (van Oort *et al.*, 2006), song consistency and perception (Grava *et al.*, 2013a) and song structure (Grava *et al.*, 2013b) of this species, despite being a habitat generalist. Elevation and presence of other chickadees can also influence their distribution and habitat preference (Campbell *et al.*, 1997).
Collectively, this information suggests the importance of a number of factors (e.g., mature woodland) for species persistence.

3.3.2 Sample collection

Using a transect-based sampling approach, approximately 20 individual birds were sampled from each location (or population) along HWY 16, the main road in the region, in British Columbia during the 2012 breeding season. Birds were captured using mist nets and call playback, and blood (< 100 µl from the brachial vein) and/or feather samples were obtained from each individual. Sampling sites were confined to a 10 km radius where possible and samples from our previous study (NWBC, BCR, SAB1 and SAB2) were included to cover a wider geographical area and to remove edge effects of the populations under study. Feather samples were used for two populations (VAN and KEL). With all individuals combined, sampling took place over ten breeding seasons (2003 – 2010, 2012 and 2013) and a total of 405 individuals from 15 populations were sampled (Figure 3.1a, Table 3.1, Appendix 2.1). Each bird was banded with a numbered metal band to prevent re-sampling and all blood samples were stored in 95% ethanol and, on return to the laboratory, stored at -80°C. Suspected family groups and juveniles were removed from the data.

3.3.3 DNA extraction and microsatellite genotyping

DNA was extracted from blood ethanol mix (10 µl) or feather samples using a modified Chelex protocol (Walsh et al., 1991). Each individual was genotyped for fourteen polymorphic microsatellite loci (Appendix 2.2). DNA was amplified for all loci (including new loci Pij02, VeCr05 and CTC101) using the same two-step annealing PCR conditions outlined in Adams & Burg (2015), except for Pij02, where
the two-step annealing temperatures were adjusted to 52°C and 54°C. All procedures following DNA amplification were conducted as in Adams and Burg (2015).

Most individuals were successfully genotyped for all 14 variable microsatellite loci. Seven populations were missing genotypes for locus PmanTAGAn45, four populations for Ppi2, two populations for Titgata02, and two populations for Pij02 (Table 3.2). All analyses were carried out with and without these four loci to determine if missing data influenced levels of observed population differentiation. In addition, we conducted analyses with and without feather sampled populations (KEL and VAN) due to missing data and the potential that genotyping errors may have occurred as amplification for some loci was problematic with lower quality DNA. However, results were not affected after removing underrepresented loci nor when feather sampled populations were removed.

3.3.4 Genetic analyses

3.3.4.1 Genetic diversity

A total of 399 individuals remained after removing those genotyped for \( \leq 5 \) loci. Errors within the data (i.e., input errors, allelic dropout, stutter and null alleles) were assessed in MICRO-CHECKER v2.2 (van Oosterhout et al., 2004). Standard statistical analyses were performed on the 399 individuals.Allelic richness was calculated in FSTAT v2.9.2.3 (Goudet, 2001) and tests for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were performed in GENEPOP v4.0.10 (Raymond and Rousset, 1995; Rousset, 2008) using default Markov chain parameters (100 batches, 1000 iterations and 1000 dememorisation steps). Both observed and expected heterozygosities were calculated in GenAIEx v6.5 (Peakall and Smouse, 2012) to determine the levels of population genetic diversity.
Lastly, levels of significance were adjusted using the modified False Discovery Rate (FDR) correction (Benjamini and Yekutieli, 2001).

### 3.3.4.2 Bayesian clustering analyses

The genetic structure was assessed using two clustering methods; STRUCTURE v2.3.4 (Pritchard et al., 2000), the standard software program for such analyses, and GENELAND v4.0.0 (Guillot et al., 2005a). Both use Bayesian models to assign individuals to clusters by maximising HWE and minimising LD, but differ in the way they use spatial information; STRUCTURE relies solely on genetic data (with the option of predefining populations with location priors) whereas GENELAND integrates spatial coordinates from individual samples to infer the number of genetic clusters.

STRUCTURE was run with the admixture model, correlated allele frequencies (Falush et al., 2003) and locations as priors (locpriors). To determine the optimal number of clusters ($K$), we conducted ten independent runs (100,000 burn in followed by 200,000 McMC repetitions) for each value of $K$ (1-10). Results were averaged using STRUCTURE HARVESTER v0.6.6 (Earl and vonHoldt, 2012) and both delta $K$ ($\Delta K$; Evanno et al., 2005) and LnPr(X|K) were used to determine the true $K$. Any populations with individuals showing mixed ancestry (e.g., 50% Q to cluster 1, and 50% Q to cluster 2) were rerun individually with two populations representing each of the two clusters involved in the mixed ancestry to determine correct assignment. This is important to check because as $K$ increases above the true $K$ value, Q values will often decrease and split clusters. This splitting of populations must be clarified prior to additional testing. Finally, if multiple populations assigned to the same genetic
cluster, those populations were rerun to test for additional substructure using the same parameters as the initial run, but only five runs for each $K$ value.

GENELAND, implemented in the program R (R Development Core Team, 2014), was run in two steps as recommended by Guillot et al. (2005a, b). First, we ran the program for ten replicates for each $K$ (1 – 10) using both the correlated allele frequencies and null allele models and 100,000 McMC iterations, 100 thinning interval, maximum rate of Poisson process of 399 (equal to the sample size), uncertainty attached to spatial coordinates was fixed to 20 km (i.e., the precision of our sample locations: 10 km radius) and the maximum number of nuclei in the Poisson–Voronoi tessellation was fixed to 1197 (three times the sample size). The number of clusters ($K$) was inferred from the modal $K$ and the run with the highest mean posterior probability. A second run was then conducted with the inferred $K$ fixed and all parameters left unchanged to allow individuals to be assigned to clusters. To determine the robustness of this model, GENELAND was run multiple times with different parameters.

3.3.4.3 Population structure

Pairwise $F_{ST}$ values were calculated in GenAlEx v6.5 to investigate the degree of genetic differentiation among the predefined populations. We also calculated $D_{EST}$ (Jost, 2008) in SMOGD v1.2.5 (Crawford, 2010), an alternative measure of diversity that accounts for allelic diversity and is shown to measure genetic differentiation more accurately than traditional $F_{ST}$ when using polymorphic microsatellite markers (Heller and Siegismund, 2009). We compared measures of $D_{EST}$ and $F_{ST}$ to determine the true level of genetic differentiation. Since the theoretical maximum of 1 for $F_{ST}$ is only
valid when there are two alleles, populationwide $F^{ST}$, standardised by the maximum $F^{ST}$ value, was also calculated in GenAlEx v6.5.

To further assess genetic structure among populations, we carried out a Principal Coordinate Analysis (PCoA; executed in GenAlEx v6.5) and a hierarchical analysis of molecular variance (AMOVA) using the groups identified in STRUCTURE (executed in ARLEQUIN v3.5 (Excoffier and Lischer, 2010)).

3.3.5 Landscape analyses

3.3.5.1 Dispersal route analyses

To assess the functional connectivity among populations, we evaluated four competing models: 1) the null model of isolation by geographical distance through suitable habitat (or IBD; Wright, 1943), 2) isolation by elevation resistance, 3) isolation by land cover resistance and 4) isolation by combined elevation and land cover resistance (i.e., both land cover and elevation raster layers were combined using “raster calculator” into one resistance layer in GIS, termed “land cover x elevation” herein). Pairwise resistance distances were calculated among all sampling sites using spatial datasets and an eight neighbour connection scheme in CIRCUITSCAPE v4.0 (McRae, 2006). This method is based on circuit theory and uses resistance distances to assess all possible pathways between two focal points (or populations) to better map gene flow across the landscape and measure isolation by resistance (IBR).

Categorized land cover and digital elevation (DEM) maps were obtained from GEOBASE (www.geobase.ca) and resistances to habitat types were assigned using ArcMap (ESRI©). Populations SAB1 and SAB2 were excluded from these analyses as geo-referenced coordinates were outside the spatial extent of the data. Given the size of our study area, all resistance surfaces were based on a 2 x 2 km resolution. As
the true costs of habitat and elevation types are unknown for our study organism, a thorough literature review facilitated the assignment of cost values. Low resistance values were assigned to suitable chickadee habitat (i.e., forest cover, particularly broadleaf and mixed forests) and low elevation ranges (< 1500 m), whereas high resistance values were given to unsuitable chickadee habitat (e.g., non-vegetated land, grassland) and high elevation (> 1500 m). The program outputs a cumulative ‘current map’ to portray the areas where resistance to gene flow is either high or low.

3.3.5.2 Statistical analyses

After resistance distances were obtained in CIRCUITSCAPE, the influence of pairwise geographical and resistance distances were compared with simple and partial Mantel tests (Mantel, 1967) using IBDWS v3.2.3 (Jensen et al., 2005) to assess their association with both linearised measures of genetic differentiation (\(F_{ST}\) and \(D_{EST}\)) (McRae & Beier, 2007). While Mantel tests allow for a comparison between two matrices, partial Mantel tests have the additional power of controlling for a third matrix (e.g., geographical distances) (Smouse et al., 1986; Spear et al., 2005). We tested statistical significance of all tests using 10,000 permutations.

Mantel tests tend to show low power (Legendre and Fortin, 2010), so we compared results with multiple matrix regression models using the package MuMIn in the program R (R Development Core Team, 2014). Predefined models (i.e., all combinations of landscape, predictor variables) were tested against both genetic distances (i.e., \(F_{ST}\) and \(D_{EST}\)) and AIC (Akaike’s Information Criterion; Akaike, 1973) was used for selecting the best model. AIC uses information theory to find the best model from a set of models by minimising the Kullback-Leibler distance (i.e., finds the model that retains most of the information, has the best fit given the data, and
fewest parameters (Burnham and Anderson, 1998)). AIC values were corrected to account for sample size (AICc) and the best model is the one with the lowest value. To compare models, differences between AICc values were calculated for each model:

$$
\Delta_i = \text{AIC}_c - \text{min AIC}_c
$$

where values of ≤ 2 provide substantial support, 4 – 7 provide less support and values ≥ 10, no support. Finally, Akaike weights were also calculated to represent the likelihood of the model using the following formula:

$$
w_i = \frac{\exp(-0.5 * \Delta_i)}{\sum \exp(-0.5 * \Delta_i)}
$$

where the relative model likelihoods (\(\exp(-0.5 * \Delta_i)\)) are normalised by dividing by the sum of the likelihoods of all the models.

3.3.5.3 GESTE analyses

Associations between environmental and genetic factors were examined using the hierarchical Bayesian program GESTE v2.0 (Foll and Gaggiotti, 2006) and default parameters. GESTE estimates population-specific \(F_{ST}\) values and relates them to environmental factors using a generalized linear model. Posterior probabilities are used to identify the factor(s) that influences genetic structure and the model with the highest posterior probabilities best explains the data.

We considered nine different factors and tested a number of scenarios to determine the models with the highest probabilities. Four common climatic variables were included (annual mean precipitation and annual minimum, mean and maximum temperatures), as well as mean summer temperature and mean summer precipitation to test if periods of summer drought influence genetic differentiation (e.g., in the southern interior). We also included two distance variables (latitude and longitude).
and, as raster data were not readily available for use in CIRCUITSCAPE, one factor to incorporate habitat loss in British Columbia (habitat fragmentation). We categorised the level of fragmentation for each population into three classes (1 = heavily fragmented, 2 = partially fragmented and 3 = no fragmentation), with heavily fragmented areas occurring primarily in the central portion of the range in the Fraser plateau and southern interior where vehicle access is easier and logging in more active. We tested a number of scenarios to identify which specific factor(s) best explains genetic structure (Wellenreuther et al., 2011; Adams & Burg, 2015).

3.4 Results

3.4.1 Genetic structure

3.4.1.1 Genetic diversity

Over all loci and populations, the number of alleles ranged from 3 – 46 alleles (Appendix 2.2). Observed heterozygosity at each site and across all loci ranged from 0.584 (KEL) to 0.683 (SAB1) followed closely by 0.681 (SAB2) and expected heterozygosity ranged from 0.572 (KEL) to 0.717 (FtStJ1; Table 3.2). Accounting for differences in sample size, allelic richness ranged from 2.42 (PG) to 2.79 (FtStJ1 and FF; Table 3.1). Eleven of the populations contained at least one private allele (Table 3.1); FtStJ1 contained the highest number of private alleles (PA = 11) followed by NBC and SAB2, each containing five. Null alleles were detected at a low frequency for a number of loci and were not consistent across populations with the exception of two loci: VeCr05 (0 – 25%) and Cuµ28 (31 – 71%). We found a large difference between observed and expected heterozygosities across populations for locus VeCr05 (Ho: 0.185, He: 0.306), but not for Cuµ28 (Ho: 0.485, He: 0.502, Table 3.2).
Exclusion of VeCr05 and/or Cuµ28 did not alter the results, and so all 14 loci were included in the final dataset.

Thirteen deviations from HWE (Table 3.2) and two pairs of loci in linkage disequilibrium were identified after corrections for multiple tests. All deviations were the result of a heterozygote deficit. Significant LD was found between loci Titgata02 and CTC101 ($P \leq 0.001$) within FtStJ1 and between loci Escu6 and Titgata02 ($P \leq 0.001$) within SAB1. As LD was not consistent across populations and genotypes showed no association, it is possible it is a type 1 error.

3.4.1.2 Bayesian clustering analyses
A hierarchical STRUCTURE approach inferred six genetic clusters (Figure 3.1b) verified by both the mean log likelihood ($Pr(X|K) = -17544.9$) and $\Delta K$ (Appendix 2.3). $\Delta K$ was also high for $K = 8$, but over-splitting of clusters was observed suggesting this result is likely a run error from lack of convergence. Populations with mixed assignment (i.e., CLU, FtStJ2, HAZ, HOU and SAB2; Figure 3.1b) were rerun to determine correct assignment; all of which clustered with NBC ($Q \geq 60\%$). A hierarchical analysis to identify additional substructure was successful for one cluster (FtStJ1 and SAB1) which showed complete differentiation of FtStJ1 and mixed ancestry of SAB1 (Figure 3.1b). In total, seven genetic groups were inferred: 1) BCR, 2) VAN and KEL, 3) NWBC, 4) PG, 5) FtStJ1 6) SAB1 and 7) all remaining populations.

Among the ten replicates in GENELAND, eight runs suggested $K = 9$ whereas two runs suggested $K = 10$. The highest posterior probability was for $K = 9$ (-958) so we took this as being the true $K$. For population membership and boundary graphs, see Appendix 2.4. GENELAND identified a number of genetic clusters similar to
STRUCTURE (BCR, NWBC, PG, KEL and VAN, and FtStJ1; Figure 3.1c), identified two additional genetic groups within the larger group (splitting NBC and CLU), and grouped SAB1 with SAB2.

3.4.1.3 Population structure

Pairwise $F_{ST}$ and $D_{EST}$ values showed a significant positive correlation ($R^2 = 0.692, P = 0.003$). Pairwise $F_{ST}$ values ranged from 0.009 to 0.316 (Table 3.3) and after corrections for multiple tests, 86 of the 105 tests were significant indicating a high level of genetic differentiation among populations. Similar levels of population structure were detected using $D_{EST}$ which ranged from 0.005 to 0.329 (Table 3.3). Overall $F'_{ST}$ was 0.240 (Appendix 2.5).

Distinct clustering of populations in PCoA was only found using $D_{EST}$ values. The first principal coordinate analysis with all 15 populations resulted in clear separation of populations KEL and VAN from all other populations with the first two axes explaining 50.59% and 17.04% of the variation (Figure 3.2a) respectively. Isolation of KEL and VAN is concordant with STRUCTURE and GENELAND. After removing KEL and VAN to identify additional structure, we see separation of PG, as well as NWBC and BCR (Coordinate 1 = 31.05%, Coordinate 2 = 19.93%; Figure 3.2b). These results conform to the groups identified in STRUCTURE and GENELAND.

