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

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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.

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LIST OF ABBREVIATIONS, ACRONYMS AND SYMBOLS

AFLP	Amplified Fragment Length Polymorphism
AIC	Akaike's Information Criterion
AIC_c	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	*g*enetic 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
$MgCl^2$	magnesium chloride
min	minutes
mtDNA	mitochondrial DNA
N	number of samples
Na	number of alleles
NSERC	Natural Sciences of Engineering Research Council of Canada
^oC	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
R^2	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
w_i	weighted AIC_c
µg	microgram
µl	microlitre
µM	micromolar
α	alpha
Δ_i	AIC_c 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

CoOR	Coastal Oregon
Ft.St.J	Fort St. James
ID	Idaho
IL	Illinois
LAB	Labrador
LETH	Lethbridge
MB	Manitoba
MI	Michigan
MO	Missouri
MT	Montana
NBC	Northern British Columbia
NC	North Carolina
NEOR	North East Oregon
NL	Newfoundland
NM	New Mexico
NSNB	Nova Scotia New Brunswick
NWBC	North West British Columbia
ON	Ontario
PG	Prince George
SAB1	Southern Alberta 1
SAB2	Southern Alberta 2
SD	South Dakota
SK	Saskatchewan
SOR	Southern Oregon
UT	Utah
WA	Washington
WV	West Virginia

Chapter 3

CLU	Cluculz Lake
FF	Fort Fraser
FrL	Francois Lake
FtStJ1	John Prince Research Station (Fort St. James)
FtStJ2	Fort St James town
HAZ	Hazelton
HOU	Houston
KEL	Kelowna
VAN	Vancouver

Chapter 4

BL	Blue Trail Park
BO	Bow River
BUF	Buffalo
BUC	Buck Lake
CR	Crowsnest River (Lundbreck)
DR	Drumheller
DY	Drywood Creek

ED	Edson
EM	Emerson Bridge
FK	The Forks
FO	Fort Macleod
GL	Glenwood
HI	Hinton
IN	Innisfail
JE	Jenner
LE	Lethbridge
NSK	North Saskatchewan River (Edmonton)
OL	Olds
OM	Oldman Dam
RD1	Red Deer 1
RD2	Red Deer 2
SB1	Southern Alberta 1
SB2	Southern Alberta 2
SSK	Southern Saskatchewan River (Medicine Hat)
StM	St. Mary River
TA	Taber
WH	Whistler Campground
WO	Woolford Provincial Park

Museums

CWS	Canadian Wildlife Service (Saskatoon)
FMC	Field Museum of Chicago
MSB	Museum of Southwestern Biology
NCM	North Carolina Museum of Natural Sciences
QUBS	Queen’s University Biological Station
UMICH	University of Michigan
UNBC	University of British Columbia
USNM	Smithsonian Museum

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. In

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. gambeli*), 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.

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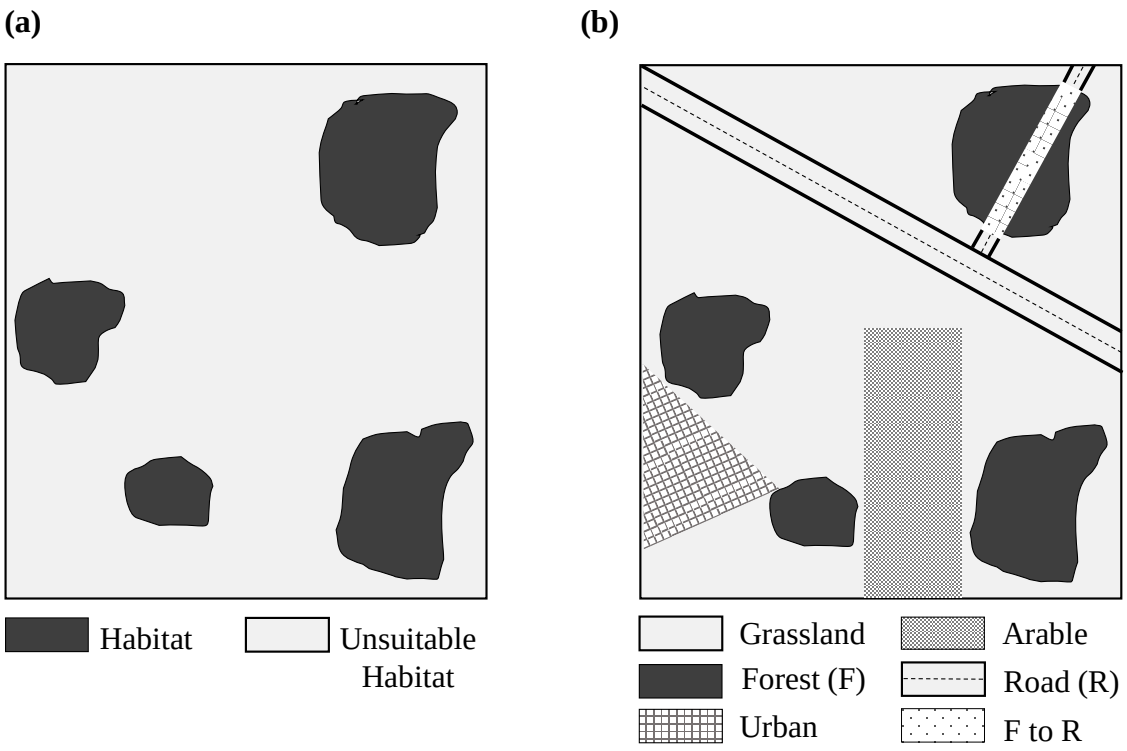

Figure 1.1. Two representations of the same landscape used to assess structural connectivity in a) classical population genetics and b) landscape genetics studies (modified from Holderegger and Wagner, 2008). In classical population genetics, the movement of individuals between populations and the rate 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.

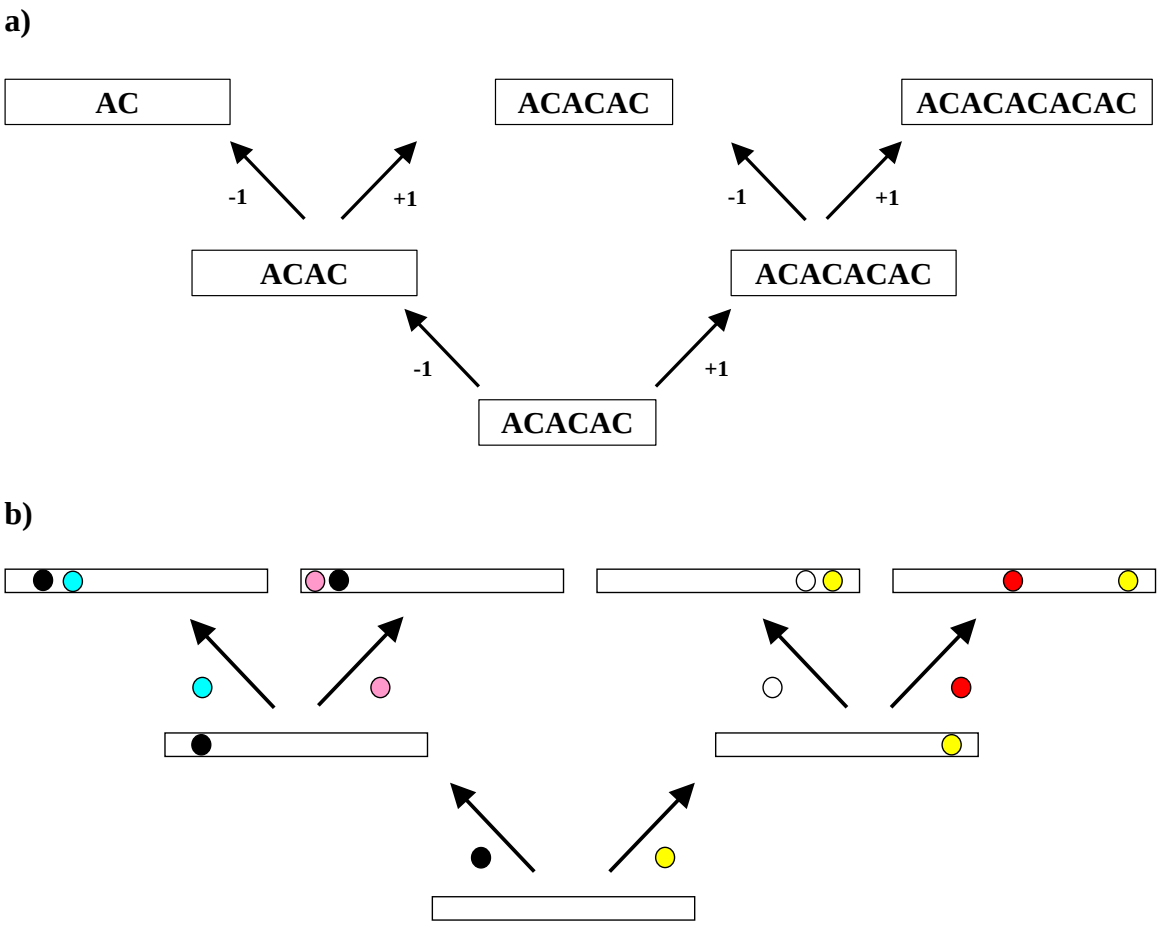

Figure 1.2. Simplified diagrams of two mutation models representing microsatellite marker evolution (modified from Walsh, 2001). The Stepwise Mutation Model (a) where each mutation results in an addition (+) or deletion (-) of a single repeat (AC) and the infinite alleles model (b) where every mutation leads to a new allele (represented by a coloured circle).

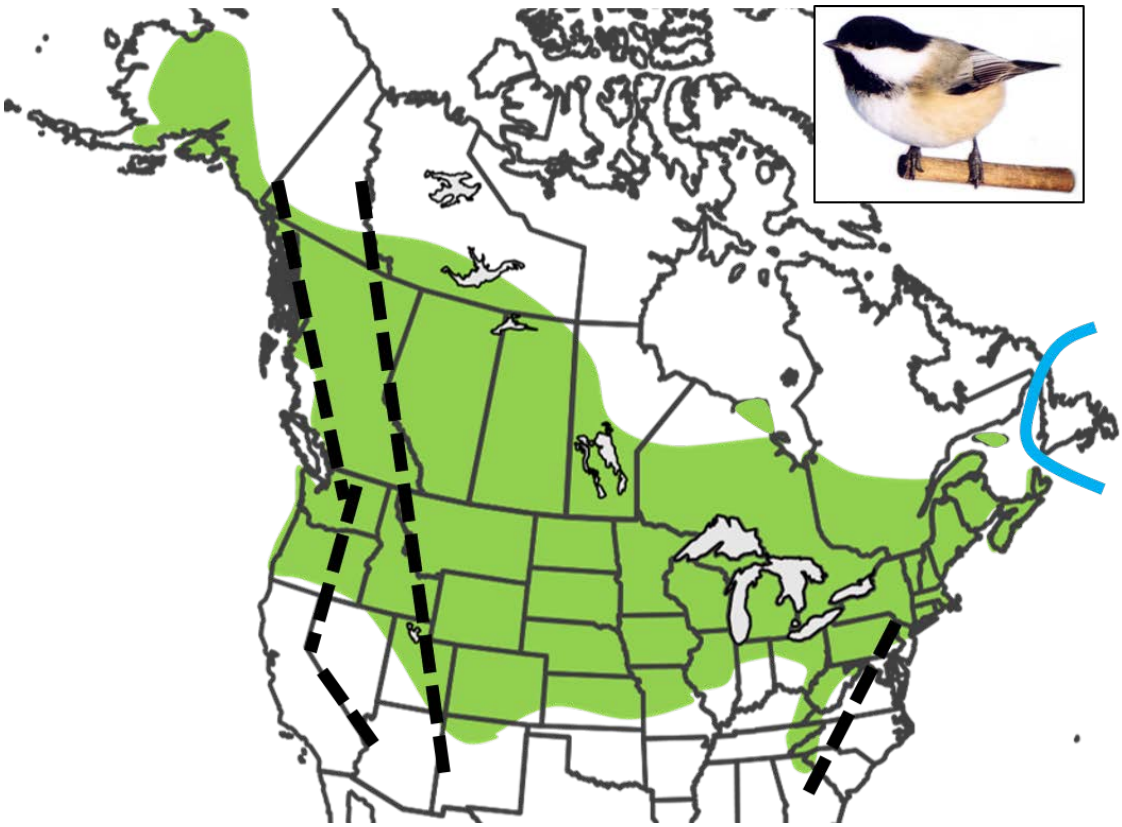

Figure 1.3. Map representing the range distribution (shaded green) of the black-capped chickadee (inset) modified from Smith (1991). Included in the map are putative physical barriers to gene flow. From west to east, black dashed lines represent the Coastal (top left), Cascades (middle left) and Sierra 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 Confromal 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

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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^{o}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), Gf06 (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 $MgCl_2$ (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^{o}C for 2 min, 50^{o}C for 45 sec and 72^{o}C for 1 min, followed by 7 cycles of 94^{o}C for 1 min, 50^{o}C for 30 sec and 72^{o}C for 45 sec, followed by 25 cycles of 94^{o}C for 30 sec, 52^{o}C for 30 sec and 72^{o}C for 45 sec, followed by a final extension step of 72^{o}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* (ΔK; 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_{MAX} = 34. BAPS searches for all values of *K* up to the value given for K_{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_{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_{MAX} with an interaction parameter (Ψ; 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_{MAX}) and lowest DIC. We also averaged DIC over all ten runs for each value of K_{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 2.5×10^5, 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 ($P \leq 0.001$; ≤ 0.001 respectively); between Escu6 and Titgata02 and Escu6 and Ppi2 within SAB1 ($P \leq 0.001$; ≤ 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.