A hierarchical AMOVA using the seven clusters (or groups) identified in STRUCTURE revealed -1.92% among group variance and 105.14% within populations. Slightly negative components in an AMOVA test are said to occur in the absence of genetic structure (Excoffier et al., 2010). In this case, where genetic structure is known to exist (Adams & Burg, 2015), it is assumed that AMOVA
struggles to partition the data when all seven groups are involved. We therefore used a number of combinations to identify the groupings that explain the largest among group variation (Appendix 2.6). The highest among group variance (2.85%) occurred using two groups (BCR and all remaining populations) followed closely by two sets of three groups; NWBC, BCR and all remaining populations as well as BCR, PG and all remaining populations (which explained 2.83% and 2.80% among group variance respectively) and finally, with four groups NWBC, BCR, PG and all remaining populations (2.64%). FtStJ1 also explained more variation (2.12%) when grouped alone, than with additional populations and groups.

3.4.2 Landscape genetics

There was a significant effect of geographical distance through suitable habitat (IBD) for both $F_{ST}$ ($R^2 = 0.168; P = 0.025$) and $D_{EST}$ ($R^2 = 0.306; P = 0.003$), but for both measures of genetic distance, the goodness of fit was relatively weak (Table 3.4a). Because of this, we carried out partial Mantel tests controlling for the effect of geographical distance. Simple and partial Mantel tests found a significant effect and high $R^2$ values for resistance distances of land cover and land cover x elevation for both $F_{ST}$ and $D_{EST}$, but not for elevation alone (Table 3.4a). Partial Mantel tests controlling for other variable effects did not significantly alter the results but controlling for elevation resistance increased the association between land cover resistance and genetic distance ($r = 0.906; Table 3.4a$).

Based on AICc, the best models varied somewhat between the genetic distance measures (Table 3.4b). For $F_{ST}$, the best model included both land cover and elevation resistance distances (AICc = -227.2) with additional support for the model including all three: land cover, elevation and geographic distance ($\Delta_i = 1.8$). For $D_{EST}$,
the best model included land cover x elevation (\( \text{AIC}_c = -182.1 \)) which also obtained the highest \( R^2 \) value for both genetic indices (Table 3.4a), however, a number of other factors were supported (\( \Delta_i = 0.2 \) – 0.7; Table 3.4b). Overall, the variable land cover x elevation is the best fitting model and the CIRCUITSCAPE resistance map reveals a number of possible pathways for gene flow (Figure 3.3).

After testing a range of models, GESTE analyses failed to identify any environmental variables significantly influencing local genetic differentiation. The constant (which excludes all tested factors and represents the null) was the best performing model with the highest probability when all factors were run together (0.806; results not shown) and individually (Table 3.5a). The sum of posterior probabilities (Table 3.5b) did not reveal any one factor having a large influence, though annual mean temperature had the highest value (0.218) followed closely by annual minimum temperature (0.209). We tested various scenarios to determine if a combination of environmental variables can help explain genetic differentiation, and again the constant was the best model for each scenario and there was no increase in performance of any other models in comparison to when factors were tested alone (results not shown). Overall, no further insights into the role of specific environmental variables in shaping the genetic structure of black-capped chickadees was found using GESTE analyses.

3.5 Discussion

3.5.1 Overall genetic structure of the black-capped chickadee

Populations of black-capped chickadees in British Columbia are spatially structured from restricted population connectivity as supported by individual based (Bayesian clustering analyses), population based (\( F_{ST} \), AMOVA, PCoA) and landscape based
analyses. Although the Bayesian programs did not infer the same number of genetic clusters, they agreed in the assignment of many groupings. Those that were not concordant could be artefacts of poor convergence or an effect of different algorithms and prior distributions. For example, clustering of SAB1 and SAB2 in GENELAND could be explained by their spatial proximity. It is therefore difficult to determine which program uses a more conservative $K$. Conflicting estimations of population structure when utilising different Bayesian clustering methods is not uncommon (Latch et al., 2006; Coulon et al., 2008; Frantz et al., 2009; Safner et al., 2011; Aurelle and Ledoux, 2013). GENELAND often overestimates the number of clusters (which was the case here) (Gauffre et al., 2008), but is better at detecting boundaries corresponding to geographical barriers (Safner et al., 2011).

Intensive sampling and additional microsatellite loci utilised in this study resulted in a finer resolution of observed genetic structure. Population genetic differentiation was observed in all regions of British Columbia from the north (NWBC) to the interior (CLU, NBC, FtStJ1, PG) to the south (VAN and KEL, BCR). Despite their vagility and generalist behaviour, black-capped chickadees are a highly sedentary species, showing strong aversion to crossing gaps in suitable habitat and this characteristic appears to have a significant impact on dispersal across fragmented landscapes. Population genetic structure is an expected evolutionary consequence of species inhabiting fragmented landscapes (Shafer et al., 2010), especially species with restricted dispersal (Unfried et al., 2012) like black-capped chickadees. Although spontaneous and highly irregular, large distance movements (i.e., irruptions) are observed in juveniles, and adults occasionally move down from high altitude localities in response to severe weather conditions or food availability; black-capped chickadees rarely disperse long distances. In one study, most (> 90%) of the 1500 banding
encounters showed no movement (i.e., birds were recaptured in the original banding location), but there were exceptions during irruptive years where birds were captured 50 to 500 km \((N = 18)\), over 500 km \((N = 8)\) and over 2000 km \((N = 1)\) away from their original banding location (Brewer et al., 2000). Distances between adjacent populations in this study are within the potential dispersal range, yet genetic differentiation was observed between populations separated by both small (e.g., ~30 km between FtStJ1 and FtStJ2) and large (e.g., ~390 km between PG and HAZ) distances (Figure 3.1a). The observed patterns suggest that factors other than geographic distance, such as habitat heterogeneity and fragmentation resulting from both natural and anthropogenic causes are influencing dispersal and gene flow.

3.5.2 Effects of landscape features on genetic differentiation

A landscape genetic approach revealed the complexity of black-capped chickadee population structuring from just two spatial datasets (land cover and elevation), and the necessity of incorporating additional landscape level data into studies of gene flow. Land cover and elevation (combined) best explained genetic differentiation for \(F_{ST} (R^2 = 0.809)\) and \(D_{EST} (R^2 = 0.684)\) (Table 3.4a). The same two landscape features are important in facilitating black bear (\(Ursus americanus\)) dispersal in northern Idaho (Cushman et al., 2006). In our study, it appears that both land cover (suitable forest cover) and elevation (low- mid elevation valleys) are important factors in explaining the observed patterns of genetic differentiation in black-capped chickadees. For example, differences in forest cover can be observed between genetically differentiated populations in Fort St. James (FtStJ1 and FtStJ2). Timber harvesting of the abundant lodgepole pine (\(Pinus contorta\)) significantly reduces the amount of suitable forest in the south (FtStJ2) in comparison to the north (FtStJ1) where the
forest is managed and protected from logging (Fondahl and Atkinson, 2007). Low resistance dispersal routes also corresponded to areas of low elevation (Figure 3.3). Black-capped chickadees frequently breed between 270 m and 1500 m elevation with the highest elevation recorded at 2300 m in British Columbia (Campbell et al., 1997). As black-capped chickadees are forest dependent and found at lower elevation, the significance of these two variables was not surprising.

Differences in land cover and elevation may reflect multiple biogeoclimatic zones across the region; characterised by variation in climate, topography and vegetation. As our populations are distributed across a number of these zones, it is possible that habitat discontinuity is playing a bigger role in genetic differentiation, than physical geographical barriers. For example, genetic differentiation in the north (NWBC) could be attributed to specific local environmental conditions; situated within the boreal-black and white spruce biogeoclimatic zone, characterised by long, extremely cold winters and short, warm summers. Our landscape analyses show high pairwise resistance values between NWBC and nearby populations for both elevation and land cover, suggesting limited dispersal. NWBC is isolated from other sampling sites by the Skeena and Omineca Mountains and to the south, there is a sharp transition from boreal-black and white spruce to Engelmann spruce-subalpine fir to interior cedar-hemlock. The Engelmann spruce-subalpine fir zone occupies the highest forested elevations in British Columbia. Our resistance map of elevation (Appendix 2.7) supports isolation of NWBC and therefore, high variability in habitat and climatic conditions combined with high elevations may explain patterns of differentiation. When gene flow is low, isolated populations may adapt to local environmental conditions as a result of divergent selection pressures (Cheviron and Brumfield, 2009).
Genetic clustering of KEL and VAN was an interesting yet unexpected result; confirmed by high, yet non-significant pairwise $F_{ST}$ (0.316). We expected reduced gene flow between the two populations because of the variable topography; particularly the presence of two prominent north-south mountain ranges. Both populations are also located in two climatically different regions; VAN is classified as oceanic or marine west coast with warm summers and cool winters with varying levels of precipitation, whereas KEL has a humid continental climate with warm, dry summers and cold winters. In addition, genetic differentiation between coastal and inland populations in British Columbia has been observed previously for other organisms such as the highly vagile grey wolf (*Canis lupus*) (Muñoz-Fuentos *et al.*, 2009). Nevertheless, gene flow between KEL and VAN appears less restricted (despite some programs implying differentiation (e.g., PCoA)) and this may be explained by low valleys within the Coastal Range, acting as important corridors to dispersal between these two populations.

3.5.3 Dispersal in fragmented landscapes

Loss of genetic diversity from habitat loss can impede a species’ ability to adapt to changes in their environment, and lead to reductions in reproductive fitness and population size (Frankham, 1995; Haag *et al.*, 2010; Woltmann *et al.*, 2012; Finger *et al.*, 2014). As such, loss of forests within low- mid elevation areas from both natural and anthropogenic processes could have a significant impact on chickadee dispersal. One reason for reduced dispersal in fragmented habitats is predation risk. Both St Clair *et al.* (1998) and Desrochers and Hannan (1997) found that black-capped chickadees are less willing to cross gaps of > 50 m of unsuitable habitat. In areas of central British Columbia where logging and other activities have fragmented
chickadee habitat, dispersal would be restricted. The size and abundance of cut-
blocks from forestry activities may be restricting dispersal, however, explicit testing at
an even smaller spatial scale is required. Unexpectedly, our resistance map (Figure
3.3) displayed a large area in the central plateau (between FrL and CLU) where
movement is impeded. This area corresponds to an area of increased agriculture
which could explain differentiation of CLU in GENELAND analyses, lower observed
allelic diversity (FF, FrL and FtStJ2; Table 3.3) and high inbreeding coefficients
(FtStJ2; Table 3.1).

Natural contributors to habitat fragmentation may also explain patterns of
genetic structure observed here. Bark beetle outbreaks have been observed in western
Canada since the 1900s (Swaine, 1918). Current outbreaks are spreading quickly with
warmer/milder winters facilitating their spread across western Canada. As mentioned
previously, the mountain pine beetle outbreak has destroyed huge portions of mature
pine forests throughout British Columbia, particularly in the central plateau region
within elevations of 800 and 1400 m (Safranyik and Wilson, 2006); areas used by
black-capped chickadees. Habitat loss could be leading to severe levels of population
isolation here, particularly in low-mid elevation forested valleys which serve as
dispersal corridors. Thus, despite being common, widely distributed and of little
conservation concern (IUCN Red List), isolated chickadee populations could
potentially be at risk from microevolutionary processes such as local adaptation.

3.5.4 Historical versus contemporary processes
Hindley (2013) examined the phylogeographic history of the black-capped chickadee
across its geographical range. Some of the same populations were also used in this
study (NWBC, SEBC (abbreviated BCR in this study) and CBC (which included
NBC). By comparing our results with patterns found with mtDNA, we can determine if patterns reflect historical processes or are a more recent origin.

Within British Columbia, Hindley found that individuals clustered into three genetic groups; SEBC (BCR in this study) clustered within a “central” group which included populations from the Intermountain West region, whereas CBC and SAB clustered within a “central north” group consisting of more northerly populations (excluding Alaska). NWBC individuals, however showed mixed assignment, with approximately one third of individuals clustering with three different genetic groups (central, central north and the Pacific group).

Differentiation of CBC and BCR was concordant with our findings and suggests long term isolation of these populations. In contrast, BCR and SAB were significantly differentiated in this study (Table 3.3). High levels of mtDNA gene flow may reflect female-biased dispersal between these two populations which is a general pattern found in birds (Greenwood, 1980). Alternatively, restricted gene flow detected by rapidly evolving microsatellite markers may reflect more recent evolutionary processes (e.g., genetic drift, selection). Interestingly in both studies NWBC showed a pattern of mixed group assignment. Hindley hypothesised that patterns found in this area may result from secondary contact following population expansion from separate Pacific and inland British Columbia refugia after the last glaciation. Our results support this hypothesis. Similar patterns have also been observed in other species in the same area (Rohwer et al., 2001; Richardson et al., 2002; Burg et al., 2006; Godbout et al., 2008).

3.6 Conclusions
Our study is the first landscape genetics study of the black-capped chickadee at a small spatial scale and produced some unexpected findings. Weak population genetic differentiation can be expected for common and widespread species with the ability to disperse among habitat patches (i.e., bird flight), but our findings suggest that generalist, resident bird species are impacted by variation and/or changes in their environment, resulting in microgeographic population structuring.

Our study shows that black-capped chickadee populations are affected by variation in landscape topography and forest cover; features critical to chickadee survival and reproductive success. Climatic differences among sampling sites may also create differential selective pressures. The importance of including additional landscape features and environmental variables when assessing connectivity and population differentiation is particularly relevant when identifying vulnerable populations and management units, as over time isolated populations may diverge through local adaptation or inbreeding. In the face of climate change, biogeographic zones will change and forest tree species are under threat of shifting and narrowing distributions (Hebda, 1997; Hamann and Wang, 2006; Wang et al., 2012) which could in turn, have a negative impact on the black-capped chickadee. Changes in precipitation and winter temperature have already driven shifts in the geographic patterns of abundance of bird populations in western North America (Illán et al., 2014). Overall, when assessing patterns of genetic differentiation of populations, not only will a smaller scale of sampling and more loci provide additional patterns of genetic structure, but incorporating both landscape features and environmental variables when explaining patterns can significantly improve our understanding of how species evolve in response to changes in their environment.
3.7 Acknowledgements

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3.8 References


Hindley, J.A. (2013) Post-Pleistocene dispersal in black-capped (Poecile atricapillus) and mountain (P. gambeli) chickadees, and the effect of social dominance on black-capped chickadee winter resource allocation. PhD, University of Lethbridge.


Table 3.1. Sampling location information including site abbreviation (Abbrev.), geographical location (latitude (Lat) and longitude (Long)), sample size ($N$). Microsatellite summary statistics for each population and all loci: number of private alleles (PA), allelic richness (AR), and inbreeding coefficients ($F_{IS}$).

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<th>Location</th>
<th>Abbrev.</th>
<th>Lat (°N)</th>
<th>Long (°W)</th>
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<th>PA</th>
<th>AR</th>
<th>$F_{IS}$</th>
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Table 3.2. Expected ($He$) and observed ($Ho$) heterozygosities, total number of alleles ($Na$) for 15 populations of black-capped chickadees at 14 microsatellite loci. Summaries are provided for across loci and across populations. Bold values indicate deviations from HWE. See Table 3.1 for sampling site abbreviations.

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Table 3.3. Pairwise $F_{ST}$ values (below diagonal) and harmonic mean estimates of $D_{EST}$ (above diagonal) for 15 black-capped chickadee populations based on 14 microsatellite loci. Bold values indicate significance after correction for multiple tests.