2.4.2 Bayesian clustering analyses

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 (Pr(X|K) = -34930) and ΔK, 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 (Pr(X|K) = -3034; Figure 2.2b). The 'main' cluster produced three clusters: western, central and eastern (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; Pr(X|K) = -14136), Pacific (WA, SOR, CoOR; Pr(X|K) = -8710), Northwest Rockies (NWBC and BCR; Pr(X|K) = -6614); Idaho (CID and ID) in the Intermountain West and finally NEOR Pr(X|K) = -2383). The central group subdivided into three clusters: eastern Rockies (MT, SD and UT; Pr(X|K) = -4041), CO and NM (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_{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_{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_{EST} which ranged from 0.030 to 0.316 (Appendix 1.6). Pairwise D_{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.

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.

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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).

Location	Site	Lat (°N)	Long (°W)	*N*	*Ho*	*He*	PA	AR
Alaska Anchorage	AKA	61.4249	149.2035	32	0.60	0.61	0	5.26
Alaska Fairbanks	AKF	64.2072	147.2111	32	0.63	0.64	0	5.35
Alaska Wrangell	AKW	61.8039	145.0931	20	0.61	0.58	0	-
Revelstoke	BCR	50.9807	118.1817	54	0.67	0.70	0	6.69
Northern British Columbia	NBC	54.8883	127.7665	43	0.65	0.70	1	7.01
Fort St. James	Ft.St.J	54.6453	124.3946	61	0.69	0.72	4	7.12
Prince George	PG	53.8936	122.8289	30	0.52	0.60	5	-
Northwest British Columbia	NWBC	58.3003	130.6677	17	0.66	0.71	2	6.67
Central Alberta	CAB	53.2981	115.1566	30	0.70	0.72	0	-
Lethbridge	LETH	49.6939	112.8625	19	0.67	0.67	1	6.64
Southern Alberta 1	SAB1	49.3450	114.4153	30	0.70	0.68	1	6.54
Southern Alberta 2	SAB2	49.0694	113.8561	22	0.63	0.70	0	6.01
Saskatchewan	SK	53.8749	106.1137	33	0.66	0.70	1	6.79
Manitoba	MB	50.2898	98.2522	11	0.67	0.70	1	6.73
Washington	WA	47.3096	121.8213	27	0.68	0.68	2	5.47
Coastal Oregon	CoOR	44.6326	123.9205	2	0.73	0.50	0	-
Northeast Oregon	NEOR	45.2441	118.0606	15	0.64	0.62	0	-
Southern Oregon	SOR	42.2981	122.7940	15	0.71	0.69	0	-
Central Idaho	CID	44.9291	116.1540	21	0.65	0.66	0	6.41
Idaho	ID	47.5010	116.7914	30	0.70	0.71	0	6.89
Montana	MT	46.0765	111.5521	29	0.71	0.70	0	5.93
South Dakota	SD	43.8065	103.4944	17	0.70	0.69	0	5.71
New Mexico	NM	35.7104	105.8804	11	0.71	0.70	2	-
Colorado	CO	40.1711	105.3413	21	0.71	0.67	1	5.61
Utah	UT	41.3436	111.2951	30	0.67	0.65	2	6.11
Illinois	IL	41.3588	88.4561	14	0.60	0.64	2	-
Michigan	MI	44.7404	85.8333	34	0.69	0.73	1	6.98
Missouri	MO	38.9053	91.9269	11	0.68	0.70	1	-
Ontario	ON	44.5666	76.3167	33	0.71	0.72	2	8
Nova Scotia/New Brunswick	NSNB	46.2215	64.0937	111	0.62	0.56	10	7.5
Labrador	LAB	53.3292	60.3700	5	0.69	0.73	1	-
North Carolina	NC	35.5164	81.1243	5	0.62	0.39	0	-
West Virginia	WV	37.5237	80.8948	13	0.72	0.69	0	-
Newfoundland	NL	49.9483	56.2473	35	0.61	0.66	2	5.76

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)

Factors	Posterior Probabilities
Constant	**0.527**
Constant, Elevation	0.473
Constant	**0.521**
Constant, Annual mean temperature	0.479
Constant	**0.526**
Constant, Precipitation	0.474
Constant	**0.531**
Constant, Latitude	0.469
Constant	**0.528**
Constant, Longitude	0.472
Constant	**0.519**
Constant, Distance to unsuitable habitat	0.481

b)

Spatial Scenario	Factors	Posterior Probabilities
i)		
	Latitude	0.155
	Longitude	0.154
	Latitude*Longitude	0.678
ii)		
	Constant	0.086
	Constant, Latitude	0.083
	Constant, Longitude	0.081
	Constant, Latitude, Longitude	0.072
	Constant, Latitude, Longitude, Latitude*Longitude	**0.678**

Climatic Scenario	Factors	Posterior Probabilities
i)	Annual mean temperature	0.385
	Precipitation	0.388
	Annual mean temperature*Precipitation	0.195
ii)		
	Constant	**0.216**
	Constant, Annual Mean Temperature	0.201
	Constant, Precipitation	0.204
	Constant, Annual Mean Temperature, Precipitation	0.184
	Constant, Annual Mean Temperature, Precipitation, Annual Mean Temperature*Precipitation	0.195

Geographic Scenario	Factors	Posterior Probabilities

i)		
	Elevation	0.384
	Distance to unsuitable habitat	0.376
	Elevation*Distance to unsuitable habitat	0.212
ii)		
	Constant	**0.214**
	Constant, Elevation	0.197
	Constant, Distance to unsuitable habitat	0.190
	Constant, Elevation, Distance to unsuitable habitat	0.186
	Constant, Elevation, Distance to unsuitable habitat, Elevation*Distance to unsuitable habitat	0.212

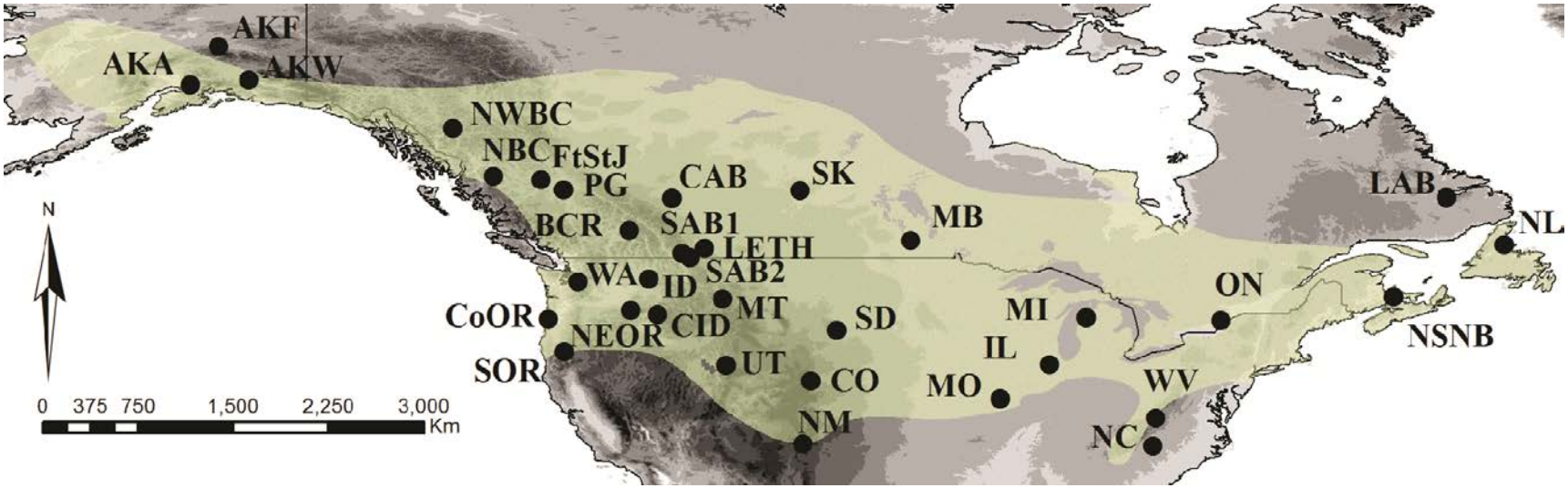

Figure 2.1. Map illustrating the current geographical distribution of the black-capped chickadee (*Poecile atricapillus*) across North America with sampling locations (See Table 2.1 for abbreviations) projected in ArcGIS® v.10.

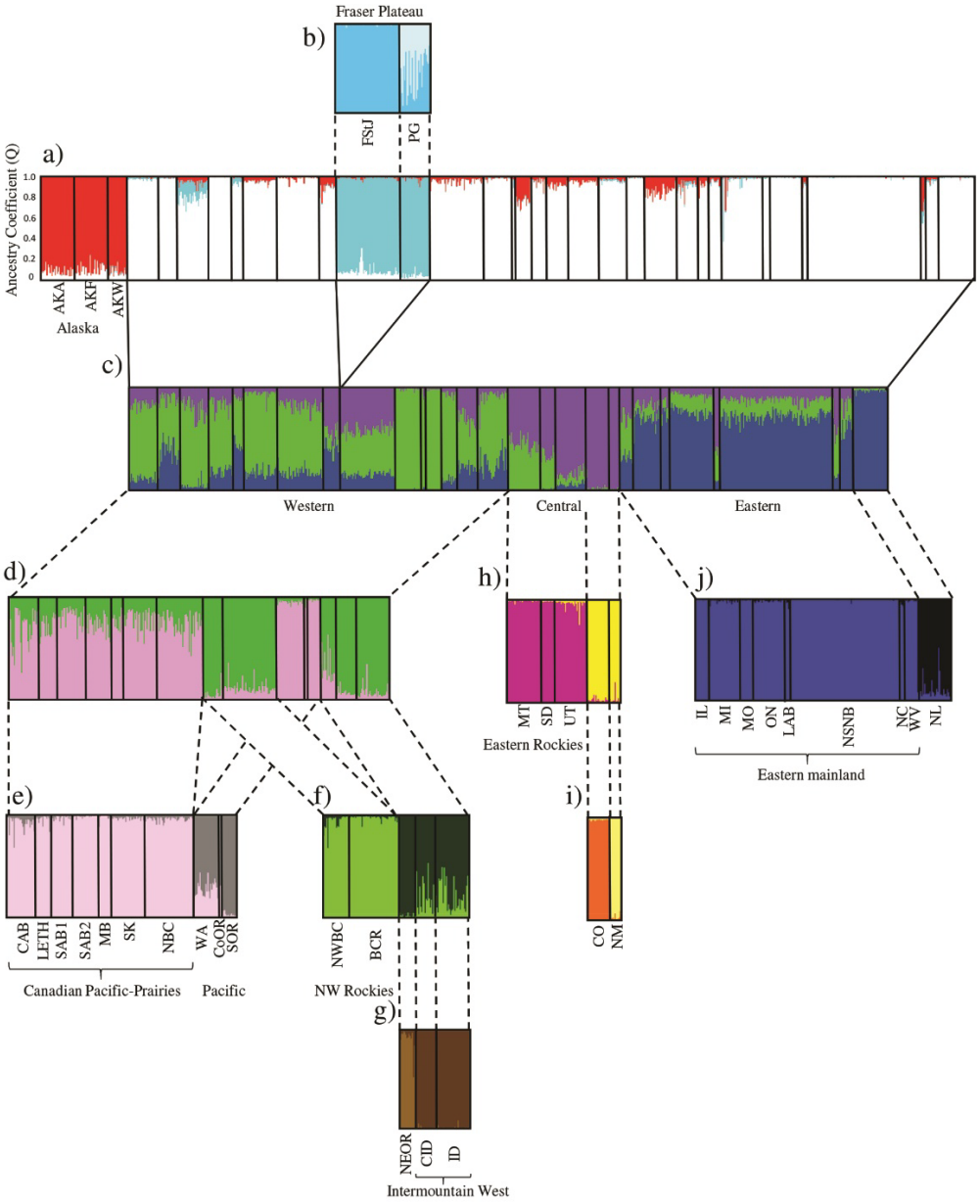

Figure 2.2. Inferred population structure of the black-capped chickadee (*Poecile atricapillus*) from eleven microsatellite loci using STRUCTURE v2.3.4 (Pritchard *et al.*, 2000) for (a) $K = 3$; all individuals from 34 populations, (b) $K = 2$; Fraser Plateau (Ft.St.J and PG), (c) $K = 3$ after removing 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.

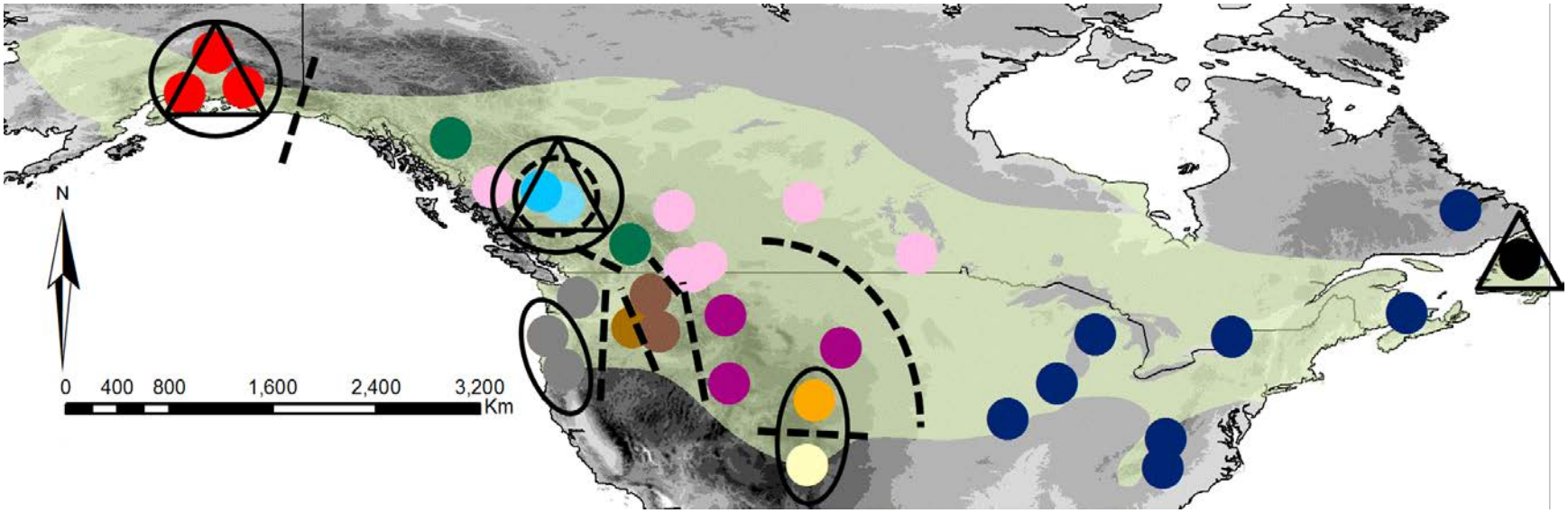

Figure 2.3. Distribution map illustrating coloured population assignment as inferred from STRUCTURE v2.3.4 for all black-capped chickadee individuals based on eleven microsatellite loci. Also included are the five genetic clusters found using BAPS v5.4 (solid circles; the fifth cluster includes the remaining 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).

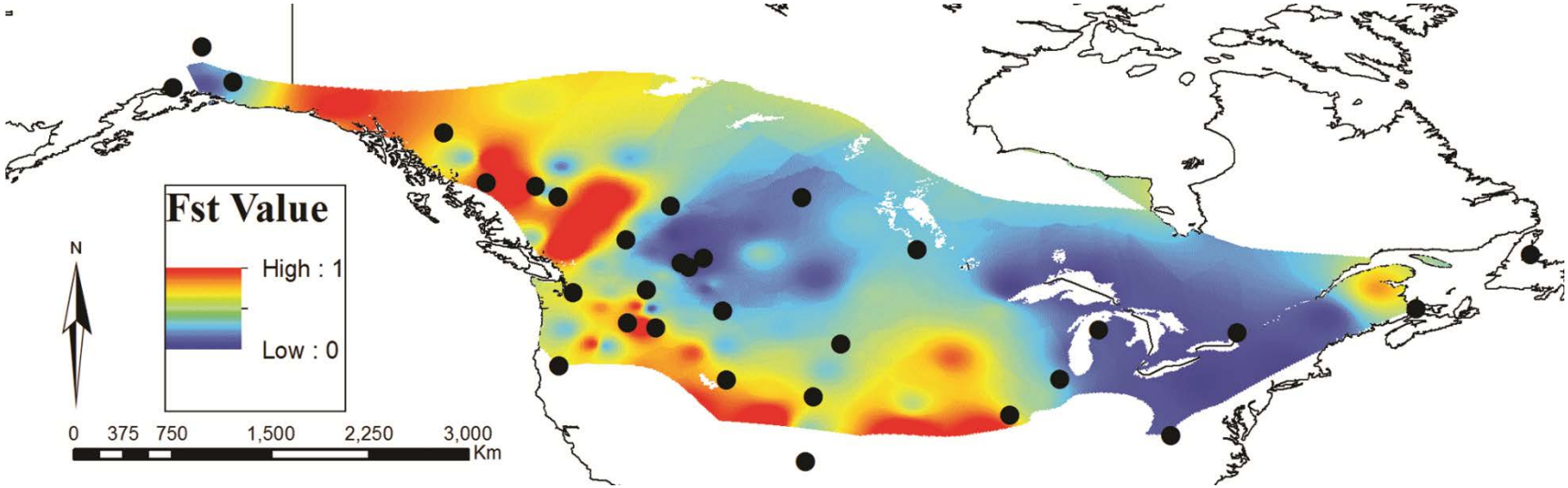

Figure 2.4. A heat map of pairwise F_{ST} values for eleven microsatellite loci in the black-capped chickadee. Red indicates high F_{ST} values and blue, low F_{ST} values. Each sampling site is represented by a black dot (see Figure 2.1 for location names).

CHAPTER 3

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

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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.*,

2011). 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^{o}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 ≤ 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 GenAlEx 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* (ΔK; 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 (AIC_c) and the best model is the one with the lowest value. To compare models, differences between AIC_c values were calculated for each model:

$$\Delta_i = AIC_c - \min AIC_c$$

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:

$$w_i = {}_{EXP}(-0.5 * \Delta_i) / \Sigma ({}_{EXP}(-0.5 * \Delta_i))$$

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 ΔK (Appendix 2.3). ΔK 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 AIC_c, 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 (AIC_c = -227.2) with additional support for the model including all three: land cover, elevation and geographic distance (Δ_i = 1.8). For D_{EST},

the best model included land cover x elevation (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 (Δ_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.

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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}).

Location	Abbrev.	Lat (°N)	Long (°W)	*N*	PA	AR	F_{IS}
Revelstoke	BCR	50.9807	118.1817	54	4	2.66	0.084
Northern BC	NBC	54.8883	127.7665	43	5	2.68	0.072
Cluculz Lake	CLU	53.9102	123.5496	20	4	2.70	0.074
Fort Fraser	FF	53.9629	124.5331	11	0	2.79	0.071
Francois Lake	FrL	54.0488	125.6988	20	1	2.64	0.081
Fort St. James Town	FtStJ2	54.4183	124.2743	18	0	2.69	0.118
Hazelton	HAZ	55.2829	128.0470	20	1	2.66	0.079
Houston	HOU	54.4043	126.6433	18	1	2.72	0.056
Kelowna	KEL	49.9200	119.3950	8	0	-	0.116
North West BC	NWBC	58.3003	130.6677	17	2	2.63	0.055
Vancouver	VAN	49.2644	123.0816	33	0	-	-0.030
John Prince Research Station	FtStJ1	54.6453	124.3949	61	11	2.79	0.089
Prince George	PG	53.8936	122.8289	30	1	2.42	0.083
Southern Alberta 1	SAB1	49.3455	114.4153	30	3	2.60	-0.003
Southern Alberta 2	SAB2	49.0694	113.8561	22	5	2.71	0.037

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.

	Locus	**PAT MP-14**	**Titgata 39**	**Escu6**	**Titgata 02**	**PAT MP-43**	**Ase18**	**Pman TAG An71**	**Cuμ28**	**Ppi2**	**Pman TAG An45**	**CcaTgu 11**	**VeCr 05**	**CtC-101**	**Pij02**	**Pop. mean across all loci**
BCR	***Na***	12	9	16	14	14	6	8	3	24	20	3	3	9	17	11
	Ho	0.600	0.593	0.852	0.774	0.769	0.370	0.759	0.566	**0.745**	0.900	0.389	0.184	0.887	0.744	0.652
	He	0.647	0.691	0.911	0.854	0.856	0.338	0.782	0.496	**0.932**	0.900	0.494	0.329	0.804	0.876	0.708
NBC	***Na***	11	7	19	14	17	6	8	3	23	16	3	2	8	19	11
	Ho	0.711	0.744	0.833	0.814	0.907	0.256	0.674	0.372	0.757	0.762	0.286	0.200	0.907	0.829	0.647
	He	0.658	0.742	0.916	0.852	0.906	0.234	0.751	0.543	0.839	0.843	0.431	0.224	0.844	0.882	0.690
CLU	***Na***	7	7	16	11	13	3	6	3	16	16	3	2	9	16	9
	Ho	0.750	0.800	1.000	0.800	0.950	0.250	0.700	0.421	0.750	**0.579**	0.250	0.350	0.850	0.700	0.654
	He	0.685	0.765	0.901	0.865	0.864	0.226	0.715	0.445	0.807	**0.896**	0.501	0.439	0.838	0.900	0.703
FF	***Na***	5	6	10	10	9	2	5	3	8	-	2	2	8	13	6
	Ho	0.556	0.400	0.900	1.000	1.000	0.167	0.900	0.700	**0.333**	-	0.300	0.111	1.000	1.000	0.644
	He	0.673	0.690	0.875	0.883	0.846	0.153	0.700	0.565	**0.861**	-	0.455	0.278	0.850	0.914	0.672
FrL	***Na***	3	6	15	10	12	4	8	3	-	-	2	3	6	14	7
	Ho	0.500	0.800	**0.650**	0.900	0.950	0.450	0.800	0.400	-	-	0.200	0.278	0.750	0.786	0.622
	He	0.524	0.663	**0.891**	0.859	0.884	0.448	0.778	0.521	-	-	0.495	0.285	0.801	0.870	0.668
FtStJ2	***Na***	3	7	12	11	14	3	8	3	-	-	3	2	9	15	8
	Ho	0.176	0.706	0.706	1.000	0.889	0.333	0.765	0.778	-	-	0.500	0.000	0.833	0.786	0.623
	He	0.403	0.775	0.874	0.893	0.889	0.290	0.765	0.554	-	-	0.551	0.245	0.843	0.918	0.667
HAZ	***Na***	5	9	13	11	13	2	8	3	12	-	2	2	7	14	8
	Ho	0.500	0.950	0.750	0.950	1.000	0.050	0.650	0.400	**0.333**	-	0.600	0.316	0.750	0.833	0.622
	He	0.540	0.821	0.886	0.801	0.878	0.049	0.760	0.521	**0.907**	-	0.480	0.499	0.805	0.915	0.682