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<th>NBC</th>
<th>CLU</th>
<th>FF</th>
<th>FrL</th>
<th>FtStJ2</th>
<th>HAZ</th>
<th>HOU</th>
<th>KEL</th>
<th>NWBC</th>
<th>VAN</th>
<th>FtStJ1</th>
<th>PG</th>
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<th>SAB2</th>
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<td>0.329</td>
<td>0.243</td>
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<td>0.218</td>
<td>0.234</td>
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<td>0.033</td>
<td>0.034</td>
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<td>0.014</td>
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Table 3.4. Results of Mantel and partial Mantel correlations (a) between two linearized pairwise estimates of genetic distance ($F_{ST}$ and $D_{EST}$) and resistance distances (variable) calculated in CIRCUITSCAPE. Controlled variables are in brackets for partial Mantel tests (e.g., “(distance)” = controlled for geographical distance through suitable habitat). For each resistance surface, the partial correlation coefficient ($r$) and coefficient of determination ($R^2$) are shown. ** indicate significant correlations ($P \leq 0.01$). Results of model selection (b) based on corrected Akaike’s Information Criterion (AICc), differences in AICc values ($\Delta_i$) and AICc weight ($w_i$) are provided for each model. Bold AICc values indicate the best model.

### a) Variable (controlled variable)

<table>
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<th>Variable (controlled variable)</th>
<th>$F_{ST}$</th>
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<th>$D_{EST}$</th>
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<td>$R^2$</td>
<td>$r$</td>
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<tr>
<td>Distance through suitable habitat</td>
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<td>0.168</td>
<td></td>
<td>0.553**</td>
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<td>Elevation (distance)</td>
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<td>-</td>
<td>-0.174</td>
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<tr>
<td>Elevation (land cover)</td>
<td>-0.280</td>
<td>-</td>
<td>-</td>
<td>0.217</td>
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<tr>
<td>Land cover</td>
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<td>0.806</td>
<td></td>
<td>0.826**</td>
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<tr>
<td>Land cover (distance)</td>
<td>0.879**</td>
<td>-</td>
<td></td>
<td>0.757**</td>
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<td>Land cover (elevation)</td>
<td>0.906**</td>
<td>-</td>
<td></td>
<td>0.818**</td>
<td>-</td>
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<td>Land cover x elevation</td>
<td>0.899**</td>
<td>0.809</td>
<td></td>
<td>0.827**</td>
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<td>Land cover x elevation (distance)</td>
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### b) Model

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<td>$w_i$</td>
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<td>$\Delta_i$</td>
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<td>0.00</td>
<td>-111.0</td>
<td>71.1</td>
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<td>0.00</td>
<td>-130.7</td>
<td>51.4</td>
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<tr>
<td>Land cover</td>
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<td>0.08</td>
<td>-181.8</td>
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<td>0.18</td>
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<td>3.4</td>
<td>0.08</td>
<td>-181.9</td>
<td>0.2</td>
<td>0.19</td>
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Table 3.5. Posterior probabilities from GESTE analyses for models of runs including a single factor (a) and sum of posterior probabilities when all nine factors were included (b). Bold values indicate the best model.

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<td>Constant</td>
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<td>Constant</td>
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<table>
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<td>Annual mean temperature</td>
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<td>Annual min temperature</td>
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<td>Summer mean temperature</td>
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<td>Annual mean precipitation</td>
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<tr>
<td>Summer mean precipitation</td>
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</table>
Figure 3.1. (a) Sampling locations of the black-capped chickadee (*Poecile atricapillus*) in British Columbia (See Table 3.1 for abbreviations) with inferred clusters from STRUCTURE $K = 6$ (pie charts) and GENELAND $K = 9$ (stars). STRUCTURE inferred 6 main genetic groups (b) with additional structure found for FtStJ1 and SAB1. GENELAND inferred nine genetic clusters (c).
Figure 3.2. Principal coordinate analysis conducted in GenAlEx based on pairwise $D_{EST}$ values for (a) all 15 populations (coordinates 1 and 2 explained 50.59% and 17.04% of the variation respectively) and (b) after removal of populations KEL and VAN (coordinates 1 and 2 explained 31.05% and 19.93% of the variation respectively).
Figure 3.3. Map showing the resistance grid output from CIRCUITSCAPE analyses for the resistance surface including land cover and elevation combined (land cover x elevation) as this variable best explained genetic differentiation in other analyses. A close up of the central plateau region is included (bottom).
CHAPTER 4

Gene flow of a forest-dependent bird across a fragmented landscape.

R. V. Adams $^{1,2}$ T. M. Burg$^1$

Prepared as manuscript for submission

$^1$University of Lethbridge, Department of Biological Sciences, 4401 University Drive, Lethbridge, AB, T1K 3M4, Canada.
$^2$Corresponding author: rachael.adams@uleth.ca
4.1 Abstract

Habitat loss and fragmentation can strongly affect the persistence of populations by reducing connectivity and restricting the ability of individuals to disperse across landscapes. Dispersal corridors promote population connectivity and therefore play important roles in maintaining gene flow in natural populations inhabiting fragmented landscapes. In the prairies, forests are restricted to riparian areas along river systems which act as important dispersal corridors across large expanses of inhospitable grassland habitat. However, natural and anthropogenic barriers within riparian systems have left these continuous linear features fragmented. In this study, we used microsatellite markers to assess the fine-scale genetic structure of a forest-dependent species, the black-capped chickadee (*Poecile atricapillus*), along 10 different river systems in Southern Alberta. Using a landscape genetic approach, a significant effect of different landscape features (e.g., land cover) on genetic differentiation was found. We discovered that populations are both genetically structured and exhibit significant $F_{ST}$ values as a result of natural breaks in continuous woodland habitat, but recent artificial barriers from dams and reservoirs have not yet restricted gene flow. In addition, significant population genetic differentiation corresponded with zones of different cottonwood (riparian poplar) species and hybrids. This study illustrates the importance of considering the impacts of habitat fragmentation at small spatial scales as well as other ecological processes to better understand how organisms respond to their environmental connectivity. Here, even in a common and widespread songbird with high dispersal potential, small breaks in continuous habitats strongly influenced the spatial patterns of genetic variation.

Keywords: black-capped chickadee, landscape genetics, microsatellites, population genetic structure, Circuitscape, fragmentation, riparian corridors
4.2 Introduction

Dispersal and gene flow in fragmented landscapes are necessary to maintain the genetic integrity of populations. However, it has long been recognised that variation within the landscape matrix separating habitat patches affects an individuals’ dispersal ability, and can subsequently break down population (and functional) connectivity (Fahrig and Merriam, 1994). Landscape genetics offers a framework to explicitly test the effects of landscape features and environmental variables on spatial patterns of genetic differentiation; providing a means to identify factors either facilitating or impeding gene flow among populations (Manel et al., 2003; Spear et al., 2005; Holderegger and Wagner, 2008).

Landscapes are spatially heterogeneous which can affect the movement characteristics of organisms and in turn influences gene flow and population dynamics (Johnson et al., 1992). In naturally heterogeneous or fragmented landscapes, suitable habitat is not continuous but is patchily distributed and gaps between suitable habitats can vary in size. In addition, habitat patches themselves can differ in their suitability for a particular organism. For example, different patches may experience different levels of food resources, predation and reproductive opportunities, which can all play a role in an organisms’ decision to disperse. A myriad of studies exist on how landscape heterogeneity affects movement and subsequent genetic structure in a variety of different organisms and its importance is growing (reviewed in Storfer et al., 2007).

One example of a heterogeneous landscape is the Great Plains in North America, a broad area of flat land found east of the Rocky Mountains and west of the Missouri River. The landscape is dominated by prairie, steppe and grassland and forested habitats are restricted to riparian areas along intervening river systems.
Riparian areas situated adjacent to streams, rivers, lakes and wetlands are among the most valuable, productive and structurally diverse habitats (Naiman et al., 1993; Naiman & Décamps, 1997; Naiman et al., 2005). This naturally rich environment provides unique habitat for wildlife (Hannon et al., 2002) be it residential or migratory species. In western North America, riparian ecosystems are dominated by poplar trees (Populus spp.) along river flood plains (Brayshaw, 1965; Rood and Mahoney, 1990) and the surrounding habitat is dominated by treeless prairie grassland. As such, riparian ecosystems are the only wooded areas in the northern Great Plains and eastern foothills of the Rocky Mountains providing critical habitat and essential dispersal corridors for forest-dependent organisms (Floate, 2004). More importantly, riparian zones have been shown to reverse the effects of habitat fragmentation by enhancing connectivity and facilitating individual movement between habitat patches that would otherwise become isolated (Gillies et al., 2008; Dallimer et al., 2012). However, even within those limited forested regions, the quality and structure of the habitat can vary spatially (i.e., upstream habitats vs. downstream) and temporally (i.e., from diversion of rivers). This demonstrates the profound effects that both natural and human-mediated processes can have on the level of habitat fragmentation in heterogeneous landscapes, even within scarcely distributed habitats patches.

River management can have long-lasting negative impacts on riparian species. Urbanisation and increasing demand for water for agriculture, industrial and domestic use has however, resulted in 82% of large rivers (> 1000 km) across North America being dammed and diverted (WWF, 2006). Changes to river flows and modifications to associated habitat can also affect the health of riparian ecosystems. Consequently, a decline in riparian forests has been observed downstream from major dams such as the Truckee River, Nevada (Rood et al., 2003), the Marias River, Montana (Rood and
Mahoney, 1995) and the Oldman River (Rood and Heinze-Milne, 1989) and Willow Creek, Alberta (Amlin et al., 2003). All studies found healthier forests upstream than downstream and, by using birds as indicators of woodland condition restoration efforts can and have been successful (Rood et al., 2003). Without these efforts, fragmentation of riparian habitats through human-mediated processes could lead to drastic reductions in population size or local extinctions particularly of riparian specialist species.

The ranges of riparian poplars within river systems can overlap resulting in zones of hybridisation. So not only is there concern over riparian forest decline and subsequent evolutionary effects, but riparian habitats may also provide unique zones of ecological transitions. These hybrid poplar zones can dramatically impact riparian biodiversity and habitat complexity with the addition of novel poplar genotypes and architectures (Brayshaw, 1965; Rood et al., 1986). In fact, studies have found that hybrid poplar zones have higher arthropod abundance such as the poplar bud gall mite (Kalischuk et al., 1997) and gall producing aphids (Whitham, 1989) which can affect the distribution of nesting birds and bird abundance (Christian et al., 1997), arthropod speciation (Evans et al., 2008) and species richness (Martinsen & Whitham, 1994; Whitham et al., 1999; Floate, 2004).

Riparian woodland are also particularly important areas for breeding, wintering and migrating birds by providing corridors through areas of unsuitable habitat (e.g., deserts and grasslands). Loss of riparian habitat could have a negative impact on populations throughout large portions of their range. A number of studies have documented the distribution, density and diversity of riparian bird species in riparian habitats (Finch, 1989; Doherty et al. 2002) particularly their response to riparian woodland fragmentation (Rottenborn, 1999; Jansen and Robertson, 2001;
Dallimer et al., 2012; Skroblin and Legge 2012; Jedlicka et al., 2014), but the effects of these habitats on the distribution of genetic variation are less well studied, perhaps because their dispersal capabilities suggest that gene flow would be unrestricted. Genetic differentiation of terrestrial (Jansson et al., 2000; Kondo et al., 2009; Van Looy et al., 2009; Mosner et al., 2012; Werth et al., 2014) and aquatic plants (Pollux et al., 2007) as well as other aquatic organisms such as fish (Heggenes and Roed, 2006; Young et al., 2011; Hudman and Gido, 2013), amphibians (Olson et al., 2007) and invertebrates (Alp et al., 2012; Phillipson and Lytle, 2012) in riparian systems are comparatively more common.

This study uses a landscape genetics approach to understand how riparian ecosystems influence dispersal and gene flow in the black-capped chickadee (*Poecile atricapillus*), a common songbird to North America (Smith, 1993). Genetically distinct populations have previously been identified in this species on both large (Gill et al., 1993; Pravosudov et al., 2012; Hindley, 2013; Adams and Burg, 2015) and small (Adams and Burg, submitted) geographical scales. As a common, widely distributed songbird that responds relatively quickly to environmental change (Gray, 1989), the black-capped chickadee is an ideal model organism for understanding the ecological state of ecosystems. Despite being a resident species, black-capped chickadees are capable of short distance dispersal, but movement is restricted to areas with sufficient forest cover. In the Great Plains, movement may be impeded within and between river systems by unsuitable habitat, reservoirs or degraded woodland as dispersal is restricted to forested riparian corridors. The purpose of this study is to identify important barriers in these ecological corridors. In addition, black-capped chickadees are known to feed on aphids, so hybrid poplar zones which harbour diverse insect communities may attract chickadees in large numbers and reduce further
movement. With growing concern over global anthropogenic change, understanding
the influence of landscape features on gene flow and population connectivity across
heterogeneous landscapes will bridge the gap in our knowledge of this species’
ecology. Where riparian forest should act as a dispersal corridor and facilitate gene
flow, additional factors may prevent gene flow in these areas. We therefore predict:
1) natural barriers restrict gene flow within and between river systems, 2)
anthropogenic barriers restrict gene flow within river systems, and 3) hybrid poplar
zones attract large numbers of individuals resulting in significant genetic
differentiation of hybrid zone associated populations.

4.3 Methods

4.3.1 Study Area

Southern Alberta is a highly heterogeneous landscape characterised by densely
forested montane habitat in the west (Rocky Mountains), transitioning to a narrow
range of aspen parkland and finally to prairie in the east, dominated by temperate
grasslands. There is also a continuous elevation gradient ranging from high elevation
in the west to low elevation in the east. Within the prairies, forested areas are
restricted to riparian habitats within river systems which flow throughout the
landscape. However, both naturally treeless river canyons and artificial reservoirs
exist along the river systems, resulting in fragmentation of the woodland corridor
(Figure 4.1). In addition, four species of riparian poplar occur: narrowleaf
cottonwood (Populus angustifolia), balsam poplar (P. balsamifera) and the closely
related black cottonwood (P. tricocarpa), and prairie or plains cottonwood (P. deltoides).
These four species hybridize to provide a globally-unique hybrid swarm.
(Kalischuk et al., 1997; Floate, 2004; Figure 4.1) that supports diverse insect communities (Floate et al., 1997).

4.3.2 Sample collection

Birds were captured using mist nets and call playback of male song or mobbing. Each individual was banded with a uniquely numbered band and blood samples (< 100 µl) were taken from the brachial vein (Appendix 3.1). Using a transect-based sampling approach, approximately 20 individuals were sampled from each location (or population) along 10 river systems and one creek in Southern Alberta. Each sampling site was confined to a 10 km radius where possible and geographic location was recorded for each site (Table 4.1). Samples from our previous study (Adams and Burg, 2015) were incorporated to cover additional river systems (i.e., CAB along the North Saskatchewan and Athabasca Rivers, SAB1 on the Castle River, and SAB2 on the Belly River). Sampling took place over eight breeding seasons (2007 – 2014).

4.3.3 Genetic diversity and population structure

DNA extraction, amplification and genotyping were performed on all individuals following the procedures described in Adams & Burg (2015) and Adams & Burg (unpubl.). Twelve polymorphic microsatellite loci were used for DNA amplifications (PAT MP-14, PAT MP-43, Escu6, Titgata39, Titgata02, CcaTgu11, Cuµ28, PmanTAGAn71, Ase18, VeCr05, CtC101 and Pij02; Appendix 3.2). Individuals genotyped for \( \leq 5 \) loci \((N = 1)\) were removed from analyses and known or suspected family groups (i.e., caught at the same time, showed patterns consistent with family groups at multiple loci) \((N = 3)\) were also removed.
Errors within the data (e.g., input errors, allelic dropout, stutter and null alleles) were assessed in MICRO-CHECKER v2.2 (van Oosterhout et al., 2004). To assess the level of genetic diversity, allelic richness was calculated in FSTAT v2.9.2.3 (Goudet, 2001) and both observed and expected heterozygosities as well as inbreeding coefficients were calculated in GenAlEx v6.5 (Peakall and Smouse, 2012). Tests for deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were performed in GENEPOP v4.0.10 (Raymond and Rousset, 1995; Rousset, 2008) using default Markov chain parameters (100 batches, 1000 iterations and 1000 dememorisation steps). Significance was tested using the modified False Discovery Rate (FDR) correction method (Benjamini and Yekutieli, 2001).