HOU	***Na***	8	6	15	10	14	3	7	2	11	-	2	1	10	15	8
	Ho	0.714	0.800	0.722	0.933	0.833	0.313	0.857	0.353	0.667	-	0.222	0.000	0.778	0.867	0.620
	He	0.804	0.691	0.907	0.873	0.887	0.275	0.827	0.457	0.833	-	0.346	0.000	0.880	0.880	0.666
KEL	***Na***	3	4	8	-	6	2	4	2	-	-	3	2	4	-	4
	Ho	0.571	0.667	0.857	-	0.857	0.167	0.750	0.200	-	-	0.750	0.400	0.625	-	0.584
	He	0.439	0.722	0.847	-	0.776	0.153	0.750	0.420	-	-	0.531	0.480	0.602	-	0.572
NWBC	***Na***	7	9	12	8	8	4	5	2	13	-	3	2	7	13	8
	Ho	0.824	0.824	0.824	0.882	0.706	0.294	0.765	0.353	0.563	-	0.588	**0.000**	0.824	0.882	0.658
	He	0.720	0.754	0.891	0.773	0.775	0.346	0.721	0.484	0.859	-	0.469	**0.291**	0.817	0.860	0.689
VAN	***Na***	5	3	13	-	8	4	6	3	-	-	4	2	8	-	6
	Ho	0.520	0.333	0.850	-	0.826	0.500	0.882	0.667	-	-	0.789	0.240	0.882	-	0.649
	He	0.460	0.573	0.889	-	0.792	0.400	0.787	0.571	-	-	0.609	0.365	0.804	-	0.625
FtStJ1	***Na***	16	8	18	14	17	6	8	3	26	16	4	2	10	22	12
	Ho	0.760	0.833	0.891	0.900	**0.733**	0.262	0.847	0.383	0.846	**0.647**	0.492	**0.138**	0.800	0.786	0.666
	He	0.741	0.759	0.912	0.875	**0.880**	0.266	0.781	0.458	0.896	**0.872**	0.511	**0.348**	0.817	0.923	0.717
PG	***Na***	11	7	17	11	14	5	6	3	2	5	3	2	9	9	7
	Ho	0.364	**0.607**	**0.583**	**0.478**	**0.481**	0.357	0.750	0.690	1.000	1.000	0.621	0.069	0.571	0.750	0.594
	He	0.748	**0.795**	**0.898**	**0.849**	**0.860**	0.528	0.633	0.499	0.500	0.750	0.499	0.238	0.815	0.750	0.669
SAB1	***Na***	10	6	20	11	13	2	7	3	9	15	2	2	10	19	9
	Ho	0.655	0.833	0.833	0.893	0.900	0.200	0.759	0.533	0.826	0.833	0.467	0.167	0.800	0.862	0.683
	He	0.640	0.686	0.902	0.839	0.882	0.180	0.727	0.455	0.813	0.877	0.464	0.299	0.851	0.861	0.677
SAB2	***Na***	7	8	16	10	13	3	8	3	16	12	3	2	11	14	9
	Ho	0.611	0.909	0.909	0.857	0.818	0.227	0.773	0.455	0.667	0.727	0.364	0.318	0.955	0.947	0.681
	He	0.702	0.791	0.912	0.815	0.863	0.241	0.778	0.538	0.909	0.819	0.501	0.268	0.874	0.892	0.707
Average for each loci	***Na***	8	7	15	10	12	4	7	3	11	8	3	2	8	13	
	Ho	0.587	0.720	0.811	0.745	0.841	0.280	0.775	0.485	0.499	0.422	0.454	0.185	0.814	0.718	
	He	0.626	0.728	0.894	0.735	0.856	0.275	0.750	0.502	0.610	0.456	0.489	0.306	0.816	0.763	

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.

	BCR	**NBC**	**CLU**	**FF**	**FrL**	**FtStJ2**	**HAZ**	**HOU**	**KEL**	**NWBC**	**VAN**	**FtStJ1**	**PG**	**SAB1**	**SAB2**
BCR	*	0.045	0.032	0.038	0.040	0.056	0.035	0.062	0.224	0.041	0.149	0.037	0.106	0.031	0.021
NBC	**0.014**	*	0.015	0.018	0.030	0.043	0.029	0.048	0.217	0.043	0.162	0.043	0.091	0.015	0.009
CLU	**0.017**	**0.020**	*	0.017	0.019	0.042	0.023	0.037	0.239	0.051	0.184	0.017	0.063	0.019	0.008
FF	**0.056**	0.054	0.058	*	0.034	0.039	0.010	0.011	0.218	0.070	0.190	0.020	0.096	0.026	0.010
FrL	**0.087**	**0.097**	0.097	0.130	*	0.048	0.040	0.052	0.202	0.070	0.167	0.049	0.098	0.030	0.024
FtStJ2	**0.088**	0.094	**0.100**	0.129	0.159	*	0.050	0.063	0.166	0.066	0.123	0.046	0.103	0.033	0.038
HAZ	**0.057**	**0.063**	0.058	0.094	**0.136**	**0.135**	*	0.044	0.202	0.052	0.157	0.029	0.094	0.039	0.018
HOU	**0.065**	**0.063**	**0.072**	0.096	**0.140**	**0.140**	**0.116**	*	0.279	0.059	0.211	0.046	0.102	0.048	0.021
KEL	**0.195**	**0.204**	**0.207**	**0.235**	**0.264**	0.253	**0.226**	**0.262**	*	0.243	0.168	0.240	0.329	0.243	0.222
NWBC	**0.018**	**0.019**	**0.025**	**0.065**	**0.101**	**0.099**	**0.069**	**0.067**	**0.212**	*	0.175	0.050	0.103	0.048	0.043
VAN	**0.172**	**0.183**	**0.189**	**0.217**	**0.246**	**0.234**	**0.218**	**0.234**	0.316	**0.188**	*	0.164	0.237	0.156	0.178
FtStJ1	**0.011**	**0.014**	**0.012**	0.053	**0.092**	**0.090**	**0.057**	**0.064**	**0.200**	**0.017**	**0.177**	*	0.091	0.013	0.025
PG	**0.035**	**0.033**	**0.034**	0.080	**0.118**	**0.121**	**0.087**	**0.081**	**0.237**	**0.036**	**0.211**	**0.031**	*	0.073	0.043
SAB1	**0.014**	**0.014**	**0.017**	0.055	**0.095**	**0.094**	**0.062**	**0.066**	**0.208**	**0.022**	**0.187**	**0.009**	**0.037**	*	0.005
SAB2	**0.013**	**0.013**	**0.019**	0.056	0.092	**0.094**	0.061	**0.065**	**0.201**	**0.021**	**0.183**	**0.013**	**0.030**	0.012	*

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 (AIC_c), differences in AIC_c values (Δ_i) and AIC_c weight (w_i) are provided for each model. Bold AIC_c values indicate the best model.

a)

Variable (controlled variable)	F_{ST}		D_{EST}	
	r	R^2	r	R^2
Distance through suitable habitat	0.414**	0.168	0.553**	0.306
Elevation	0.062	-0.004	0.283	0.129
Elevation (distance)	-0.352	-	-0.174	-
Elevation (land cover)	-0.280	-	0.217	-
Land cover	0.898**	0.806	0.826**	0.682
Land cover (distance)	0.879**	-	0.757**	-
Land cover (elevation)	0.906**	-	0.818**	-
Land cover x elevation	0.899**	0.809	0.827**	0.684
Land cover x elevation (distance)	0.881**	-	0.757**	-

b)

Model	F_{ST}			D_{EST}		
	AIC_c	Δ_i	w_i	AIC_c	Δ_i	w_i
Distance through suitable habitat	-114.2	113.0	0.00	-129.2	52.9	0.00
Elevation	-101.5	125.7	0.00	-111.0	71.1	0.00
Elevation + distance	-123.9	103.3	0.00	-130.7	51.4	0.00
Land cover	-223.9	3.3	0.08	-181.8	0.3	0.18
Land cover + distance	-223.8	3.4	0.08	-181.9	0.2	0.19
Land cover + elevation	**-227.2**	0.0	0.42	-181.4	0.7	0.15
Land cover + elevation + distance	-224.9	2.3	0.13	-179.7	2.4	0.06
Land cover x elevation	-224.8	2.4	0.13	**-182.1**	0.0	0.21
Land cover x elevation + distance	-225.4	1.8	0.17	-181.9	0.2	0.19

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.

a)

Factors	Posterior Probabilities
Constant	**0.913**
Constant, latitude	0.087
Constant	**0.936**
Constant, longitude	0.064
Constant	**0.924**
Constant, habitat fragmentation	0.076
Constant	**0.834**
Constant, annual max temperature	0.166
Constant	**0.812**
Constant, annual mean temperature	0.188
Constant	**0.813**
Constant, annual min temperature	0.187
Constant	**0.895**
Constant, summer mean precipitation	0.105
Constant	**0.813**
Constant, summer mean temperature	0.187
Constant	**0.920**
Constant, annual mean precipitation	0.080

b)

Factors	Sum of Posterior Probabilities
Latitude	0.197
Longitude	0.161
Habitat fragmentation	0.181
Annual max temperature	0.190
Annual mean temperature	0.218
Annual min temperature	0.209
Summer mean temperature	0.156
Annual mean precipitation	0.112
Summer mean precipitation	0.130

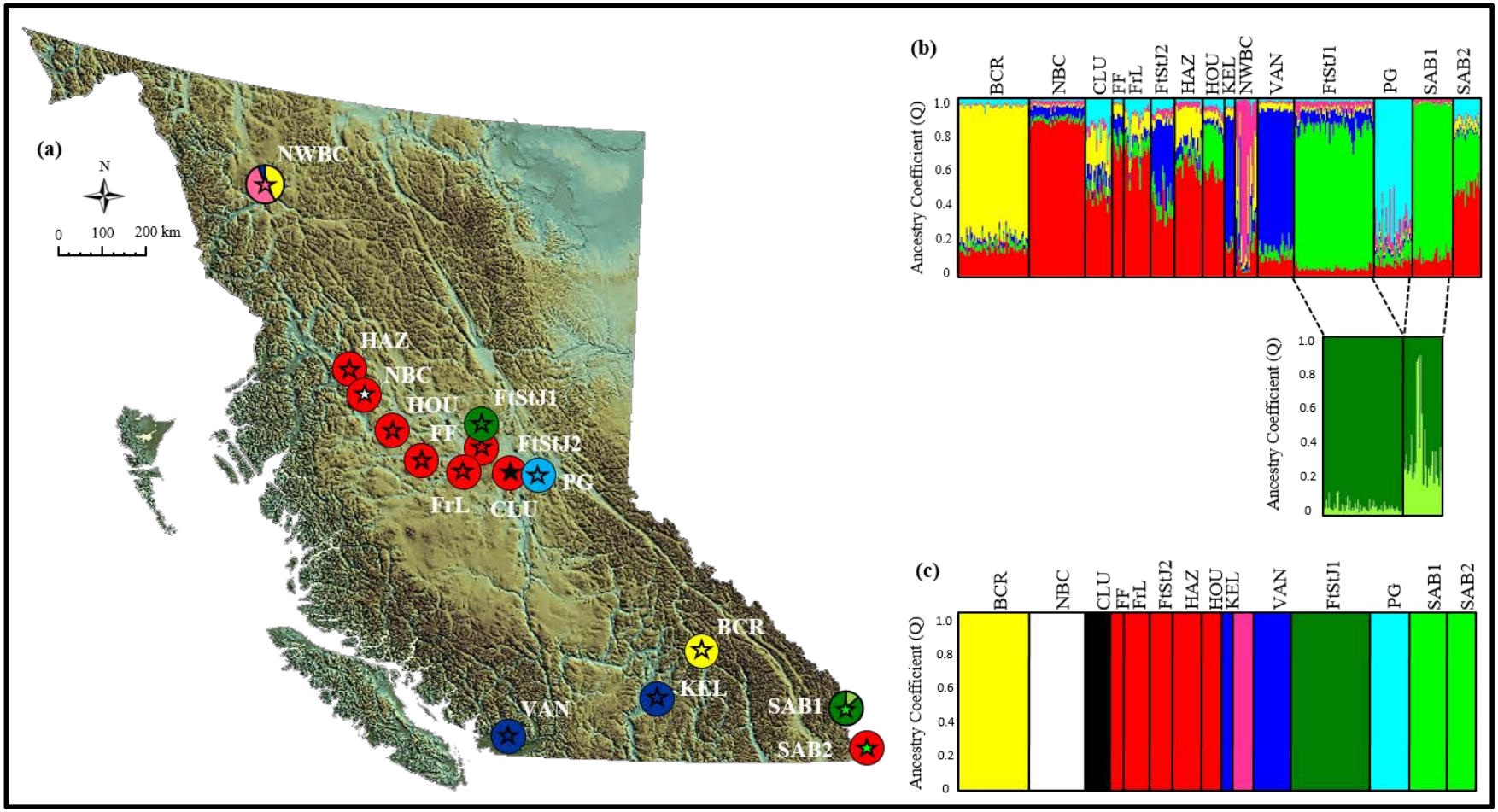

Figure 3.1. (a) Sampling locations of the black-capped chickadee (*Poecile atricapillus*) in British Columbia (See Table 3.1 for abbreviations) with inferred clusters from STRUCTURE $K = 6$ (pie charts) and GENELAND $K = 9$ (stars). STRUCTURE inferred 6 main genetic groups (b) with additional structure found for FtStJ1 and SAB1. GENELAND inferred nine genetic clusters (c).

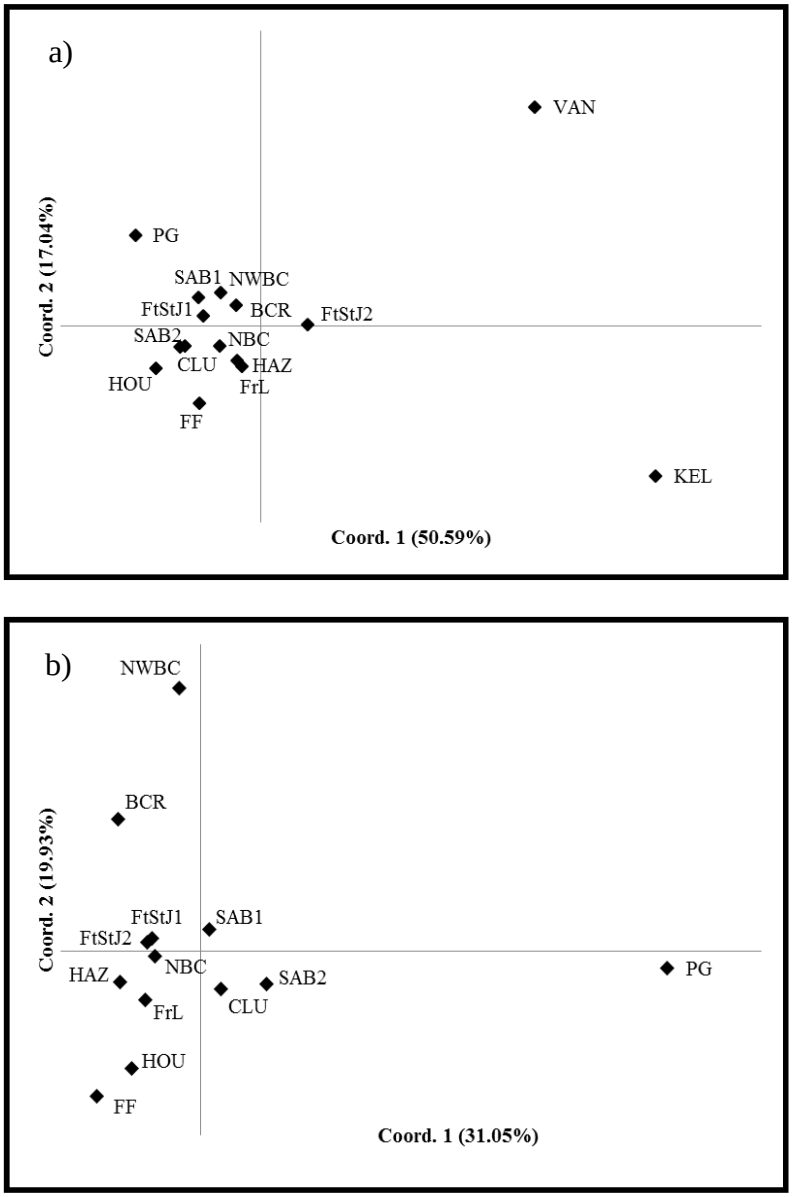

Figure 3.2. Principal coordinate analysis conducted in GenAlEx based on pairwise D_{EST} values for (a) all 15 populations (coordinates 1 and 2 explained 50.59% and 17.04% of the variation respectively) and (b) after removal of populations KEL and VAN (coordinates 1 and 2 explained 31.05% and 19.93% of the variation respectively).

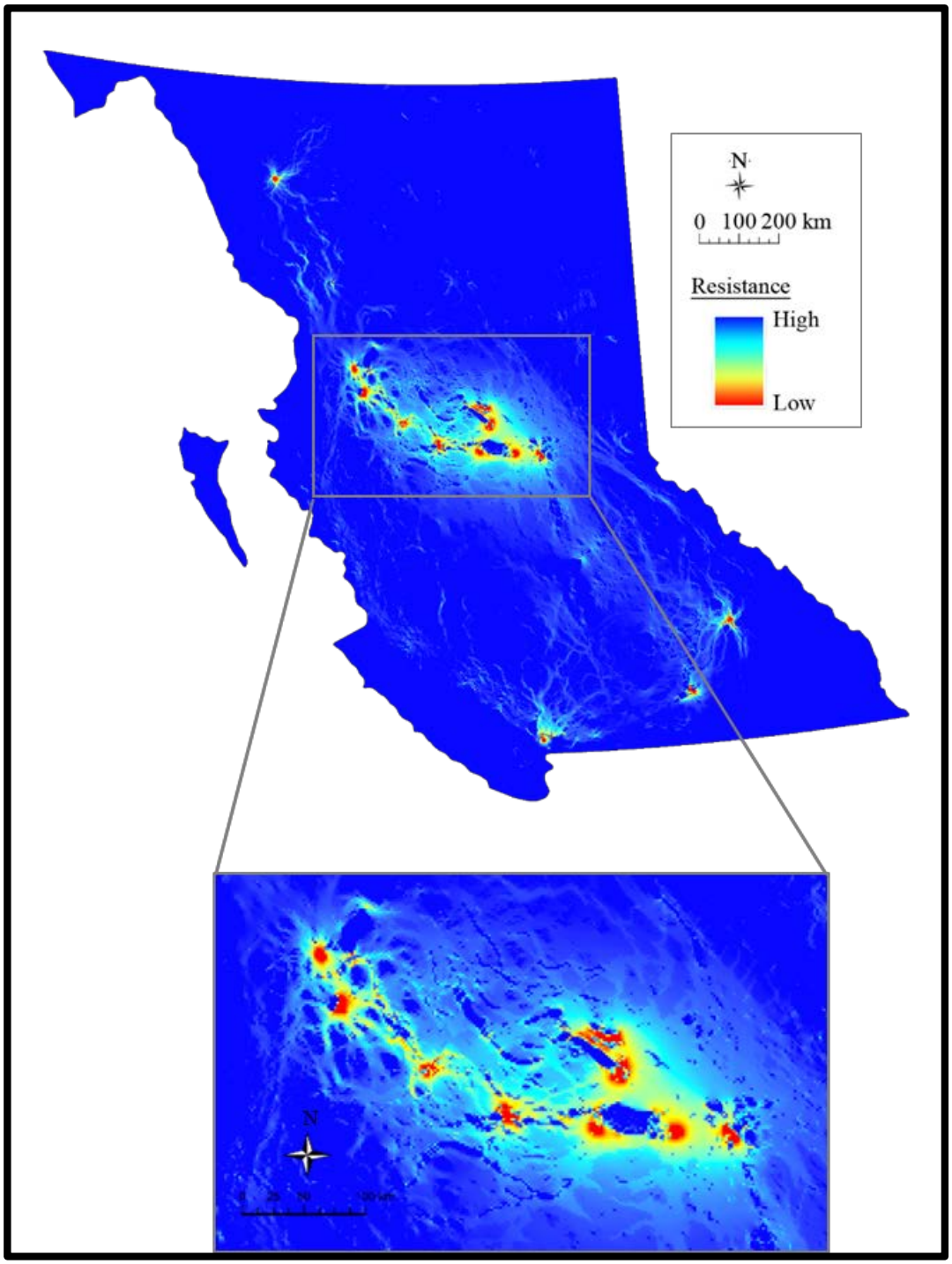

Figure 3.3. Map showing the resistance grid output from CIRCUITSCAPE analyses for the resistance surface including land cover and elevation combined (land cover x elevation) as this variable best explained genetic differentiation in other analyses. A close up of the central plateau region is included (bottom).

CHAPTER 4

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

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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; Phillipsen 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 ≤ 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 $\leq$ 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 ($N \leq 5$). 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 (≤ 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 (Δ_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* (ΔK) and mean log likelihood (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 ΔK ($K = 2$) 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 ΔK) 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 (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 (AIC_c = -359.1 (F_{ST}) and -280.5 (D_{EST})). Those that had the lowest 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 (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 Δ_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 distibutions 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.

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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_{IS}).

Pop.	Abbrev.	Associated river system	Lat (°N)	Long (°W)	*N*	PA	AR	F_{IS}
Whistler	WH	Athabasca River	52.8491	118.0797	1	0	-	-
Edson	ED	Athabasca River	53.6286	116.8019	1	0	-	-
Hinton	HI	Athabasca River	53.3936	117.5843	2	0	-	-
Buck Lake	BUC	North Saskatchewan River	52.9721	114.6046	7	2	4.18	-0.122
Edmonton	NSK	North Saskatchewan River	53.4974	113.5357	23	3	4.68	0.001
Olds	OL	Red Deer River	51.7637	114.4128	4	1	-	
Innisfail	IN	Red Deer River	52.0415	113.9703	9	0	4.33	0.111
Red Deer 1	RD1	Red Deer River	52.3135	113.7858	18	0	4.51	0.204
Red Deer 2	RD2	Red Deer River	52.3376	113.1258	19	3	4.6	0.012
Drumheller	DR	Red Deer River	51.4609	112.7258	20	1	4.6	0.072
Emerson Bridge	EM	Red Deer River	50.9161	111.9007	4	0	-	-
Jenner	JE	Red Deer River	50.8440	111.1527	2	0	-	-
Buffalo	BUF	Red Deer River	50.8494	110.6970	1	0	-	-
Wyndam-Carseland PP	BO	Bow River	50.8290	113.4220	20	2	4.57	0.051
Southern Alberta 2	SB2	Waterton River	49.0694	113.8561	29	2	4.54	0.059
Drywood Creek	DY	Drywood Creek	49.2978	114.0225	20	0	4.66	0.103
Southern Alberta 1	SB1	Castle River	49.3908	114.3397	30	5	4.29	-0.006
Crownest	CR	Crowsnest River	49.5740	114.2405	20	2	4.79	0.004
Oldman River Reservoir	OM	Oldman River	49.5584	113.8210	10	1	4.58	0.061
Blue Trail Park	BL	Waterton River	49.4295	113.4961	4	0	-	-
Glenwood	GL	Waterton River	49.4019	113.5933	3	1	-	-
Fort Macleod	FO	Oldman River	49.7328	113.3990	15	1	4.21	0.001
Lethbridge	LE	Oldman River	49.6960	112.8633	48	10	4.34	0.094
St.Mary	StM	St Mary River	49.5891	112.8889	5	2	-	-
Woolford PP	WO	St Mary River	49.1750	113.1876	3	1	-	-
Taber	TA	Oldman River	49.8133	112.1701	4	0	-	-
Forks	FK	Oldman/ Bow/ S.Sask confluence	49.9249	111.6908	1	0	-	-
Medicine Hat	SSK	South Saskatchewan River	50.0412	110.6631	20	1	4.01	0.068

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.

	Locus	**PAT MP-14**	**Titgata 39**	**Escu 6**	**Titgata 02**	**PAT MP-43**	**Ase18**	**PmanTA GAn71**	**Cuμ28**	**CcaTgu 11**	**VeCr05**	**CtC-101**	**Pij02**	**Population mean across all loci**
BUC	***Na***	3	6	9	5	7	2	5	2	2	2	8	6	**5**
	Ho	0.714	1.000	1.000	0.714	1.000	0.429	0.857	0.429	0.429	0.286	1.000	0.714	**0.714**
	He	0.541	0.806	0.867	0.745	0.837	0.337	0.714	0.459	0.337	0.408	0.806	0.735	**0.633**
NSK	***Na***	7	7	16	12	15	3	7	3	2	2	11	17	**9**
	Ho	0.652	0.870	0.905	0.957	0.826	0.174	0.826	0.696	0.348	0.238	0.870	0.833	**0.683**
	He	0.677	0.798	0.876	0.873	0.895	0.162	0.766	0.540	0.476	0.337	0.805	0.906	**0.676**
IN	***Na***	4	5	10	8	7	2	7	2	3	2	9	9	**6**
	Ho	0.714	0.556	0.889	0.889	0.889	0.111	0.889	0.125	0.556	0.111	0.889	0.778	**0.616**
	He	0.541	0.636	0.877	0.852	0.827	0.278	0.815	0.492	0.475	0.278	0.852	0.790	**0.643**
RD1	***Na***	5	6	14	10	12	3	8	2	3	2	7	13	**7**
	Ho	0.533	0.667	0.882	0.833	0.833	0.111	0.833	0.389	0.389	0.000	0.611	0.688	**0.564**
	He	0.662	0.756	0.898	0.836	0.877	0.156	0.779	0.461	0.508	0.305	0.810	0.875	**0.660**
RD2	***Na***	6	7	16	10	13	5	7	2	3	2	10	15	**8**
	Ho	0.625	0.737	0.833	0.947	0.842	0.684	0.842	0.368	0.421	0.294	0.842	0.947	**0.699**
	He	0.650	0.713	0.903	0.863	0.859	0.579	0.787	0.450	0.536	0.327	0.810	0.886	**0.697**
DR	***Na***	9	9	13	10	11	3	6	3	3	2	9	13	**8**
	Ho	0.700	0.800	0.850	0.750	0.900	0.300	0.700	0.600	0.474	0.125	0.900	0.900	**0.667**
	He	0.789	0.765	0.895	0.821	0.863	0.261	0.781	0.611	0.522	0.469	0.836	0.886	**0.708**
BO	***Na***	12	7	14	9	10	4	8	2	3	2	9	14	**8**
	Ho	0.750	0.750	0.950	0.800	0.800	0.200	0.900	0.600	0.400	0.188	0.750	0.684	**0.648**
	He	0.723	0.781	0.894	0.818	0.835	0.186	0.801	0.495	0.509	0.342	0.855	0.893	**0.678**

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**
DY	***Na***	6	6	14	11	12	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**
SB1	***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**
CR	***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**
OM	***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**
FO	***Na***	7	8	13	10	11	3	7	3	2	2	8	5	**7**
	Ho	0.923	0.929	0.857	0.786	0.786	0.286	0.714	0.571	0.267	0.111	0.800	0.538	**0.631**
	He	0.710	0.804	0.898	0.857	0.865	0.255	0.781	0.482	0.320	0.105	0.856	0.760	**0.641**
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 loci	***Na***	**7**	**7**	**14**	**10**	**11**	**3**	**7**	**3**	**3**	**2**	**9**	**12**	
	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**	
	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**	

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.