Populations with ≤ 5 individuals were removed from population based analyses. Genetic structure was quantified for all pairwise combinations of populations using $F_{ST}$ implemented in GenAlEx v6.5 (Peakall and Smouse, 2012). To complement the conventional $F$-statistic we calculated an additional pairwise estimate of genetic differentiation ($D_{EST}$) in SMOGD v1.2.5 (Crawford, 2010; Jost, 2008) and standardised $F'_{ST}$ in GenAlEx v6.5 and significance was tested by the FDR correction method (Benjamini and Yekutieli, 2001). To further assess population genetic structure we carried out a hierarchical analysis of molecular variance (AMOVA) in ARLEQUIN v3.5 (Excoffier and Lischer, 2010) using the groups identified in Bayesian clustering analyses.

4.3.4 Genetic clustering analyses

We assessed the overall population genetic structure using two individual based Bayesian clustering methods, STRUCTURE v2.3.4 (Pritchard et al., 2000) and GENELAND v4.0.0 (Guillot et al., 2005a, b), and one non-Bayesian exploratory
clustering method, Discriminant Analysis of Principal Components (DAPC; Jombart et al., 2010). STRUCTURE and GENELAND both identify the most likely number of genetic clusters (K) by assigning individuals to said clusters while maximising HWE and minimising LD, but only GENELAND incorporates spatial coordinates of sampled individuals. All individuals were included as assignments are based on individual multilocus genotypes and not influenced by populations with small sample sizes (N ≤ 5). STRUCTURE was run with the admixture model, correlated allele frequencies (Falush et al., 2003) and locations as priors (locpriors). Ten independent runs (50,000 burn in followed by 200,000 McMC repetitions) were conducted for each value of K (1-10) to infer the optimal number of clusters (K). Results were averaged and the true K was determined using STRUCTURE HARVESTER v0.6.6 (Earl and vonHoldt, 2012) from both delta K (ΔK; Evanno et al., 2005), and mean log likelihood LnPr(X|K). Any individual showing mixed ancestry (e.g., 50% to cluster 1, and 50% to cluster 2) was rerun to determine correct assignment and furthermore, if individuals from multiple populations assigned to one genetic cluster, a hierarchical analysis was carried out to test for additional substructure within those clusters (using the same parameters as the initial run, but only five runs for each K value).

In addition to assessing population genetic structure across the whole study area, we tested an additional two hypotheses to determine if 1) natural or 2) artificial barriers influence population genetic structure. Populations separated by a known extensive break in riparian woodland include LE, SSK and BO (Figure 4.1). Populations separated by artificial barriers include CR and OM separated by the Oldman Reservoir, and SB2 and GL/BL by the Waterton Reservoir (Figure 4.1). Populations StM and WO are separated by both an artificial (St. Mary Reservoir) and a gap in woodland. Prior to the establishment of the St. Mary Reservoir, this river
system was composed of sparsely distributed poplar woodland (Dawson, 1885), however, the reservoir has since had a negative impact on downstream riparian woodland, leading to the complete loss of woodland (Rood et al., 1995). STRUCTURE was run for each pair of populations separated by a “barrier” to determine if these factors drive differentiation at small geographical scales. This method removes noise present from additional data and allows the determination of population structuring at very small spatial scales.

GENELAND, implemented in R (R Development Core Team, 2008) was run in two steps. First, the program was run for ten replicates for varying \( K (1 – 10) \) using both the correlated allele frequencies and null allele models, and 100,000 McMC iterations, 100 thinning interval, maximum rate of Poisson process of 343 (equal to the sample size as suggested by Guillot et al. (2005a)), uncertainty attached to spatial coordinates fixed to 20 km (i.e., the precision of our sample locations: 10 km radius), and the maximum number of nuclei in the Poisson–Voronoi tessellation fixed to 1029 (3 times the sample size as recommended by Guillot et al. (2005a)). The \( K \) number of populations was selected from the run with the highest mean posterior probability and a second run was then conducted with \( K \) fixed and the same parameters to allow individuals to be assigned to clusters. We then compared the output maps of clusters to a geographic map to link genetic breaks with potential barriers to gene flow. GENELAND was run multiple times with various parameters to see if the same estimate of \( K \) was estimated.

DAPC is a multivariate method implemented in the R package ADEGENET (Jombart, 2008) designed to identify and visualise diversity among groups without using geographical information (Jombart et al., 2010). Unlike STRUCTURE and GENELAND, DAPC does not assume HWE or LD. For DAPC analysis (function
 dapc), first a principal component analysis (PCA) is performed on predefined populations (i.e., sampling site) where the genotypic data are transformed into principal components. The PCA variables are then used in the discriminant analysis (DA). This initial PCA step ensures that no correlated variables are input into the DA and that a weighted and reduced number of variables are included; 50 principal components (PCs) were retained corresponding to > 85% of the variance. DAPC defines groups by minimising within group variation and maximising among group variation. Small populations ($N \leq 5$) were removed from analyses.

4.3.5 Identification of landscape variables

After calculating geographic distances (i.e., shortest distance through suitable habitat) among pairs of populations to test for isolation by distance (IBD; Wright, 1943), we also calculated pairwise resistance distances for different landscape variables using a circuit model of landscape connectivity in CIRCUITSCAPE v4.0 (McRae, 2006) to test for isolation by resistance (IBR). The IBR model calculates all possible pathways of least resistance to gene flow using circuit theory. Small populations ($\leq 5$ individuals) were excluded as genetic distance data ($F_{ST}$ and $D_{EST}$) was unavailable and therefore, could not be compared to resistance distance data.

Rather than performing the resistance distance calculations on the whole map of Alberta, we clipped our resistance raster maps in ArcMap (ESRI©) so that analyses were only performed on the study area (a buffer remained to leave enough landscape available for bird dispersal). We used categorised land cover (grouped into 9 classes) and topographical maps (6 ranges) from GEOBASE (www.geobase.ca) with a 100 m resolution and reclassified pixel values for each class or range to hypothetical resistance values to dispersal in ArcMap (ESRI©). For land cover, we assigned high
resistance values to non-forested areas (e.g., grassland) and low resistance values to forested regions (particularly, broadleaf and mixed forest; preferred habitat of black-capped chickadees). For elevation, high resistance values were given to ranges that exceeded 2300 m and the lowest values were assigned to the 201 – 500 m range; where chickadees are more prevalent. We created additional raster resistance maps (modified from Figure 4.1 in Floate, 2004) to represent the different poplar zones among river systems in Southern Alberta. To determine if hybrid zones influence chickadee dispersal we created two hypothesised resistance layers; one in which hybrid zones restrict dispersal ("hybrid-") and another where hybrid zones facilitate dispersal ("hybrid+"). For hybrid zone based models and analyses, 12 populations sampled in hybrid zones were included: Drywood Creek and the Red Deer, Oldman, Crowsnest, Waterton, St. Mary and South Saskatchewan Rivers. We also combined resistance surfaces using “raster calculator” in ArcMap to better represent the landscape with multiple factors (e.g., hybrid- x elevation x land cover).

4.3.6 Comparison of landscape distance on genetic distance

To determine whether geographic and/ or landscape resistance distances influence gene flow, each distance matrix was compared with linearised pairwise genetic distances ($F_{ST}$ and $D_{EST}$) using simple and partial Mantel tests in IBDWS v3.2.3 (Jensen et al., 2005). Statistical significance was determined by 10,000 permutations. Mantel tests were performed for all 15 populations for the 4 resistance distance matrices (geographical distance through suitable habitat, land cover, elevation and combined land cover x elevation), and then again for 12 populations after incorporating hybrid- and hybrid+ resistance distances.
As Mantel tests are often criticised by their low power (Legendre and Fortin, 2010; Cushman, 2013), we also conducted multiple matrix regression models for a comparison. Genetic distances ($F_{ST}$ and $D_{EST}$) served as the dependent variable and landscape distances as independent (predictor) variables using the package MuMIn in the program R (R Development Core Team, 2014). All possible combinations of candidate models (with single parameter resistance distances and combined resistance distances) were tested and the best model was chosen based on the Akaike’s Information Criterion (AIC - Akaike, 1973; Burnham and Anderson, 1998; Roach et al., 2001). AIC is based on information theory and estimates the information lost when a given model is used and measures the overall fit of a regression model to a given data set, thus providing a trade-off between goodness of fit of the model and model complexity. AIC values were adjusted to correct for sample size (AIC$_c$), differences between AIC$_c$ values ($\Delta_i$) were calculated (as recommended by the authors) to determine which models showed the most support (≤ 2 provides substantial support, 4 – 7 provides moderate support and ≥ 10, no support), and AIC$_c$ values were weighted ($w_i$) to represent the likelihood of the model. The model with the lowest AIC$_c$ represents the best model. Model selection was conducted in two steps. First, landscape resistance and geographical distances were combined and tested for all 15 populations. Second, we incorporated the hybrid- and hybrid+ distance measures and tested the 12 populations in the hybrid zones.

### 4.4 Results

#### 4.4.1 Genetic diversity and population structure

A total of 343 individuals from 28 locations were successfully genotyped for 12 variable microsatellite loci (Table 4.1; Figure 4.2a). The presence of null alleles was
detected in eight populations (with inconsistencies across populations) and the frequency was low with the exception of two loci. Null allele frequencies in locus VeCr05 ranged from 0 – 70% and in locus Cuµ28, this range increased from 0 - 73%; these same loci showed evidence of null alleles in Adams and Burg (submitted), but at much smaller frequencies. Large discrepancies between observed and expected heterozygosities were found for both loci (Table 4.2), but this was not consistent across populations. We therefore carried out all additional analyses with and without those two loci for comparison, but as no considerable differences in results were observed, both VeCro05 and Cuµ28 were retained. Allelic richness ranged from 4.01 (SSK) to 4.79 (CR; Table 4.1). The number of alleles per locus ranged from 2 – 33 alleles (Appendix 3.2) and overall observed and expected heterozygosities ranged from 0.564 (RD1) to 0.714 (BUC), and 0.633 (BUC) to 0.708 (DR and CR; Table 4.2) respectively. Population LE contained the largest number of private alleles (PA = 10) followed by SB1 (PA = 5). After corrections for multiple tests, we found two deviations from HWE and three pairs of loci in disequilibrium. LE deviated from HWE at two loci; VeCr05 and Pij02 and significant LD was found between loci Titgata39 and CTC101 ($P \leq 0.001$) within RD2 and between loci PAT MP 2-14 and Titgata39 ($P \leq 0.001$) within populations SSK and LE ($P \leq 0.001$).

Pairwise values of both $F_{ST}$ and $D_{EST}$ showed low to moderate genetic differentiation among population comparisons ranging from 0.007 – 0.049 ($F_{ST}$) and 0.000 – 0.089 ($D_{EST}$). Population wide $F'_{ST}$ was 0.060. After corrections for multiple tests, 50 ($D_{EST}$) and 52 ($F_{ST}$) of the 105 tests were significant (Table 4.3). For $F_{ST}$, three populations (LE, DR and SSK) were significantly differentiated from all other populations; two of which (LE and DR) are situated within a poplar hybrid zone. In
addition, BO was significantly differentiated from all populations south of the Bow River. Significant pairwise $D_{EST}$ values confirm these patterns.

An analysis of molecular variance with no hierarchy generated an $F_{ST}$ of 0.020 and 2.04% of the variance was among populations and 97.96% within populations; $P \leq 0.0001$). When groups were separated hierarchically based on STRUCTURE and $F_{ST}$ analyses, less of the variance was explained among groupings and AMOVA failed to identify additional structure (Appendix 3.3).

### 4.4.2 Genetic clustering results

Delta $K$ ($\Delta K$) and mean log likelihood ($\text{LnPr(X|R)}$) and for the initial STRUCTURE runs involving all 343 individuals showed two and three groups respectively (Figure 4.3a; Appendix 3.4). Assignments for $K = 3$ had individuals with Q values suggesting mixed ancestry (Figure 4.3a (ii)) which implies oversplitting of populations, therefore, we chose $K = 2$ (Figure 4.3a (i)) as our true initial $K$. We then ran admixed individuals from StM and WO (Figure 4.3a (i)) with one pure population from each of the two clusters and confirmed that StM and WO individuals clustered with LE individuals. Using a hierarchical approach and removing the LE, StM and WO cluster, SSK formed a distinct cluster. Again, there was disagreement between $\Delta K$ ($K = 2$) and mean log likelihood ($K = 3$) over the true $K$ (Figure 4.3b). For $K = 3$, clustering of populations BO and NSK is evident (Figure 4.3b (ii)), however, when these populations were run together with RD1 (to represent the large genetic cluster), STRUCTURE identified only one genetic group ($K = 1$) suggesting that splitting of BO and NSK was an overestimation and so we took $K = 2$ as the true value (Figure 4.3b (i)). Overall, STRUCTURE identified three genetic clusters (cluster 1: LE, StM and WPP; cluster 2: SSK and cluster 3: all remaining populations; Figure 4.2a).
STRUCTURE analyses confirmed that populations separated by natural gaps in riparian woodland were genetically structured from each other whereas those separated by artificial barriers were not (Table 4.4). These results are concordant with pairwise $F_{ST}$ and $D_{EST}$. Structuring of LE and SSK was determined in previous runs but more importantly, STRUCTURE inferred two clusters (confirmed by $Pr(X|R)$ and $\Delta K$) when assessing BO with all populations in the south and confirms significant $F_{ST}$ values. These results suggest natural gaps in the woodland play a role in genetic differentiation of chickadee populations. In contrast, populations separated by reservoirs clustered as one genetic group and therefore do not appear to act as dispersal barriers.

GENELAND identified four genetic clusters from multiple, independent runs. Cluster 1 (Figure 4.2b) included populations within the Red Deer River from DR downstream; cluster 2 (Figure 4.2c) contained SSK; cluster 3 (Figure 4.2d) included populations LE, StM and WO, and cluster 4 (Figure 4.2e) included all remaining populations including upstream populations on the Red Deer River (OL, IN, RD1, and RD2). Clusters 2 and 3 are concordant with STRUCTURE analyses.

For DAPC analysis, we see separation of SSK and LE on the x axis with some overlap (Figure 4.4); comparable with genetic structuring identified in STRUCTURE. DAPC fails to cluster StM and WPP with LE. All other populations form one clearly defined cluster.

4.4.3 Influence of the landscape on genetic distance

All statistically significant Mantel correlations were positive suggesting isolation by landscape resistance between populations (Table 4.5). IBD was significant with $D_{EST}$ ($P = 0.02$), but not with $F_{ST}$ ($P = 0.17$). Partial Mantel tests did not significantly alter
the results. Overall, correlations were greater for land cover as well as combinations that included the factor hybrid- (i.e., hybrid zones restrict dispersal), but not when hybrid- was tested alone. For both measures of genetic distances, corresponding AIC model results confirmed Mantel correlation results. The best model over 15 populations included land cover ($\text{AIC}_c = -604.6$ ($F_{ST}$) and -433.3 ($D_{EST}$)), and over 12 populations included the resistance surface combining hybrid-, elevation and land cover ($\text{AIC}_c = -359.1$ ($F_{ST}$) and -280.5 ($D_{EST}$)). Those that had the lowest $\text{AIC}_c$ also had the highest $R^2$ values.