	BUC	**NSK**	**IN**	**RD1**	**RD2**	**DR**	**BO**	**SB2**	**DY**	**SB1**	**CR**	**OM**	**FO**	**LE**
BUC	*	**0.036**	0.008	0.001	0.006	0.038	**0.036**	0.004	0.007	0.000	0.007	**0.039**	0.005	**0.044**
NSK	0.031	*	0.015	0.012	0.026	**0.051**	0.012	0.012	0.016	**0.031**	**0.044**	**0.036**	0.020	**0.039**
IN	0.052	0.029	*	0.000	0.006	0.026	**0.050**	0.013	0.023	0.005	0.013	0.012	0.007	**0.062**
RD1	0.029	0.015	0.027	*	0.000	0.019	0.012	0.003	0.000	0.001	0.006	0.015	0.000	**0.026**
RD2	0.028	0.022	0.029	0.017	*	0.007	**0.047**	0.007	0.000	0.005	0.000	0.022	0.000	**0.023**
DR	**0.042**	**0.024**	**0.032**	**0.023**	**0.024**	*	**0.057**	**0.019**	**0.022**	**0.039**	**0.014**	0.059	0.012	**0.089**
BO	**0.035**	0.012	0.033	0.014	0.023	**0.025**	*	**0.013**	**0.028**	**0.029**	**0.041**	**0.087**	**0.032**	**0.044**
SB2	0.026	0.012	0.031	0.011	0.016	**0.025**	0.013	*	0.000	0.000	0.005	**0.042**	0.000	**0.036**
DY	0.027	0.017	0.034	0.015	0.016	**0.026**	**0.021**	0.010	*	0.003	0.001	0.028	0.001	**0.019**
SB1	0.026	**0.017**	0.030	0.010	**0.016**	**0.027**	**0.017**	0.007	0.014	*	**0.013**	**0.040**	0.006	**0.025**
CR	0.028	0.020	0.028	0.017	0.010	**0.022**	**0.021**	0.014	0.014	**0.017**	*	0.023	0.002	**0.047**
OM	0.039	**0.036**	0.049	0.033	0.026	**0.041**	**0.043**	**0.035**	0.030	**0.036**	0.028	*	0.008	**0.042**
FO	**0.035**	0.023	0.046	0.020	0.024	**0.042**	**0.028**	0.012	0.019	0.018	0.025	0.036	*	**0.015**
LE	**0.035**	**0.017**	**0.040**	**0.015**	**0.023**	**0.032**	**0.018**	**0.015**	**0.021**	**0.014**	**0.024**	**0.034**	**0.021**	*
SSK	**0.039**	**0.030**	**0.039**	**0.027**	**0.022**	**0.037**	**0.034**	**0.024**	**0.025**	**0.026**	**0.023**	**0.035**	**0.036**	**0.032**

Table 4.4. Results from STRUCTURE analysis of individuals from populations separated by hypothesised artificial or natural barriers to gene flow within river systems.

Hypothesis	Impediment	Approx. distance of barrier (river km)	Populations	Number of clusters (*K*)
Natural	Gap in woodland	98	LE & SSK	2
	Gap in woodland	150	BO & southern populations	2
Artificial	Oldman Reservoir	20	CR & OM	1
	St. Mary Reservoir	17	StM & WO	1
	Waterton Reservoir	10	SB1 & GL/BL	1
	St. Mary Reservoir/ gap in woodland	80	StM & WO	1

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, Δ_i = differences in AIC_c values, w_i = AIC_c weights. ** indicates significant correlations ($P \leq 0.05$).

Variable (controlled variable)	F_{ST}					D_{EST}				
	r	R^2	AIC_c	Δ_i	w_i	r	R^2	AIC_c	Δ_i	w_i
Distance through suitable habitat	0.16	0.02	-569.9	34.7	0	0.33**	0.11	-427.1	6.2	0.04
Elevation	-0.35	0.12	-580.2	24.4	0	-0.28	0.08	-427.5	5.8	0.04
Elevation (distance)	-0.34					-0.26				
Elevation (land cover)	-0.14					-0.15				
Land cover	0.59**	0.35	**-604.6**	**0**	0.44	0.38**	0.15	**-433.3**	0	0.78
Land cover (distance)	0.58**					0.30				
Land cover (elevation)	0.52**					0.29				
Land cover x elevation	0.57**	0.33	-601.7	2.9	0.1	0.35	0.12	-429.9	3.4	0.14
Land cover x elevation (distance)	0.56**					0.25				
Hybrid-	0.18	0.03	-340.8	18.3	0	0.02	0	-262.7	17.8	0
Hybrid- (distance)	0.01					-0.35				
Hybrid+	0.15	0.02	-340.6	18.5	0	-0.04	0	-263.1	17.4	0
Hybrid+ (distance)	-0.06					-0.52				
Hybrid- x elevation	0.33**	0.11	-344.2	14.9	0	0.27**	0	-263.5	17	0
Hybrid- x elevation (distance)	0.23					0.02				
Hybrid+ x elevation	-0.06	0	-340.2	18.9	0	-0.08	0.01	-263.9	16.6	0
Hybrid+ x elevation (distance)	-0.28					-0.39				
Hybrid- x land cover	0.46**	0.22	-350.9	8.2	0.02	0.42**	0.18	-268.9	11.6	0
Hybrid- x land cover (distance)	0.47**					0.26				
Hybrid+ x land cover	0.04	0	-339.8	19.3	0	-0.01	0	-262.7	17.8	0
Hybrid+ x land cover (distance)	-0.19					-0.37				
Hybrid- x elevation x land cover	0.57**	0.33	**-359.1**	**0**	0.98	0.53**	0.28	**-280.5**	0	1
Hybrid- x elevation x land cover (distance)	0.55**					0.50**				
Hybrid+ x elevation x land cover	-0.15	0.02	-340.8	18.3	0	-0.24	0.06	-266.5	14	0
Hybrid+ x elevation x land cover (distance)	-0.21					-0.34				

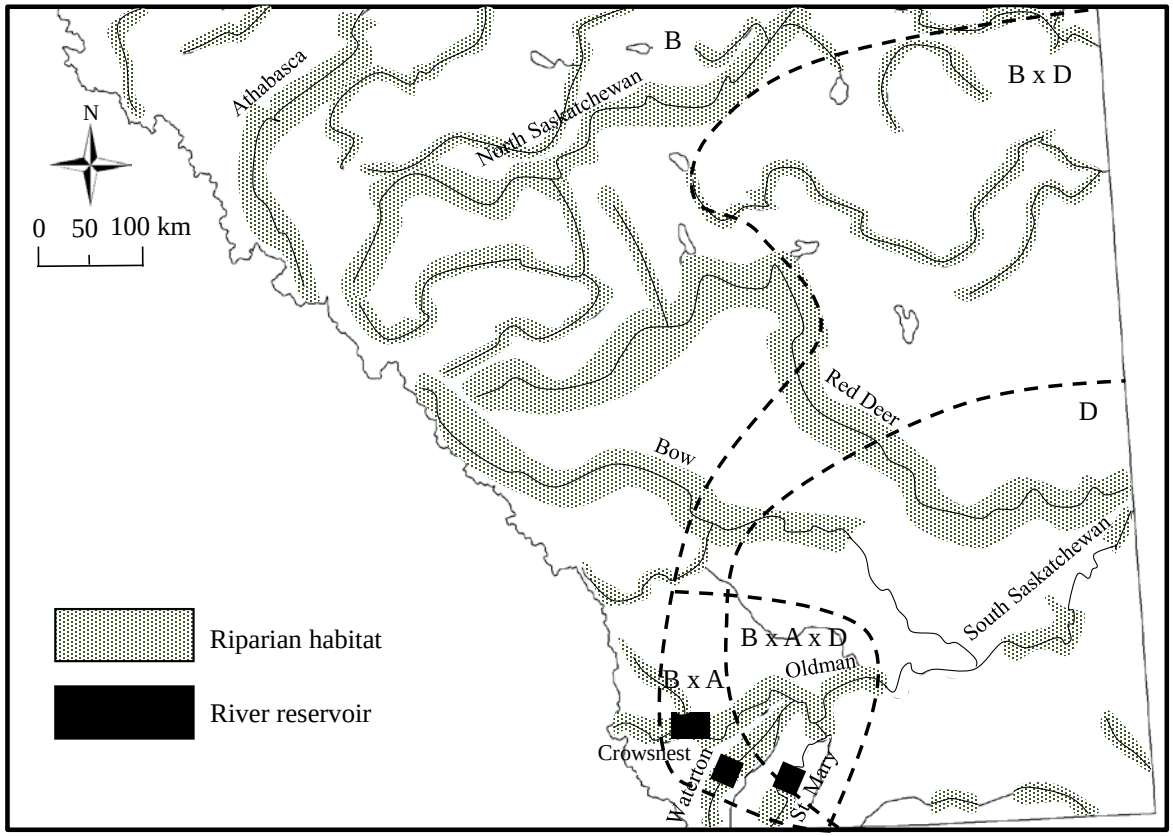

Figure 4.1. Map of Southern Alberta illustrating the presence (shaded area) and absence (e.g., downstream of the Bow River) of riparian woodland within each river system under study. Artificial barriers (i.e., river reservoirs) are located in black rectangles. Approximate regions of pure and hybrid poplar 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*).

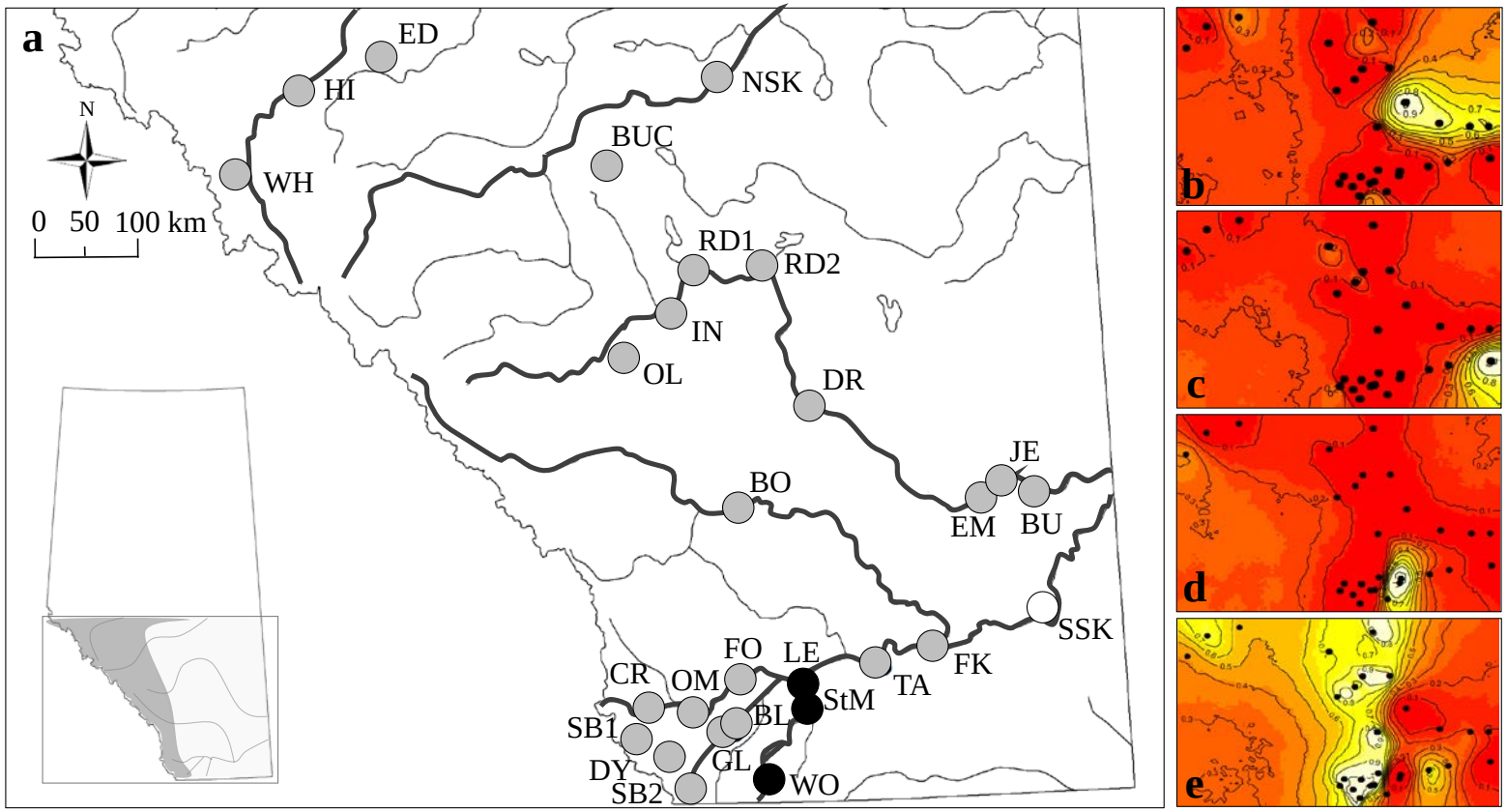

Figure 4.2. Sampling locations (a) of black-capped chickadee (*Poecile atricapillus*) in Southern Alberta (See Table 4.1 for abbreviations and associated river systems) with inferred clusters from STRUCTURE (coloured circles; $K = 3$; see Figure 4.3). Inset illustrates forest cover in the area (dark 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).

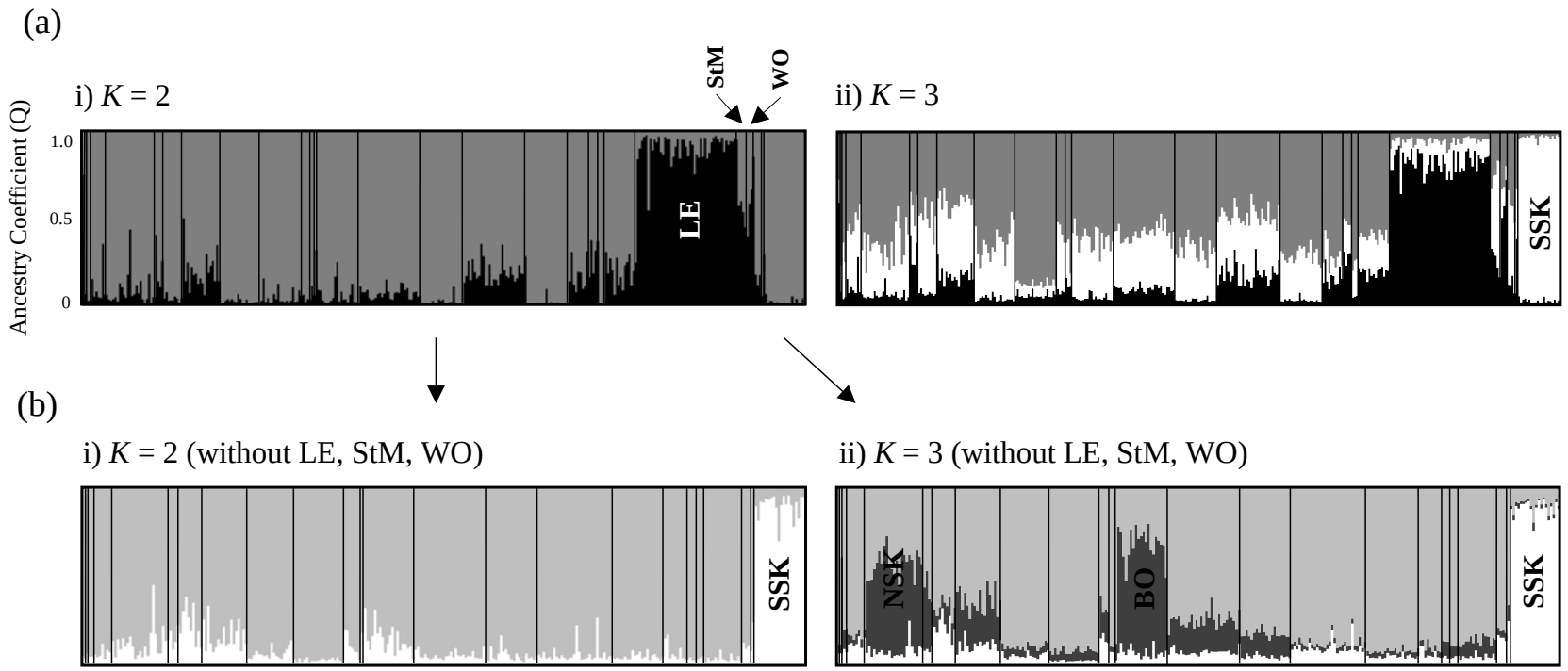

Figure 4.3. Inferred population structure of the black-capped chickadee (*Poecile atricapillus*) from 12 microsatellite loci using STRUCTURE. Two runs were conducted, but the optimal number of clusters to describe the data was unclear for each run. The initial run (a) for all individuals from 28 localities resulted in contrasting values of true *K*: (i) *K* = 2 (Δ*K*) and ii) *K* = 3 (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 (Δ*K*) and ii) *K* = 3 (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).

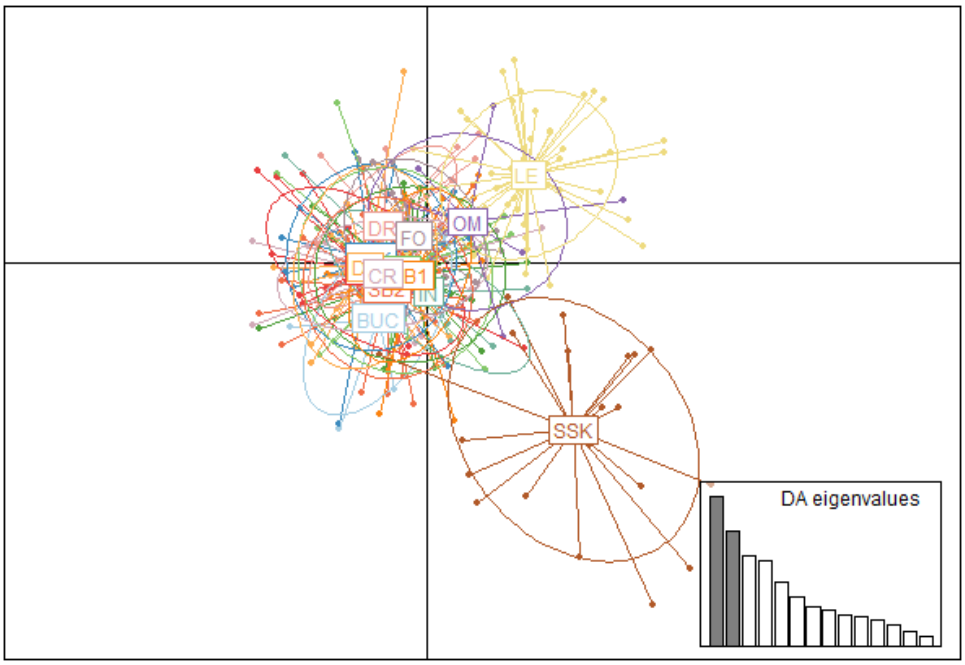

Figure 4.4. A representation of genetic relatedness between geographical clusters of black-capped chickadee populations (N = 15) obtained by discriminant analysis of principal components (DAPC). The graphs represent individuals as dots and the populations as inertia eclipses (population abbreviations can be found in Table 1) and scatterplots are based on the first two principal 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 caeuleus*) 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.

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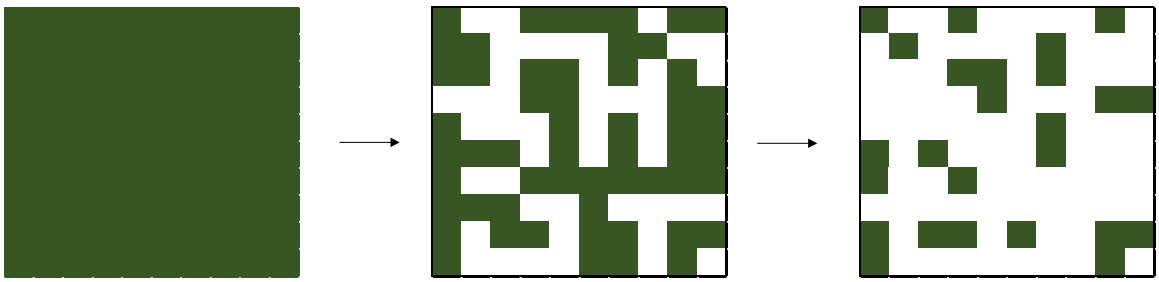


Figure 5.1. Simplified diagram illustrating the process of habitat fragmentation of a single habitat patch (suitable habitat = green; removed habitat = white). Modified from Fahrig, (2003).

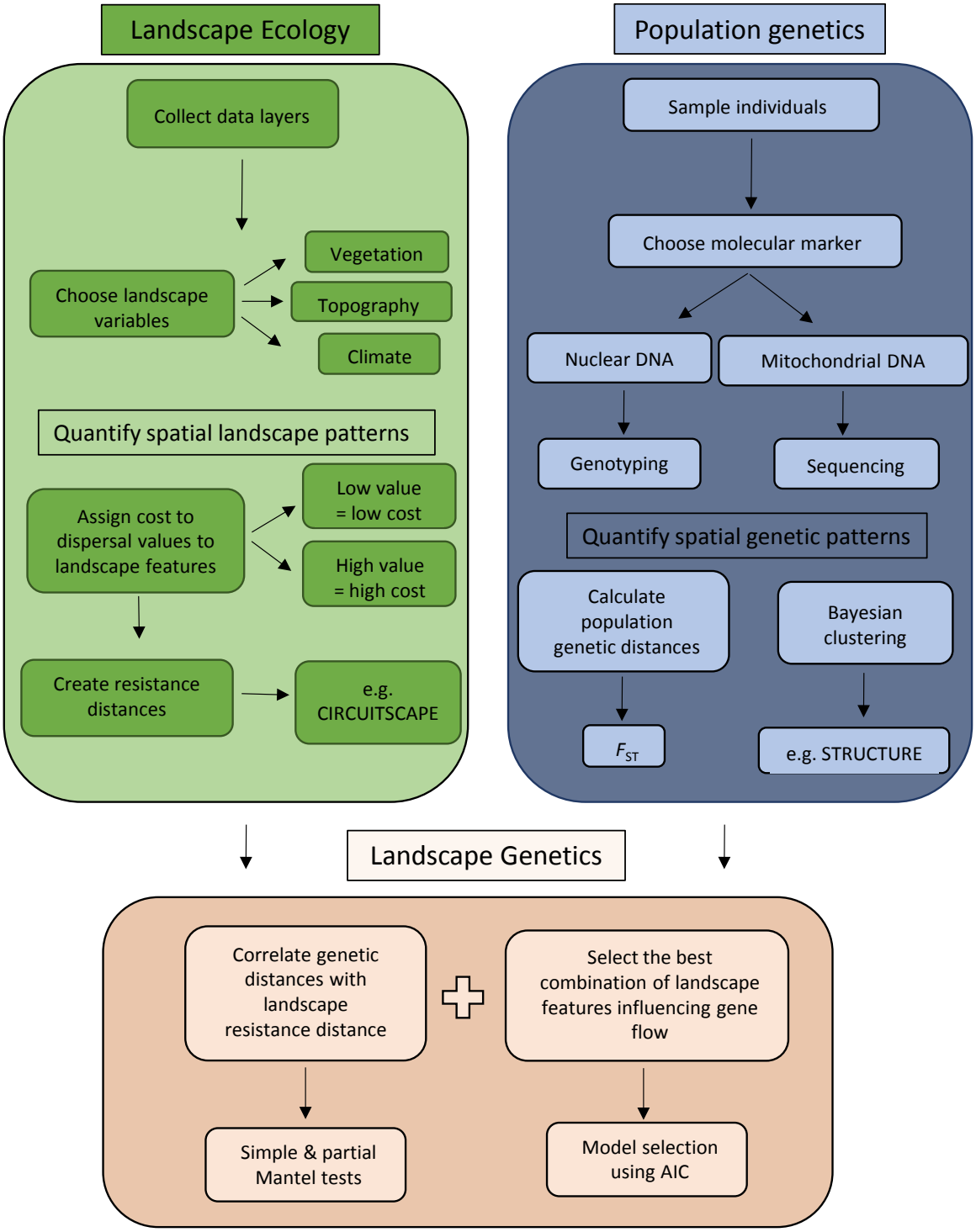


Figure 5.2. Simplified model illustrating the steps necessary to carry out a landscape genetics study.

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).