When a full model AIC evaluation was carried out on all possible model combinations given the landscape variables available, we found some unexpected results, particularly when the effects of hybrid poplar zones were included (Appendix 3.5). Firstly for 15 populations, the best model for $F_{ST}$ included land cover + elevation ($\text{AIC}_c = -605.8$) but two other models (land cover as well as land cover + elevation + distance ($D_{EST}$’s best model)) were also well supported (both $\Delta_i = 1.2$). This indicates that elevation and geographical distance are both important factors to take into consideration when explaining genetic differentiation. When the effect of hybrid zones were tested on 12 populations results varied within and between the genetic distance measures. Generally, models incorporating the factor hybrid- had lower AIC values than those with hybrid+, consistent with Mantel test results. However, when combined resistance surfaces were incorporated into the models (e.g., hybrid- x elevation) AIC favoured models that included hybrid+, which conflicts with Mantel test results. This illustrates the importance of carefully selecting a small set of candidate models (Table 4.5) as if too many models (or hypotheses) are tested at the same time, some relationships may occur by chance and lead to misleading conclusions (Johnson and Omland, 2004).
4.5 Discussion

4.5.1 Overall population genetic structure

Gene flow and population dynamics are complex especially in heterogeneous environments. Habitat fragmentation can lead to reduced population connectivity, dispersal and gene flow which can lead to population isolation and genetic differentiation. Forested habitats are naturally fragmented in prairie landscapes and further fragmentation occurs within these linear features by anthropogenic processes which can have significant implications on the movement characteristics and genetic variability of forested-dependent species.

In this study, we established the importance riparian woodlands for dispersal and gene flow of black-capped chickadee populations within the prairies of Southern Alberta. Both Bayesian and exploratory clustering programs identified up to four genetic clusters and the two most concordant groups include SSK within the South Saskatchewan River as a discrete genetic unit as well as LE, StM and WO populations within the Oldman and St. Mary Rivers. In comparison to STRUCTURE, GENELAND inferred an additional cluster on the Red Deer River which included populations DR, EM, JE and BU. Although the correlated model in GENELAND is more powerful, it has been shown to overestimate the true $K$ (Chen et al., 2007; Munguia-Vega et al., 2013; Tucker et al. 2014). It is uncertain whether this genetic cluster exists but owing to the landscape composition downstream of DR (i.e., open floodplains, scattered poplar distributions) it is possible. Differentiation of BO from southern populations is concordant with measures of genetic distance and illustrates the importance of assessing population genetic structure at small spatial scales (Phillipsen and Lytle, 2012).
4.5.2 Landscape effects on gene flow

Heterogeneous landscapes can vary in terms of topography, vegetation and climate. Here, a significant effect of landscape resistance distances on genetic distance suggests that variation in landscape features influence chickadee dispersal. Both Mantel correlations and model selection indicated a significant effect of land cover and elevation as well as geographical distance through suitable habitat on genetic differentiation, which given the fragmented nature of the study area, the variation in distribution of tree species with elevation and the dependence of birds on riparian woodland for movement, was not surprising. Considering all possible landscape factors influencing dispersal (be it large or small) is essential, as here, even small gaps in continuous habitat act as significant impediments to gene flow in a generalist and widespread species.

4.5.2.1 Anthropogenic barriers

Human-mediated disturbances have had a huge impact on the health and survival of riparian ecosystems, and consequently, declines in riparian woodland (Rood and Mahoney, 1990) and disruptions to riverine communities (Janssen et al., 2000; Neraas and Spruell, 2001) have been observed. Contrary to our original hypothesis, artificial reservoirs do not act as barriers to gene flow within river systems (Tables 4.3 & 4.4). Gaps as large as 20 km do not appear to restrict gene flow despite a number of gap crossing studies of forest-dependent birds showing evidence of reduced movement by much smaller gaps (≤ 100 m) in forest cover (Seiving et al., 1996; Desrochers and Hannon, 1997; Laurance et al., 2002; Robertson and Radford, 2009). A temporal lag may explain why genetic differentiation was not observed, as the introduction of some
barriers may be too recent to impact spatial genetic structure. Landguth et al. (2010) found that the time to detect a genetic signal after the establishment of a barrier was approximately 15 generations for Mantel’s $r$ whereas for $F_{ST}$, it was ten times longer. With the oldest reservoir built in 1951 (St. Mary River), and the average lifespan of chickadees being 1.5 - 3 years (although some individuals can live up to 12 years), it is possible that genetic differentiation is not yet detectable using $F_{ST}$.

Agricultural practices (the conversion of semi-natural areas into cultivated cropland) have intensified worldwide and long term and intensive grazing on river valleys are becoming a serious concern for the health of riparian woodlands, as well as abundance and diversity of riparian bird communities (Jansen and Robertson, 2001). These processes may have contributed to patterns of genetic differentiation from limited movement between nearby river systems separated by large areas of agricultural fields (e.g., between St. Mary and Waterton Rivers). Even highly vagile migratory species such as the American robin (Turdus migratorius), the brown thrasher (Toxostoma rufum) and the loggerhead shrike (Lanius ludovicianus) have been shown to preferentially cross agricultural landscapes through connecting woodland corridors (Haas, 1995), highlighting the importance of natural corridors for dispersal.

Finally, artificial plantations of poplars are common in southern Alberta to promote woodland replenishment, and one example of this occurs in Taber (population TA). This may explain the anomaly in our clustering analyses with individuals in TA (as well as one individual in FK) clustering with the large genetic group in STRUCTURE (grey cluster; Figure 1a) and GENELAND (Figure 1e), instead of neighbouring genetic groups (i.e. LE, StM and WO, and SSK).
4.5.2.2 Natural barriers

Natural breaks in the landscape can play a key role in genetic differentiation of populations, and corresponds to a number of genetic breaks observed for the black-capped chickadee. For example, populations along the Red Deer River (e.g., DR) are isolated from southern river systems by prairie grassland (supported by the southern boundary of cluster 1 identified in GENELAND (Figure 4.2b)). Rivers that cross the plains are confined to coulees (or valleys) of varying depth, but coulees themselves are separated by large expanses of grassland and low shrubby vegetation with scattered depressions (i.e., ponds, marshes or lakes) where patches of forest sometimes exist. Black-capped chickadees would need to disperse approximately 100 km across unsuitable habitat between river systems which, given their low dispersal potential, is highly unlikely. While a number of populations located on different rivers systems showed a lack of genetic differentiation particularly in the west (e.g., FO and OL), they are connected upstream by forests along the foothills. This suggests that patterns of dispersal and gene flow are largely determined by habitat connectivity such that an abundance of treed habitat in the parkland and foothill regions facilitate dispersal between disconnected river systems. Similar patterns of habitat connectivity between river systems, but in a topographical complex landscape were found in populations of the Pacific jumping mouse (*Zapus trinotatus*; Vignieri, 2005).

As well as between rivers systems, natural gaps within river systems can also restrict dispersal and gene flow. The distribution of woodland is influenced by survival, establishment and regeneration of riparian poplars (e.g., adequate river flows, flooding, channel shifting, climate; Gom and Rood, 1999) and because of this, natural breaks in riparian woodland can occur. For example, SSK acts as an isolated island within the South Saskatchewan River, genetically distinct from all other
populations as a result of large stretches of unforested river valleys upstream and downstream. Furthermore, BO appears to be isolated from southern populations (Tables 4.3 & 4.4) because no riparian woodland is present downstream for approximately 150 km. The size of gaps seems to play a role in dispersal, with gaps ≥ 100 km impeding gene flow. Similar effects were found for a declining riparian specialist, the purple-crowned fairy-wren (*Malurus coronatus*), where functional isolation of populations from natural stretches of treeless river (~ 140 km) contributed to patterns of genetic differentiation (Skroblin *et al.*, 2014).

The density of woodland within river systems can also affect dispersal and gene flow. If trees are more sparsely distributed, predators become a bigger risk as well as increased competition for breeding sites. Differences in riparian environments (Rocky Mountains to foothills to semi-arid prairies), substrate type (coarse gravel in west vs. fine sand in east) and climatic variability (precipitation and temperature) all play an important role in the distribution of poplars. In this study, a gradual elevational gradient sloping from 1200 m in the west to 600 m in the east (Brayshaw, 1965), contributes to variation in ecoclimatic zones which in turn affects poplar spp. distributions along river systems. For example, Alberta has a semi-arid or dry continental climate as a result of a rainshadow effect from the Rocky Mountains in addition to its’ isolation from large water bodies. Despite this dry climate, rainfall is higher in the northern and western parts of the province (i.e. with increasing with elevation and latitude). As such, the densely populated *P. balsamifera* and *P. angustifolia* are found in the Rocky Mountains and foothills in the west, whereas the sparsely distributed *P. deltoides* are found in semi-arid grasslands of the east (Brayshaw, 1965). This corresponds to differentiation of DR and downstream populations found in *P. deltoides* sections of the river. Clinal variation in landscape,
climate and vegetation may explain genetic patterns seen here with less differentiation observed in the western regions. Chickadees may therefore favour poplars from this section due to their wider distribution and denser stands (Gom and Rood, 1999).

Overall, we found that large expanses of prairie grassland and breaks within the riparian corridor are important factors impeding gene flow at lower elevations where suitable habitat is limited. In the west, genetic differentiation is low suggesting that the Rocky Mountains and associated foothills provide sufficient treed habitat that maintains connectivity between headwaters of river systems and allowing dispersal eastward.

4.5.3 Influence of hybrid poplar zones on genetic differentiation

When hybrid poplar zones were given high resistance values in comparison to pure zones, a significant effect on genetic differentiation was observed in comparison to when low resistance values were tested. Pairwise genetic distances ($F_{ST}$ and $D_{EST}$) were high and significant across all comparisons for hybrid zone-associated chickadee populations (e.g., DR and LE). Boundary analysis in GENELAND also depicted areas of overlap and hybridisation (i.e., upstream of DR (Figure 4.2b), and surrounding LE (Figure 4.2d)). As hypothesised, these results suggest that hybrid poplar zones may be influencing movement decisions due to their ecologically rich and diverse community; particularly favourable for insectivorous, cavity nesting birds.

It has been widely recognised that hybridisation is important for plant speciation (Soltis and Soltis, 2009), but there has been increasing evidence of the importance of hybrid poplar zones in influencing the abundance (Whitham et al., 1996ab), preference (Whitham, 1989; Kalischuk et al., 1997), performance (Whitham et al., 1999) and genetic diversity (Evans et al., 2008; Evans et al., 2012) of dependent
species. Poplar hybrids often differ in tree architecture, phenology and chemical defences from their parental species and these characteristics have contributed to differences in arthropod distributions (Whitham et al., 2006; Evans et al., 2008; Floate et al., in review) and can drive population genetic differentiation in mite populations (Evans et al., 2012). Can they then drive genetic differentiation in chickadee populations as observed in this study? If they can influence the evolution of dependent arthropods, then they also have the potential to impact a wide range of taxa within the riparian community (e.g., microbes and vertebrates) and thus have important ecological and evolutionary roles for dependent organisms. As such, conservation efforts should prioritise the preservation of these important habitats.

Alternatively, genetic structuring found in this study coincides with the distributions of cottonwood species rather than the hybrid zones. For example, GENELAND grouped DR, a site in a poplar hybrid zone, with all downstream populations, coinciding with the distribution of the *P. deltoides* within that river system. Similarly, SSK coincides with *P. deltoides*, whereas the genetic cluster containing LE, StM and WO coincides with the distribution of *P. angustifolia*.

### 4.6 Conclusions

Fragmented landscapes are important study areas as they are structurally complex, can influence dispersal and gene flow, and affect population dynamics and evolutionary potential. One impact of reduced dispersal is population isolation which can lead to reduced population size. Over time small, isolated populations will begin to diverge as microevolutionary forces (e.g., genetic drift) act on them and may lead to extinction. Understanding the role that landscape features play on the genetic diversity of populations can help in the design of effective management strategies to
maintain their genetic integrity and survival. This study demonstrated the importance of assessing dispersal and gene flow on small spatial scales as both additional substructure and the effects of specific environmental variables or landscape factors may go undetected at large geographical scales.

Here we found significant genetic structuring of a common, resident riparian species which was not observed at the rangewide scale. Differentiation within the prairie riparian habitats can be attributed to habitat fragmentation from external factors (i.e., natural breaks in riparian corridors). Furthermore, genetic differences that cannot be explained by gaps in woodland, coincide with poplar hybrid zones. These areas may influence movement decisions due to the favourable conditions that they provide (i.e., they act as pest sinks) and may lead to genetic differentiation. These areas may have important conservation implications as they have already been shown to promote local adaptation and subsequent divergence in other poplar-dependent organisms.

4.7 Acknowledgements

Funding for the project was provided by the Alberta Conservation Association. We thank L. Lait, K. Dohms, J. Hindley, P. Pulgarin-Restrepo, A. Curtis, E. Carpenter and P. Narváez for help with sample collection for this project as well as C. Goater and H. Jiskoot for their constructive comments. We are also grateful to C. Langhorn, C. Bonifacio and L. Philipsen for their GIS expertise as well as Dr. Stewart Rood (University of Lethbridge) and Dr. Kevin Floate (Agriculture and Agri-Food Canada, Lethbridge) for their expertise and knowledge of riparian systems and associated woodland in southern Alberta.
4.8 References


Dawson, G.M. (1885) Geological map of the region in the vicinity of the Bow and Belly rivers embracing the southern portion of the District of Alberta and part of Assiniboia, North West Territory. Geological and Natural History Survey and Museum of Canada. Dawson Bros., Montreal, Quebec.


Table 4.1. Information for each sampling site including population name (Pop.), site abbreviation (Abbrev.), location (latitude (Lat) and longitude (Long)), sample size (N) as well as microsatellite summary statistics for each population across all loci: number of private alleles (PA), allelic richness (AR) and inbreeding coefficients (F\text{IS}).

<table>
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<th>Pop.</th>
<th>Abbrev.</th>
<th>Associated river system</th>
<th>Lat (°N)</th>
<th>Long (°W)</th>
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<th>PA</th>
<th>AR</th>
<th>F\text{IS}</th>
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Table 4.2. Microsatellite diversity measures (expected \((He)\) and observed \((Ho)\) heterozygosities, total number of alleles \((Na)\)) for 15 populations of black-capped chickadees at 12 microsatellite loci. See Table 1 for sampling site abbreviations.

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<td>8</td>
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<tr>
<td></td>
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<td>1.000</td>
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<td>0.261</td>
<td>0.781</td>
<td>0.611</td>
<td>0.522</td>
<td>0.469</td>
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<td>0.886</td>
</tr>
<tr>
<td>BO</td>
<td>Na</td>
<td>12</td>
<td>7</td>
<td>14</td>
<td>9</td>
<td>10</td>
<td>4</td>
<td>8</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>9</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Ho</td>
<td>0.750</td>
<td>0.750</td>
<td>0.950</td>
<td>0.800</td>
<td>0.800</td>
<td>0.200</td>
<td>0.900</td>
<td>0.600</td>
<td>0.400</td>
<td>0.188</td>
<td>0.750</td>
<td>0.684</td>
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<tr>
<td></td>
<td>He</td>
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<td>0.781</td>
<td>0.894</td>
<td>0.818</td>
<td>0.835</td>
<td>0.186</td>
<td>0.801</td>
<td>0.495</td>
<td>0.509</td>
<td>0.342</td>
<td>0.855</td>
<td>0.893</td>
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</tbody>
</table>

162
| SB2 | Na  | 9   | 8   | 17  | 11  | 13  | 4   | 8   | 3   | 3   | 2   | 11  | 14  | 9  |
|     | Ho  | 0.560 | 0.828 | 0.862 | 0.893 | 0.862 | 0.241 | 0.793 | 0.345 | 0.276 | 0.241 | 0.897 | 0.923 | 0.643 |
|     | He  | 0.719 | 0.769 | 0.917 | 0.829 | 0.864 | 0.248 | 0.795 | 0.518 | 0.463 | 0.212 | 0.877 | 0.896 | 0.676 |
| SB1 | Na  | 6   | 6   | 14  | 11  | 13  | 3   | 8   | 3   | 4   | 2   | 9   | 13  | 8  |
|     | Ho  | 0.550 | 0.700 | 0.750 | 0.800 | 0.800 | 0.400 | 0.650 | 0.650 | 0.350 | 0.118 | 0.900 | 0.750 | 0.618 |
|     | He  | 0.651 | 0.741 | 0.891 | 0.840 | 0.881 | 0.339 | 0.703 | 0.551 | 0.545 | 0.291 | 0.830 | 0.875 | 0.678 |
| CR  | Na  | 10  | 6   | 20  | 11  | 13  | 2   | 7   | 3   | 2   | 2   | 10  | 19  | 9  |
|     | Ho  | 0.655 | 0.833 | 0.833 | 0.893 | 0.900 | 0.200 | 0.759 | 0.533 | 0.467 | 0.167 | 0.800 | 0.862 | 0.659 |
|     | He  | 0.640 | 0.686 | 0.902 | 0.839 | 0.882 | 0.180 | 0.727 | 0.455 | 0.464 | 0.299 | 0.851 | 0.861 | 0.649 |
| OM  | Na  | 7   | 6   | 15  | 14  | 16  | 6   | 7   | 3   | 4   | 2   | 9   | 15  | 9  |
|     | Ho  | 0.600 | 0.600 | 0.850 | 0.889 | 0.800 | 0.500 | 0.900 | 0.650 | 0.650 | 0.278 | 0.900 | 0.765 | 0.698 |
|     | He  | 0.645 | 0.770 | 0.885 | 0.884 | 0.898 | 0.508 | 0.821 | 0.501 | 0.546 | 0.313 | 0.825 | 0.905 | 0.708 |
| FO  | Na  | 7   | 6   | 6   | 8   | 8   | 3   | 7   | 3   | 3   | 2   | 7   | 8   | 6  |
|     | Ho  | 0.700 | 0.600 | 0.667 | 0.900 | 0.900 | 0.500 | 0.800 | 0.400 | 0.600 | 0.222 | 0.800 | 0.556 | 0.637 |
|     | He  | 0.705 | 0.720 | 0.750 | 0.820 | 0.860 | 0.540 | 0.825 | 0.445 | 0.445 | 0.444 | 0.750 | 0.796 | 0.675 |
| LE  | Na  | 12  | 8   | 22  | 13  | 14  | 5   | 7   | 3   | 2   | 2   | 10  | 14  | 9  |
|     | Ho  | 0.674 | 0.702 | 0.833 | 0.891 | 0.896 | 0.125 | 0.689 | 0.447 | 0.396 | 0.068 | 0.833 | 0.773 | 0.611 |
|     | He  | 0.773 | 0.732 | 0.916 | 0.868 | 0.872 | 0.120 | 0.728 | 0.439 | 0.437 | 0.283 | 0.791 | 0.885 | 0.654 |
| SSK | Na  | 5   | 5   | 11  | 6   | 10  | 4   | 7   | 2   | 2   | 2   | 7   | 7   | 6  |
|     | Ho  | 0.750 | 0.700 | 0.800 | 0.850 | 0.900 | 0.600 | 0.700 | 0.350 | 0.650 | 0.053 | 0.650 | 0.722 | 0.644 |
|     | He  | 0.723 | 0.719 | 0.846 | 0.735 | 0.864 | 0.588 | 0.729 | 0.439 | 0.489 | 0.301 | 0.765 | 0.813 | 0.667 |
| Average for each locus | Na  | 7   | 7   | 14  | 10  | 11  | 3   | 7   | 3   | 3   | 2   | 9   | 12  | 9  |
|     | Ho  | 0.673 | 0.751 | 0.851 | 0.853 | 0.862 | 0.324 | 0.790 | 0.477 | 0.445 | 0.167 | 0.829 | 0.762 | 0.667 |
|     | He  | 0.677 | 0.746 | 0.881 | 0.832 | 0.865 | 0.316 | 0.770 | 0.489 | 0.472 | 0.314 | 0.821 | 0.851 | 0.667 |
Table 4.3. Pairwise $F_{ST}$ values (below diagonal) and harmonic mean estimates of $D_{EST}$ (above diagonal) for 15 black-capped chickadee populations based on 12 microsatellite loci. Bold values indicate statistical significance after FDR correction.

<table>
<thead>
<tr>
<th></th>
<th>BUC</th>
<th>NSK</th>
<th>IN</th>
<th>RD1</th>
<th>RD2</th>
<th>DR</th>
<th>BO</th>
<th>SB2</th>
<th>DY</th>
<th>SB1</th>
<th>CR</th>
<th>OM</th>
<th>FO</th>
<th>LE</th>
</tr>
</thead>
<tbody>
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<td>BUC</td>
<td>0.036</td>
<td>0.008</td>
<td>0.001</td>
<td>0.006</td>
<td>0.038</td>
<td>0.036</td>
<td>0.004</td>
<td>0.007</td>
<td>0.000</td>
<td>0.007</td>
<td>0.039</td>
<td>0.005</td>
<td>0.044</td>
<td></td>
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<tr>
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<td>0.015</td>
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<td>0.026</td>
<td><strong>0.051</strong></td>
<td>0.012</td>
<td>0.012</td>
<td>0.016</td>
<td><strong>0.031</strong></td>
<td><strong>0.044</strong></td>
<td><strong>0.036</strong></td>
<td>0.020</td>
<td>0.039</td>
</tr>
<tr>
<td>IN</td>
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<td>0.029</td>
<td>*</td>
<td>0.000</td>
<td>0.006</td>
<td>0.026</td>
<td><strong>0.050</strong></td>
<td>0.013</td>
<td>0.023</td>
<td>0.005</td>
<td>0.013</td>
<td>0.012</td>
<td>0.007</td>
<td>0.062</td>
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<tr>
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<td>0.015</td>
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<td>0.019</td>
<td>0.012</td>
<td>0.003</td>
<td>0.000</td>
<td>0.001</td>
<td>0.006</td>
<td>0.015</td>
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<tr>
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<td>0.022</td>
<td>0.029</td>
<td>0.017</td>
<td>*</td>
<td>0.007</td>
<td><strong>0.047</strong></td>
<td>0.007</td>
<td>0.000</td>
<td>0.005</td>
<td>0.000</td>
<td>0.022</td>
<td>0.000</td>
<td>0.023</td>
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<tr>
<td>DR</td>
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<td><strong>0.032</strong></td>
<td><strong>0.023</strong></td>
<td><strong>0.024</strong></td>
<td>*</td>
<td><strong>0.057</strong></td>
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<td><strong>0.022</strong></td>
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<td><strong>0.014</strong></td>
<td>0.059</td>
<td>0.012</td>
<td>0.089</td>
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<tr>
<td>BO</td>
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<td>0.033</td>
<td>0.014</td>
<td>0.023</td>
<td><strong>0.025</strong></td>
<td>*</td>
<td>0.013</td>
<td><strong>0.028</strong></td>
<td>0.029</td>
<td><strong>0.041</strong></td>
<td>0.087</td>
<td><strong>0.032</strong></td>
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<tr>
<td>SB2</td>
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<td>0.031</td>
<td>0.011</td>
<td>0.016</td>
<td>0.025</td>
<td>0.013</td>
<td>*</td>
<td>0.000</td>
<td>0.000</td>
<td>0.005</td>
<td><strong>0.042</strong></td>
<td>0.000</td>
<td>0.036</td>
</tr>
<tr>
<td>DY</td>
<td>0.027</td>
<td>0.017</td>
<td>0.034</td>
<td>0.015</td>
<td>0.016</td>
<td>0.026</td>
<td>0.021</td>
<td>0.010</td>
<td>*</td>
<td>0.003</td>
<td>0.001</td>
<td>0.028</td>
<td>0.001</td>
<td>0.019</td>
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<td>0.010</td>
<td>0.016</td>
<td>0.027</td>
<td>0.017</td>
<td>0.007</td>
<td>0.014</td>
<td>*</td>
<td><strong>0.013</strong></td>
<td><strong>0.040</strong></td>
<td>0.006</td>
<td>0.025</td>
</tr>
<tr>
<td>CR</td>
<td>0.028</td>
<td>0.020</td>
<td>0.028</td>
<td>0.017</td>
<td>0.010</td>
<td>0.022</td>
<td>0.021</td>
<td>0.014</td>
<td>0.014</td>
<td><strong>0.017</strong></td>
<td>*</td>
<td>0.023</td>
<td>0.002</td>
<td>0.047</td>
</tr>
<tr>
<td>OM</td>
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<td>0.026</td>
<td>0.041</td>
<td><strong>0.043</strong></td>
<td><strong>0.035</strong></td>
<td>0.030</td>
<td><strong>0.036</strong></td>
<td>0.028</td>
<td>*</td>
<td>0.008</td>
<td>0.042</td>
</tr>
<tr>
<td>FO</td>
<td>0.035</td>
<td>0.023</td>
<td>0.046</td>
<td>0.020</td>
<td>0.024</td>
<td>0.042</td>
<td>0.028</td>
<td>0.012</td>
<td>0.019</td>
<td>0.018</td>
<td>0.025</td>
<td>0.036</td>
<td>*</td>
<td>0.015</td>
</tr>
<tr>
<td>LE</td>
<td><strong>0.035</strong></td>
<td><strong>0.017</strong></td>
<td><strong>0.040</strong></td>
<td><strong>0.015</strong></td>
<td><strong>0.023</strong></td>
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<td><strong>0.021</strong></td>
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<td><strong>0.024</strong></td>
<td><strong>0.034</strong></td>
<td><strong>0.021</strong></td>
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<tr>
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<td>0.024</td>
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<td>0.023</td>
<td>0.035</td>
<td>0.036</td>
<td>0.032</td>
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Table 4.4. Results from STRUCTURE analysis of individuals from populations separated by hypothesised artificial or natural barriers to gene flow within river systems.

<table>
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<tr>
<th>Hypothesis</th>
<th>Impediment</th>
<th>Approx. distance of barrier (river km)</th>
<th>Populations</th>
<th>Number of clusters (K)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Natural</td>
<td>Gap in woodland</td>
<td>98</td>
<td>LE &amp; SSK</td>
<td>2</td>
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<tr>
<td></td>
<td>Gap in woodland</td>
<td>150</td>
<td>BO &amp; southern populations</td>
<td>2</td>
</tr>
<tr>
<td>Artificial</td>
<td>Oldman Reservoir</td>
<td>20</td>
<td>CR &amp; OM</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>St. Mary Reservoir</td>
<td>17</td>
<td>StM &amp; WO</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Waterton Reservoir</td>
<td>10</td>
<td>SB1 &amp; GL/BL</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>St. Mary Reservoir/ gap in woodland</td>
<td>80</td>
<td>StM &amp; WO</td>
<td>1</td>
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Table 4.5. Summary of Mantel and partial Mantel test results comparing the effect of different resistance distances on genetic distance ($F_{ST}$ and $D_{EST}$) for 15 populations (above dashed line) and 12 populations located within hybrid poplar zones (below dashed line). Controlled variable for partial Mantel test stated in brackets (e.g., “(distance)” = controlled for geographical distance through suitable habitat). Results include $r =$ partial coefficient, $R^2 =$ coefficient of determination, $AIC_c =$ corrected Akaike’s Information Criterion, $\Delta_i =$ differences in $AIC_c$ values, $w_i =$ $AIC_c$ weights. ** indicates significant correlations ($P \leq 0.05$).

<table>
<thead>
<tr>
<th>Variable (controlled variable)</th>
<th>$F_{ST}$</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>$D_{EST}$</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$R^2$</td>
<td>$AIC_c$</td>
<td>$\Delta_i$</td>
<td>$w_i$</td>
<td>$r$</td>
<td>$R^2$</td>
<td>$AIC_c$</td>
<td>$\Delta_i$</td>
<td>$w_i$</td>
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<tr>
<td>Distance through suitable habitat</td>
<td>0.16</td>
<td>0.02</td>
<td>-569.9</td>
<td>34.7</td>
<td>0</td>
<td>0.33**</td>
<td>0.11</td>
<td>-427.1</td>
<td>6.2</td>
<td>0.04</td>
</tr>
<tr>
<td>Elevation</td>
<td>-0.35</td>
<td>0.12</td>
<td>-580.2</td>
<td>24.4</td>
<td>0</td>
<td>-0.28</td>
<td>0.08</td>
<td>-427.5</td>
<td>5.8</td>
<td>0.04</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td>-0.26</td>
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<td></td>
</tr>
<tr>
<td>Elevation (land cover)</td>
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<td></td>
<td></td>
<td></td>
<td>-0.15</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Land cover</td>
<td>0.59**</td>
<td>0.35</td>
<td>**-604.6</td>
<td>0</td>
<td>0.44</td>
<td>0.38**</td>
<td>0.15</td>
<td>**-433.3</td>
<td>0</td>
<td>0.78</td>
</tr>
<tr>
<td>Land cover (distance)</td>
<td>0.58**</td>
<td></td>
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<td>Land cover x elevation</td>
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<td>0.33</td>
<td>-601.7</td>
<td>2.9</td>
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<td>0.35</td>
<td>0.12</td>
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<td>Land cover x elevation (distance)</td>
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<tr>
<td>Hybrid-</td>
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<td>0.03</td>
<td>-340.8</td>
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<tr>
<td>Hybrid+</td>
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<td>0.02</td>
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<td>-0.04</td>
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<td>-263.1</td>
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<td>14.9</td>
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<td>0.27**</td>
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<td>-263.5</td>
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<td></td>
<td></td>
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<tr>
<td>Hybrid+ x elevation</td>
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<td>-340.2</td>
<td>18.9</td>
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<td>-0.08</td>
<td>0.01</td>
<td>-263.9</td>
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<td>0</td>
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<td>0</td>
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Figure 4.1. Map of Southern Alberta illustrating the presence (shaded area) and absence (e.g., downstream of the Bow River) of riparian woodland within each river system under study. Artificial barriers (i.e., river reservoirs) are located in black rectangles. Approximate regions of pure and hybrid poplar zones (not to scale) are separated by the dashed lines (B = pure *Populus balsamifera*; B x D = hybrid zone between *P. balsamifera* and *P. deltoides*; B x A = hybrid zone between *P. balsamifera* and *P. angustifolia*; B x A x D = trispecific hybrid zone between *P. balsamifera*, *P. angustifolia* and *P. deltoides*; D = pure *P. deltoides*).
Figure 4.2. Sampling locations (a) of black-capped chickadee (*Poecile atricapillus*) in Southern Alberta (See Table 4.1 for abbreviations and associated river systems) with inferred clusters from STRUCTURE (coloured circles; $K = 3$; see Figure 4.3). Inset illustrates forest cover in the area (dark grey = forest; light grey = grassland). Included in the figure are GENELAND boundary maps ($K = 4$) for (b) cluster 1 (DR, M, JE and BU), (c) cluster 2 (SSK), (d) cluster 3 (LE, StM and WO) and (e) cluster 4 (all remaining populations).
**Figure 4.3.** Inferred population structure of the black-capped chickadee (*Poecile atricapillus*) from 12 microsatellite loci using STRUCTURE. Two runs were conducted, but the optimal number of clusters to describe the data was unclear for each run. The initial run (a) for all individuals from 28 localities resulted in contrasting values of true $K$: (i) $K = 2$ ($\Delta K$) and ii) $K = 3$ ($\text{LnPr}(X|K)$). We chose $K = 2$ and after removing structure populations (LE, StM and WO) in a hierarchical fashion, our second run (b) also presented contrasting results: (i) $K = 2$ ($\Delta K$) and ii) $K = 3$ ($\text{LnPr}(X|K)$). Due to mixed assignment of NSK and BO, we chose $K = 2$ as the true $K$. No additional structure was identified after removing population SSK. Overall, STRUCTURE identified 3 genetic clusters (cluster 1: LE, StM and WO; cluster 2: SSK and cluster 3: all remaining populations).
Figure 4.4. A representation of genetic relatedness between geographical clusters of black-capped chickadee populations ($N = 15$) obtained by discriminant analysis of principal components (DAPC). The graphs represent individuals as dots and the populations as inertia eclipses (population abbreviations can be found in Table 1) and scatterplots are based on the first two principal(196,477),(813,831) components. Populations with $N \leq 5$ were excluded.
CHAPTER 5: General Discussion

5.1 Patterns of population genetic structure

This study revealed high levels of genetic differentiation and complex patterns of population genetic structure in the black-capped chickadee at both large and small geographical scales. These findings were unexpected given the dispersal potential of this species (i.e., flight capabilities). Dispersal and gene flow in black-capped chickadees seem to be the result of variation within the landscape. The rangewide genetic patterns were consistent with previous studies (e.g., clustering of Alaska, Newfoundland and a Pacific group (Gill et al., 1993; Pravosudov et al., 2012; Hindley, 2013)), but high resolution microsatellite markers enabled us to identify substructuring of populations particularly in the western portion of the range. In addition, this was the first time a fine-scale landscape genetics approach was adopted in this species. Our findings support the idea that variation in the landscape matrix can affect an organisms’ ability to disperse between populations (Manel et al., 2003).

Dispersal is an important life history trait which maintains population and species integrity. In nature, extrinsic factors can reduce population connectivity; restricting dispersal and subsequent gene flow among populations leading to isolation. Reduced number of migrants and reduced gene exchange increase genetic differences between populations and lower genetic diversity within populations (Frankham, 2005). Over time, small isolated populations may become susceptible to high levels of inbreeding from mating with closely related individuals (Keller and Waller, 2002) and in extreme cases, become vulnerable to local extinctions (Frankham, 2005). Alternatively, isolated populations may adapt through natural selection to different environmental conditions. For example, speciation can be driven by geographic
isolation and the absence of gene flow, where continuous populations are divided into smaller discrete populations which independently experience different environmental conditions and selection pressures. The differential effects of genetic isolation stress the importance of monitoring and tracking the movements of individuals, to determine how they are coping as a species in different environments, and ultimately to identify populations or species that require conservation management. Here in a widespread species, large topographical features (e.g., rivers, mountains), historical processes (e.g., glaciation, island formation) as well as current ecological processes (e.g., habitat fragmentation) left genetic imprints on contemporary patterns of genetic variation. Teasing apart the effects of different processes on patterns of population genetic structure was necessary to prevent errors in interpretation, and was assisted by comparing findings with studies using different molecular markers. Moreover, this study demonstrated the complexity of different landscapes and their subsequent effects on gene flow; highlighting the need to understand how different organisms interact with their environment. This information can then be used to facilitate predictions of future environmental change on their survival.

5.1.1 Macrogeographical features

5.1.1.1 Isolation by distance

Highly mobile organisms that are continuously distributed across a variety of habitats are expected to show limited genetic differentiation across their geographic range. Given the broad geographical range of the black-capped chickadee, isolation by distance (IBD) played an important role in reducing gene flow between western and eastern populations, with large expanses of unsuitable habitat (e.g., the Great Plains) further exacerbating the effects of IBD. However, some of the patterns identified (i.e.,
genetic differentiation between neighbouring populations) suggest that other factors are affecting dispersal and gene flow. The expectation of unrestricted gene flow in widespread, highly mobile organisms therefore does not always apply as broad scale patterns of genetic differentiation can be explained by a number of different processes (e.g., historical, ecological and behavioural) and not restricted to IBD (Foll and Gaggiotti, 2006; Razgour et al., 2014; Liu et al., 2013).

5.1.1.2 Mountains
In western North America, genetic differentiation in black-capped chickadees corresponded to an east-west split between the central Rocky and Cascade Mountains (e.g., Pacific and Intermountain West groups) which is consistent with phylogeographic patterns (Hindley, 2013) and supports the hypothesis that large mountain ranges cause a physical impediment to dispersal. Genetic discontinuities resulting from impermeable mountain ranges have also been observed in a number of animal and plant species (reviewed in Shafer et al., 2010) including chickadees (Spellman et al., 2007; Lait et al., 2012). Contrary to the original hypothesis, not all mountain ranges impede gene flow. The Appalachian Mountains did not restrict gene flow in the east (evident from one eastern genetic cluster), nor did the northern Rocky Mountains in the west (evident from clustering of CBC with the Canadian Pacific-Prairies Group). These findings suggest that a series of low elevation, forested valleys or passes facilitate dispersal and prevent genetic isolation. This same pattern was found in other widely distributed chickadees (Lait and Burg, 2013) as well as less mobile organisms associated with different mountain ranges (Zhan et al., 2009). Therefore, the assumption that mountains act as barriers to gene flow is not definitive.
5.1.1.3 Large water bodies

The eastern portion of the range showed weak genetic differentiation with high levels of connectivity and gene flow, with the exception of Newfoundland (NL). Chickadees on NL were genetically distinct from continental populations. Similar levels of genetic differentiation on this island have been observed for multiple organisms (McGowan et al., 1999; Boys et al., 2005; Colbeck et al., 2008). Isolation of island populations is not uncommon due to large water bodies acting as a physical impediment (Mayr, 1963). In addition, island populations are generally smaller in size and likely experience high levels of genetic drift, resulting in rapid fixation of neutral alleles and reduced overall genetic variation (Frankham, 1998). Interestingly, black-capped chickadees are absent from other offshore islands in North America (e.g., Haida Gwaii, Alexander Archipelago and Victoria Island), suggesting that large bodies of water may restrict dispersal and that their presence on NL was driven by additional factors.

5.1.1.4 Historical processes

Oftentimes, signatures of historical processes (e.g., Pleistocene glaciations) are present in contemporary genetic patterns. For example, the east-west split observed here, combined with an additional north-south split within the central and southern Rockies, are consistent with ancient vicariance events, such as isolation in multiple refugia during the Pleistocene, and periods of secondary contact (Brunsfeld et al., 2001; Good and Sullivan, 2001; Reding et al., 2012).

Furthermore, genetic isolation on NL was supported by both microsatellite (Chapter 2) and mtDNA (Hindley, 2013) data, in addition to morphological differences such that a subspecies has been described (*Poecile atricapillus bartelli*).
This body of evidence supports a previous hypothesis (Gill et al., 1993) that NL likely served as a glacial refugium.

5.1.2 Microgeographical features

Unusual patterns of spatial genetic structure, that cannot be explained from geographical isolation or historical processes, are often influenced by less obvious features such as variation in landscape and environmental variables (e.g., climate, vegetation, anthropogenic disturbance) (McRae et al., 2005; Reding et al., 2012; Wang, 2012; McGraughran et al., 2014; Wasserman et al., 2014). This was the first time regional patterns of spatial genetic structure were examined in the black-capped chickadee and results suggest that dispersal and subsequent gene flow are largely influenced by landscape heterogeneity.

5.1.2.1 Habitat fragmentation

Environmental change is an important driver of population isolation. Habitats are becoming increasingly fragmented or degraded by natural and/ or anthropogenic barriers (Figure 4.1 and 5.1) which not only alters the layout of the environment, but can change microclimates within fragments from edge effects. Natural barriers, such as changes in forest composition, restrict gene flow in a number of species (Su et al., 2003; McRae et al., 2005; Funk et al., 2005) including chickadees. For example, this thesis showed genetic differentiation increased in black-capped chickadee populations isolated by large natural gaps in continuous woodland (e.g., geological breaks in riparian forest). The effects of human activities and demands for resources on population connectivity are similar (Epps et al., 2005; Cushman, 2006). Although artificial barriers within riparian woodland did not reduce gene flow in black-capped
chickadees, excessive removal of suitable chickadee habitat in central British Columbia from forestry practices seem to have an effect on gene flow, with high levels of genetic differentiation observed between neighbouring populations each experiencing different levels of human mediated habitat loss (e.g., FtStJ1 and FtStJ2). An important implication of habitat fragmentation is that fragmented populations may develop different behaviours (e.g., mating strategies) which may lead to reproductive isolation. As such, gaining an understanding of the spatial distribution of genetic variation across heterogeneous landscapes can provide interesting and sometimes unexpected insights into how organisms interact with their environment and the mechanisms of evolutionary diversification.

5.1.2.2 Habitat suitability

Dispersal among populations can be strongly influenced by the complexity of the landscape matrix (i.e., the stretch of land between habitat patches) (Manel et al., 2003). Black-capped chickadees are highly dependent on continuous suitable habitat for dispersal, and gene flow is sensitive to variation in ecological conditions, particularly large gaps in woodland. At the landscape level, ecological variables such as topography (elevation) and landscape configuration (forest cover) had a significant effect on gene flow. Predictably, genetic differentiation increased with high elevation (e.g., montane habitats) and unsuitable habitat (e.g., pure coniferous forest, grassland) and decreased with lower elevation and suitable habitat (e.g., mixed/deciduous forest, riparian habitat). Higher elevation habitats are often associated with a transition from mixed forests to pure coniferous forests and the presence of competitors (e.g., mountain, boreal and chestnut-backed chickadees) which limits the distribution of black-capped chickadees in heterogeneous landscapes (Campbell et al. 1997).
Furthermore, patterns of genetic differentiation on a regional scale (i.e., in British Columbia) corresponded to different ecoregions characterized by differences in physical conditions (e.g., climatic variables). This would suggest that the observed genetic patterns may have arisen through local adaptation to different environments (Cheviron and Brumfeld, 2009), however, analyses (e.g., GESTE) failed to find a significant relationship between specific climatic factors and genetic differentiation which was unexpected given that the extreme heterogeneity of British Columbia’s landscape for example. Similar results were found in organisms that are more sensitive to climatic differences than birds (e.g., amphibians (Muir et al., 2013) and fish (Leclerc et al., 2008)). Given that black-capped chickadees are present in a range of different environments, from the extreme winters in Alaska to extreme desert conditions in southern US, it is possible that individuals originating in one climate can successfully breed in another. Habitat suitability (old-growth forests), resource availability (e.g., food availability, nesting sites) and dispersal corridors seem to be more important factors influencing gene flow and driving genetic differentiation in chickadees than climatic conditions.

5.2 Landscape genetics

5.2.1 Cryptic patterns of genetic structure

A landscape genetics approach (Figure 5.2) helped resolve cryptic patterns of genetic structure in this species at a regional scale, and revealed additional insights into the distribution of genetic variation and the environmental factors influencing genetic patterns. Cryptic genetic structure is important because populations may be subjected to other ecological and evolutionary processes, related to factors such as habitat differences, social complexities, behavioural changes or other demographic causes.
For example, cryptic subdivisions in large terrestrial animals (Ernest et al., 2003; Geffen et al., 2004) have been attributed to social cohesion (i.e., dispersing to habitats similar their natal habitat) and habitat quality (Sacks et al., 2005). In this thesis, cryptic substructuring of black-capped chickadee populations corresponded to small gaps in forested habitat, changes in woodland density and composition, as well as environmental differences (e.g., biogeoclimatic zones). Reduced population connectivity at a microgeographic scale here suggests that chickadees are extremely sensitive to even small changes in their environment and that variation in habitat quality is a key driver of population isolation and genetic structure. For black-capped chickadees, the maintenance of suitable forested habitat and dispersal corridors over large areas may be critical to the integrity of populations.

5.2.2 Prioritising populations for conservation in widespread species

Previously, conservation efforts and management strategies have focused primarily on geographic areas, ecosystems, individual species and often species of concern (Myers et al., 2000). While isolated populations may be at risk from reduced population size, lowered genetic diversity or local extinctions, they may also undergo local adaptation as a result of selection or genetic drift (i.e., different behaviour, morphology or life-history traits may evolve in diverse environments). For example, Mediterranean blue tits (Parus caeruleus) altered the timing of their breeding season and clutch size in response to an earlier food supply in a deciduous habitat, in comparison to populations in evergreen habitats that experienced later leafing and insect emergence (Blondel et al., 1993). This thesis has illustrated the negative effects of environmental variation on a species that has a stable conservation status with no economic importance. Genetics studies should therefore not be limited to study organisms of economic
importance, in decline, with limited dispersal capabilities or with small, disjunct distributions because even in a common widespread species, genetically distinct populations were identified that may require additional monitoring.

The identification and conservation of discrete units below the species level (e.g., subspecies, populations) is becoming an increasingly accepted priority (Taylor et al., 2013; Volkmann et al., 2014; Mee et al., 2015). In widespread species, distinct populations play important roles in different types of ecosystems, and their extinction may lead to important changes in ecosystem dynamics (Taylor et al., 2013). Landscape genetics approaches, such as isolation by resistance, can improve detection of discrete population genetic structure which might represent subspecies or other evolutionary significant units in different environments, in comparison to larger phylogeographic studies where patterns are often attributed to range dimensions (McRae and Beier, 2007). Mee et al. (2015) identified 36 distinct units in the geographically widespread lake whitefish species complex (Coregonus spp.) based on four criteria developed to capture evolutionary and ecologically relevant processes at multiple temporal and spatial scales (e.g., reproductive isolation, phylogeographic history, local adaptation and biogeographic separation). Their criteria were effective and can be applied to any widespread taxon with complex phylogeographic histories and ecological diversity, which includes black-capped chickadees. The only criterion that has not yet been evaluated in black-capped chickadees is “local adaptation” which would be the obvious next research objective to help identify significant conservation units in this species.

5.2.3 Future directions

5.2.3.1 Incorporation of additional ecological factors
The main challenge in landscape genetics is assigning resistance values to reflect the true influence of different cover types on gene flow. To do this, studies have to rely on field data (e.g., homing experiments, Bélisle et al., 2001) and expert opinion (Amos et al., 2012). When this information is unavailable or inaccurate, studies employ a model optimization method whereby multiple resistance surfaces are created for the same landscape feature(s) which are then statistically compared (using $r$, $R^2$, or AIC) to determine which resistance surface best fits the genetic data (Spear et al., 2010). For example, if one is unsure of the effect of agricultural land on gene flow, different levels of resistance can be assigned (e.g., low = 1, medium = 10 and high = 100). A more complex method was described in Cushman et al. (2006) where 108 different landscape resistance surfaces were created to account for various levels of relative resistance for land cover, slope, roads and elevation to identify the factors influencing connectivity in black bears (*Ursus americanus*). The results from model optimization can be further validated by landscape genetic simulations of empirical datasets to determine if the best fitting resistance model is ecologically meaningful (Cushman and Landguth, 2010a).

All landscape processes are tightly interrelated, so a combined land cover resistance layer with single resistance values assigned to each cover type (using expert opinion) was used in this thesis (Chapters 3 and 4) to provide an overall picture of the effects of habitat heterogeneity in the black-capped chickadee. Further research into the processes governing gene flow would benefit from investigating the effect of individual landscape features and from modelling varying levels of resistances for each landscape feature. For example, rather than combining all land cover types into the one resistance layer, generating multiple resistance layers of single cover types (e.g., rivers, lakes, shrubs, broadleaf forest, non-vegetated land) and different
variables within those features (e.g., canopy cover, curvature of rivers) would provide a better indication of the processes driving genetic differentiation in the black-capped chickadee.

5.2.3.2 Species-specific spatial scale

When sampling and analyses are conducted at spatial scales similar to that of dispersal and gene flow, the relationship between gene flow and ecological factors are often much stronger (Anderson et al., 2010; Cushman and Landguth, 2010b). Presumably, this is because variation in the landscape can affect individual movement at different spatial scales. One study, identified distinct patterns of genetic structure across the geographical range of the highly mobile grey long-eared bat (*Plecotus austriacus*), but additional fine-scale population structure driven by small gaps in meadows was also identified, illustrating the importance of assessing the effects of landscape features on gene flow at appropriate scales (Razgour et al., 2014). Furthermore, in the widespread, cooperative breeding bird, the superb fairy-wren (*Malurus cyaneus*), long distance dispersal was constrained by geographical distance as expected, but mating systems were disrupted by limited gene flow in heavily fragmented agricultural landscapes (i.e., reduced tree cover) on a small geographical scale leading to fine-scale population structure (Harrisson et al., 2012).

The landscape extent investigated in British Columbia (Chapter 3) was double the average dispersal distance of juvenile chickadees (assuming average post fledging dispersal distances of 1.1 km) and 10 times the average dispersal distance of adults (average independent individual dispersal distance of 204 m (Weise and Meyer, 1979)), so the patterns emerged from the influence of landscape features between populations at a regional scale. This is still highly informative, and the scale was
necessary because populations were distributed throughout the province and substantially reduced computing power due to the high resolution of the data. Despite finding a significant effect of landscape features on functional connectivity, a future consideration may be to further reduce the scale so that gene flow is measured at a scale relevant to dispersal. For example, investigating gene flow among the central plateau populations only may provide better picture of the specific environmental processes driving genetic differentiation as additional landscape and environmental variables can be assessed individually (e.g., variation in forest cover, roads, water, agricultural land, urbanisation, and climate variables).

The emergence of landscape genetics studies have often focused on assessing the effects of the landscape matrix between locations on dispersal, but it is also likely that variation within the local environment influences patterns of genetic differentiation (Murphy et al., 2010; Wang et al., 2013; Coster et al., 2015). Landscape heterogeneity can influence the three stages of dispersal: immigration, transience and emigration. Local conditions may differ in the number of resources available, number of competitors or patch size, which may influence genetic patterns by facilitating or deterring dispersal (i.e., immigration and emigration stage). In addition, variation in the landscape matrix (e.g., habitat boundaries, physical barriers, perceived predation risk) affect movement characteristics between patches (i.e., transience) (Pflüger and Balkenhol, 2014). A few studies have incorporated local environmental conditions (and matrix qualities) into landscape genetics analyses and found that local factors are important in explaining gene flow and spatial patterns of genetic structure (Murphy et al., 2010; Wang et al., 2013; Wang, 2013; Nowakowski et al., 2015). Weckworth et al. (2013) found that local effective population size as well as preferred habitat helped explain genetic relationships in the endangered
woodland caribou (*Rangifer tarandus*). Other studies have found that matrix variables between localities were better predictors of gene flow than local features (Coster *et al.*, 2015). This illustrates the importance of including both sets of data as some species may be affected more by local patterns than the landscape matrix, or vice versa. An interesting follow up to this thesis therefore would be to take a small subset of populations to determine if local conditions may further elucidate some unexpected patterns of genetic differentiation observed in the black-capped chickadee (e.g., FtStJ1 and PG).

### 5.2.3.3 Comparative landscape genetics

Understanding how one species is affected by different ecological factors does not imply that all species respond in the same way. Often, species exhibit variation in demography and life history traits which implies that they may respond to their environment in different ways (Baguette and Van Dyck, 2007). A number of studies investigating species-specific landscape genetic patterns have focused on amphibians, presumably because they are more sensitive to landscape change due to their low vagility and physiological constraints (Coster *et al.*, 2015; Nowakowski *et al.*, 2015). The variety of responses in amphibians likely originates from divergent life histories as well as species-specific tolerance to landscape change. I propose that these comparative studies should be extended to other organisms as they too may show important species-specific differences.

The transition from landscape genetics studies focusing on single species to multiple species within the same landscape will enable us to determine if patterns are consistent across species, or if species-specific differences can be identified. In this case, comparing the relationship between gene flow and environmental features
between different resident bird species may provide additional insight into whether patterns observed here are specific to black-capped chickadees or shared between different species inhabiting the same area. This additional effort would essentially “kill two birds with one stone” and would likely prevent errors in conservation strategies for a species that is based on patterns found in another similar species.

5.3 General conclusions
A more comprehensive sampling approach combined with high resolution microsatellite markers provided a more complete picture of the overall spatial distribution of genetic variation of the black-capped chickadee, in comparison to previous studies. High levels of genetic differentiation across North America were identified and attributed to large physical barriers and a complex phylogeographic history; the evolutionary consequences of these processes should be monitored. At smaller geographical scales, substructuring was observed by a landscape genetics approach and was explained by variation in the landscape matrix. In addition, their resident status combined with their dependence on continuous woodland for dispersal and gene flow means that geographical distance through suitable habitat can impede movement between distant populations. Additional habitat fragmentation may isolate populations further which could result in negative evolutionary effects.

This work advances current approaches aimed at investigating the genetic structure of black-capped chickadees as it is the first time a landscape genetics approach was implemented in this species. By employing this method, we were the first to identify and explain cryptic patterns of genetic structure in a widespread and stable species with dispersal potential. We showed that not only are chickadees isolated by large physical barriers across their range, but also that gene flow is
restricted at small spatial scales in heterogeneous landscapes and can lead to significant population genetic differentiation. This study has therefore provided additional insight into how black-capped chickadees are influenced by their environment, and in doing so, has opened the door to a multitude of questions concerning gene flow in different landscapes, but also how future environment change may impact not only black-capped chickadees, but other species with similar life history characteristics.
5.4 References


Hindley, J.A. (2013) Post-Pleistocene dispersal in black-capped (Poecile atricapillus) and mountain (P. gambeli) chickadees, and the effect of social dominance on black-capped chickadee winter resource allocation. PhD, University of Lethbridge.


Figure 5.1. Simplified diagram illustrating the process of habitat fragmentation of a single habitat patch (suitable habitat = green; removed habitat = white). Modified from Fahrig, (2003).
Figure 5.2. Simplified model illustrating the steps necessary to carry out a landscape genetics study.
APPENDIX 1: Supplementary Information for Chapter 2

Influence of ecological and geological features on rangewide patterns of genetic structure in a widespread passerine
Appendix 1.1. Details of black-capped chickadee samples used in analyses. Sources include Burg lab (wild), Smithsonian Museum (USNM); Queen’s University Biological Station (QUBS); CWS Saskatoon (CWS); University of Northern British Columbia (UNBC); North Carolina Museum of Natural Sciences (NCM), University of Michigan (UMICH), Field Museum of Chicago (FMC) and the Museum of Southwestern Biology at the University of New Mexico (MSB).

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<td>47.536</td>
<td>122.263</td>
<td>Wild</td>
<td>2540-23017</td>
</tr>
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<td>47.536</td>
<td>122.263</td>
<td>Wild</td>
<td>2540-23018</td>
</tr>
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Appendix 1.2. Repeat type (if known), primer sequence, allele size range (bp), number of alleles ($N_a$) and MgCl$_2$ concentration for each microsatellite locus used to genotype black-capped chickadee individuals.

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<tr>
<th>Locus</th>
<th>Repeat type</th>
<th>Sequence (5’ to 3’)</th>
<th>Size range (bp)</th>
<th>$N_a$</th>
<th>MgCl$_2$ (mM)</th>
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<tr>
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<td>322-488</td>
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<td>Martinez et al., 1999</td>
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Appendix 1.3. Log likelihood plots (LnPr(X|K)) over K for each STRUCTURE run as shown in Figure 2. Runs involving only two populations (Figures 2b and 2i) could not be plotted. For each plot, Delta $K$ was also provided. The most likely number of populations $K$ is determined by the highest estimated log probability of the data and delta $K$ infers the correct number of clusters from the difference of LnPr(X|K).
Appendix 1.4. Plot of DIC averaged over 10 runs for each $K_{\text{MAX}}$ (2 – 13) following 50,000 burn in sweeps and 100,000 McMC sweeps, under the CAR model and $\psi$ 0.6, conducted in the program TESS v.2.3.
Appendix 1.5. Clusters as determined by TESS v2.3.
Appendix 1.6. Pairwise $F_{ST}$ values (below diagonal) and harmonic mean estimates of $D_{EST}$ (above diagonal) for 31 black-capped chickadee populations based on eleven microsatellite loci. Values in bold indicate significant pairwise $F_{ST}$ comparisons after FDR correction ($\alpha = 0.008$). Populations with $n < 5$ were removed from the analysis.
Appendix 1.7. Pairwise $F_{ST}$ values for 31 black-capped chickadee populations based on eleven microsatellite loci. Populations with $n < 5$ were removed from the analyses.

|       | AKA | AKF | AKW | NWBC | NBC | FSM1 | PG | BCR | CAB | LETH | SAR1 | SAR2 | MB | SK | WA | SOHR | NEOR | CID | ID | MT | SD | UT | CD | NM | IL | MI | MO | ON | NSNB | WV | NL |
|-------|-----|-----|-----|------|-----|------|----|-----|-----|------|------|------|----|----|----|------|------|-----|----|----|----|----|-----|----|----|----|----|------|----|----|
| AKA   | 0.00 |     |     |      |     |      |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| AKF   | 0.014| 0.00 |     |      |     |      |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| AKW   | 0.01 | 0.00 | 0.00 |      |     |      |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| NWBC  | 0.18 | 0.16 | 0.20 | 0.00 |     |      |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| NBC   | 0.18 | 0.16 | 0.20 | 0.00 | 0.00 |      |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| FSM1  | 0.32 | 0.29 | 0.30 | 0.37 | 0.35 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| PG    | 0.87 | 0.83 | 0.73 | 0.81 | 0.77 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| BCR   | 0.23 | 0.23 | 0.23 | 0.23 | 0.23 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| CAB   | 0.21 | 0.18 | 0.23 | 0.08 | 0.24 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| LETH  | 0.19 | 0.17 | 0.19 | 0.19 | 0.19 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| SAR1  | 0.23 | 0.19 | 0.25 | 0.07 | 0.34 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| SAR2  | 0.15 | 0.06 | 0.31 | 0.14 | 0.29 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| MB    | 0.28 | 0.28 | 0.30 | 0.06 | 0.06 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| SK    | 0.25 | 0.18 | 0.22 | 0.06 | 0.14 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| WA    | 0.31 | 0.29 | 0.28 | 0.28 | 0.28 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| SOHR  | 0.19 | 0.11 | 0.16 | 0.04 | 0.16 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| NEOR  | 0.16 | 0.08 | 0.10 | 0.02 | 0.10 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| CID   | 0.25 | 0.22 | 0.25 | 0.11 | 0.10 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| ID    | 0.24 | 0.21 | 0.27 | 0.07 | 0.08 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| MT    | 0.23 | 0.20 | 0.23 | 0.01 | 0.01 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| SD    | 0.17 | 0.17 | 0.17 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| UT    | 0.17 | 0.17 | 0.17 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| CO    | 0.15 | 0.15 | 0.15 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| NM    | 0.19 | 0.19 | 0.19 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| IL    | 0.15 | 0.15 | 0.15 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| MO    | 0.24 | 0.24 | 0.24 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| ON    | 0.24 | 0.24 | 0.24 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| NSNB  | 0.23 | 0.23 | 0.23 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| WV    | 0.22 | 0.22 | 0.22 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |
| NL    | 0.21 | 0.21 | 0.21 | 0.00 | 0.00 | 0.00 |    |     |     |      |      |      |    |    |    |      |      |     |    |    |    |    |     |    |    |    |    |      |    |    |

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Appendix 1.8. Summary of population genetic structure of the black-capped chickadee from previous studies. Hindley (2013) revealed five genetic groups (depicted by squares) using mtDNA data; Alaska (AK), Newfoundland (NL), Pacific (WA, SOR), SE Rockies (MT, UT, CO) and a main group. The main group includes populations northwest BC, southeast BC, northeast Oregon, coastal Oregon, Idaho, Alberta (incl. SAB1, SAB2, LETH and CAB), Saskatchewan, Manitoba, Missouri, Illinois, Michigan, Ontario, West Virginia, North Carolina, Nova Scotia/ New Brunswick and Labrador (represented by the black dots). Pravosudov et al., (2012) detected four genetic groups (depicted by circles) using AFLP markers; Alaska (AK), Washington (WA), and Interior group (BC, MT), and an Eastern group (MN, KS, IA, ME, CO).
APPENDIX 2: Supplementary Information for Chapter 3

Influence of landscape features on the microgeographic genetic structure of a
resident songbird
Appendix 2.1. Details of black-capped chickadee sampled. Sample IDs in grey were removed from analyses. Sources include Burg lab (wild), and University of Northern British Columbia (UNBC).

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<th>Long (°W)</th>
<th>Source</th>
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Appendix 2.2. Repeat type (if known), primer sequence, allele size range (bp), number of alleles (Na) and MgCl₂ concentration for each microsatellite locus used to genotype black-capped chickadee individuals. *indicates new primer designed during this study.

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Appendix 2.3. (a) Log likelihood plots (LnPr(X|K)) for STRUCTURE runs. Runs involving only two populations (Figure 3.1b) could not be plotted. (b) Delta $K$ was also provided.
Appendix 2.4. GENELAND output including the modal number of clusters ($K = 9$), map of population membership, and map boundaries for each of the nine clusters inferred.
Appendix 2.5. Pairwise $F'_{ST}$ values for 15 black-capped chickadee populations based on 14 microsatellite loci with significant values in bold ($P \leq 0.05$). Populations with $N \leq 5$ were removed from the analyses.

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Appendix 2.6. Hierarchical analysis of molecular variance showing the percentage of variation for each of the three levels (among groups, among populations within groups and within populations) and across different group combinations. Groups that included > 1 population are separated by “&” and the number of groups for each test are provided (# groups).

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<th>Among Groups</th>
<th>Among populations within groups</th>
<th>Within populations</th>
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Appendix 2.7. Maps showing the resistance grid output from CIRCUITSCAPE analyses for the resistance surfaces (a) elevation and (b) land cover.
APPENDIX 3: Supplementary Information for Chapter 4

Gene flow of a forest-dependent bird across a fragmented landscape
## Appendix 3.1. Details of black-capped chickadee samples used in analyses. Sample ID’s in grey were removed from analyses.

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### Appendix 3.2.

Repeat type (if known), primer sequence, allele size range (bp), number of alleles ($N_a$) and MgCl$_2$ concentration for each microsatellite locus used to genotype black-capped chickadee individuals.

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<th>Size range (bp)</th>
<th>$N_a$</th>
<th>MgCl$_2$ (mM)</th>
<th>Reference</th>
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Appendix 3.3. Hierarchical analysis of molecular variance showing the percentage of variation for each of the three levels (among groups, among populations within groups and within populations) and across different group combinations.

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<th>Grouped populations</th>
<th>Among Groups</th>
<th>Among populations within groups</th>
<th>Within populations</th>
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Appendix 3.4. Delta $K$ ($\Delta K$) and log likelihood ($\text{LnPr}(X|K)$) plots for STRUCTURE runs as shown in Figure 4.3. The most likely number of populations $K$ is determined by the highest estimated log probability of the data and delta $K$ infers the correct number of clusters from the difference of $\text{LnPr}(X|K)$. 
**Appendix 3.5.** AIC evaluation of all possible model combinations given the landscape variables available for 15 populations (above dashed line) and 12 populations within hybrid poplar zones (below dashed line). Results include AICc = corrected Akaike’s Information Criterion, Δi = differences in AICc values, wi = AICc weights. Bold values indicate the best models based on AIC.

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