ID	Location	Lat (°N)	Long (°W)	Source	Band/ Museum ID
AKA001	Eagle River Campground, AK	61.307	149.571	Wild	2540-22801
AKA002	Eagle River Campground, AK	61.306	149.571	Wild	2540-22803
AKA003	Eagle River Campground, AK	61.306	149.571	Wild	2540-22804
AKA004	Eagle River Campground, AK	61.306	149.571	Wild	2540-22805
AKA005	Eagle River Campground, AK	61.306	149.571	Wild	2540-22806
AKA006	Eagle River Campground, AK	61.307	149.571	Wild	2540-22807
AKA007	Eagle River Campground, AK	61.306	149.572	Wild	2540-22808
AKA008	Eagle River Campground, AK	61.306	149.567	Wild	2540-22809
AKA009	Eagle River Campground, AK	61.306	149.567	Wild	2540-22810
AKA010	Eagle River Campground, AK	61.307	149.569	Wild	2540-22813
AKA011	Eklutna Rd, AK	61.423	149.202	Wild	2540-22815
AKA012	Eklutna Rd, AK	61.411	149.156	Wild	2540-22816
AKA013	Eagle River Rd x Roop Rd, AK	61.278	149.378	Wild	2540-22817
AKA014	Eagle River Rd x Vantage Av, AK	61.276	149.375	Wild	2540-22818
AKA015	Eagle River Rd x Vantage Av, AK	61.276	149.375	Wild	2540-22819
AKA016	Eagle River Rd x Vantage Av, AK	61.276	149.375	Wild	2540-22820
AKA017	Eagle River Rd x Vantage Av, AK	61.276	149.375	Wild	2540-22821
AKA018	Eagle River Rd x "Fill site", AK	61.268	149.348	Wild	2540-22825
AKA019	Eagle River Rd x Clemens Cres, AK	61.282	149.389	Wild	2540-22827
AKA020	Eagle River Rd x Clemens Cres, AK	61.282	149.389	Wild	2540-22828
AKA021	Eagle River Don and Sherry Shiesl's, AK	61.567	149.373	Wild	2540-22839
AKA022	Eagle River Don and Sherry Shiesl's, AK	61.567	149.373	Wild	2540-22840
AKA023	Eagle River Don and Sherry Shiesl's, AK	61.567	149.373	Wild	2540-22841
AKA024	Anchorage Don and Nancy Podgorski, AK	61.550	149.550	Wild	2540-22886

AKA025	Anchorage Don and Nancy Podgorski, AK	61.550	149.550	Wild	2540-22887
AKA026	Anchorage Don and Nancy Podgorski, AK	61.550	149.550	Wild	2540-22888
AKA027	Anchorage Don and Nancy Podgorski, AK	61.550	149.550	Wild	2540-22889
AKA028	Norh Fork Eagle river, AKA	61.297	149.532	Wild	2540-22926
AKA029	Eagle river campground, AKA	61.308	149.520	Wild	2540-22928
AKA030	Knik river, AKA	61.451	148.821	Wild	2540-22932
AKA031	Knik river, AKA	61.451	148.821	Wild	2540-22933
AKA032	Knik river, AKA	61.451	148.821	Wild	2540-22934
AKF001	Old Nanana Rd, AK	64.816	148.188	Wild	2540-22845
AKF002	Standard Crk Rd, AK	64.812	148.209	Wild	2540-22847
AKF003	Standard Crk Rd, AK	64.812	148.209	Wild	2540-22848
AKF004	Spinach Crk Rd, AK	64.929	148.010	Wild	2540-22851
AKF005	Miller Hill Rd, AK	64.868	147.881	Wild	2540-22852
AKF006	Miller Hill Rd, AK	64.868	147.881	Wild	2540-22853
AKF007	Miller Hill Rd, AK	64.868	147.881	Wild	2540-22858
AKF008	Spinach Crk Rd, AK	64.942	148.088	Wild	2540-22859
AKF009	Spinach Crk Rd, AK	64.942	148.088	Wild	2540-22860
AKF010	Tanana Valley Campground, AK	64.865	147.759	Wild	2540-22864
AKF011	Birch Hill Rec Area, AK	64.871	147.647	Wild	2540-22869
AKF012	Two Rivers Road, AK	64.878	147.043	Wild	2540-22875
AKF013	Two Rivers Road, AK	64.878	147.043	Wild	2540-22876
AKF014	Two Rivers Road, AK	64.870	147.043	Wild	2540-22877
AKF015	Steese Hwy, AK	64.207	147.211	Wild	2540-22879
AKF016	Steese Hwy, AK	64.207	147.211	Wild	2540-22880
AKF017	Nordale Rd, AK	64.858	147.405	Wild	2540-22882
AKF018	Tanana Valley Campground, AK	64.864	147.761	Wild	2540-22883
AKF019	Murphy Dome Rd, AK	64.924	148.989	Wild	2540-22849
AKF020	Murphy Dome Rd, AK	64.924	148.989	Wild	2540-22850
AKF021	Sheep creek road, AKF	64.877	147.907	Wild	2540-22908
AKF022	Sheep creek road, AKF	64.877	147.907	Wild	2540-22909
AKF023	Sheep creek road, AKF	64.877	147.907	Wild	2540-22912

AKF024	Sheep creek road, AKF	64.877	147.907	Wild	2540-22913
AKF025	Sheep creek road, AKF	64.877	147.907	Wild	2540-22916
AKF026	Jones road, AKF	64.927	147.896	Wild	2540-22918
AKF027	Jones road, AKF	64.927	147.896	Wild	2540-22919
AKF028	Jones road, AKF	64.927	147.896	Wild	2540-22920
AKF029	Waldheim Dr, AKF	64.936	147.916	Wild	2540-22921
AKF030	Waldheim Dr, AKF	64.936	147.916	Wild	2540-22922
AKF031	ABO, AKF	64.863	147.717	Wild	2540-22923
AKF032	ABO, AKF	64.863	147.717	Wild	2370-52235
AKW01	Old Edgerton HWY, AKW	61.751	144.990	Wild	2540-23169
AKW02	Old Edgerton HWY, AKW	61.751	144.990	Wild	2540-23171
AKW03	Old Edgerton HWY, AKW	61.767	145.022	Wild	2540-23174
AKW04	Old Edgerton HWY, AKW	61.767	145.022	Wild	2540-23175
AKW05	Old Edgerton HWY, AKW	61.767	145.022	Wild	2540-23176
AKW06	Old Edgerton HWY, AKW	61.767	145.022	Wild	2540-23177
AKW07	Old Edgerton HWY, AKW	61.767	145.022	Wild	2540-23178
AKW08	Old Edgerton HWY, AKW	61.775	145.036	Wild	2540-23179
AKW09	Old Edgerton HWY, AKW	61.775	145.036	Wild	2540-23180
AKW10	Old Edgerton HWY, AKW	61.775	145.036	Wild	2540-23182
AKW11	Old Edgerton HWY, AKW	61.775	145.036	Wild	2540-23184
AKW12	Old Edgerton HWY, AKW	61.794	145.071	Wild	2540-23187
AKW13	Old Edgerton HWY, AKW	61.794	145.071	Wild	2540-23188
AKW14	Old Edgerton HWY, AKW	61.794	145.071	Wild	2540-23191
AKW15	Old Edgerton HWY, AKW	61.819	145.141	Wild	2540-23193
AKW16	Richardson HWY x Old Edgerton HWY, AKW	61.825	145.219	Wild	2540-23196
AKW17	Richardson HWY x Old Edgerton HWY, AKW	61.825	145.219	Wild	2540-23197
AKW18	WISE headquarters, AKW	61.804	145.093	Wild	2540-23200
AKW19	WISE headquarters, AKW	61.804	145.093	Wild	2540-22901
AKW20	Old Edgerton HWY, AKW	61.822	145.171	Wild	2540-22907
BC-MI-155	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61093
BC-MI-156	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61094

BC-MI-157	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61096
BC-MI-158	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61097
BC-MI-159	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36344
BC-MI-160	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61098
BC-MI-161	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61099
BC-MI-162	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61100
BC-MI-163	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75979
BC-MI-164	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75802
BC-MI-165	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75803
BC-MI-166	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75804
BC-MI-167	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75981
BC-MI-168	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2359-75980
BC-MI-169	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75699
BC-MI-170	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75805
BC-MI-171	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75807
BC-MI-172	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75808
BC-MI-173	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-76030
BC-MI-174	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75801
BC-MI-175	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2590-61108
BC-MI-177	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75857
BC-MI-178	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75852
BC-MI-179	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75853
BC-MI-180	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75854
BC-MI-184	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75856
BC-MI-37	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75681
BC-MI-38	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75926
BC-MI-39	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75727
BC-MI-40	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75703
BC-MI-41	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36368
BC-MI-42	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-76006
BC-MI-43	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36334

BC-MI-44	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75916
BC-MI-45	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75732
BC-MI-46	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36327
BC-MI-47	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75921
BC-MI-48	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75920
BC-MI-49	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75919
BC-MI-50	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36308
BC-MI-51	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36307
BC-MI-52	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36329
BC-MI-53	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36302
BC-MI-54	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75908
BC-MI-55	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75729
BC-MI-56	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36309
BC-MI-57	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36339
BC-MI-58	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36349
BC-MI-59	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36354
BC-MI-60	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36340
BC-MI-61	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75924
BC-MI-62	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36301
BC-MI-63	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75911
BC-MI-64	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	1950-36342
BC-MI-65	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75933
BC-MI-66	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-76009
BC-MI-67	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75939
BC-MI-68	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-76082
BC-MI-69	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75938
BC-MI-70	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-75931
BC-MI-71	John Prince Research Station, Ft St James BC	54.645	124.395	UNBC	2350-76015
BC-PU-01	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36098
BC-PU-02	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36100
BC-PU-03	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36213

BC-PU-04	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36214
BC-PU-05	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36217
BC-PU-06	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36218
BC-PU-07	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36220
BC-PU-08	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36227
BC-PU-09	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36228
BC-PU-10	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36229
BC-PU-11	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36240
BC-PU-12	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36252
BC-PU-13	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36257
BC-PU-14	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36263
BC-PU-15	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36264
BC-PU-16	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36157
BC-PU-17	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36164
BC-PU-18	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36177
BC-PU-19	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36223
BC-PU-20	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36294
BC-PU-21	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36295
BC-PU-22	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36296
BC-PU-23	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36298
BC-PU-24	UNBC, Prince George BC	53.894	122.829	UNBC	1950-36300
BC-PU-25	UNBC, Prince George BC	53.894	122.829	UNBC	2350-75601
BC-PU-26	UNBC, Prince George BC	53.894	122.829	UNBC	2350-75602
BC-PU-27	UNBC, Prince George BC	53.894	122.829	UNBC	2350-75603
BC-PU-28	UNBC, Prince George BC	53.894	122.829	UNBC	2350-75604
BC-PU-29	UNBC, Prince George BC	53.894	122.829	UNBC	2350-75605
BC-PU-30	UNBC, Prince George BC	53.894	122.829	UNBC	2350-75606
BCR001	Revelstoke, BC	50.981	118.182	Wild	2490-57684
BCR002	Revelstoke, BC	50.981	118.182	Wild	2490-57685
BCR003	Revelstoke, BC	50.983	118.179	Wild	bcch 3
BCR004	Mt Revelstoke Ski Chalet, BC	51.007	118.191	Wild	2490-57686

BCR005	Mt Revelstoke Ski Chalet, BC	51.007	118.191	Wild	2490-57687
BCR006	Mt Revelstoke Ski Chalet, BC	51.014	118.203	Wild	2490-57688
BCR007	Mt Revelstoke Ski Chalet, BC	51.014	118.203	Wild	2490-57689
BCR008	Mt Revelstoke Ski Chalet, BC	51.006	118.182	Wild	2490-57690
BCR009	Revelstoke field, BC	50.982	118.180	Wild	2490-57691
BCR010	Revelstoke Resort, BC	50.970	118.172	Wild	2490-57692
BCR011	Revelstoke Resort, BC	50.970	118.174	Wild	2490-57693
BCR012	Begbie Falls Revelstoke, BC	50.944	118.205	Wild	2490-57694
BCR013	Mount MacPherson Revelstoke, BC	50.942	118.223	Wild	2490-57695
BCR014	9 mile Revelstoke, BC	50.897	118.114	Wild	2490-57696
BCR015	Smokey Bear Revelstoke, BC	50.989	118.278	Wild	2490-57697
BCR016	Frisby Rd Revelstoke, BC	51.066	118.194	Wild	2490-57698
BCR017	Frisby Rd Revelstoke, BC	51.066	118.194	Wild	2490-57699
BCR018	Frisby Rd Revelstoke, BC	51.052	118.219	Wild	2490-57700
BCR019	Frisby Ridge Rd Revelstoke, BC	51.059	118.206	Wild	2490-57701
BCR020	Frisby Ridge Rd Revelstoke, BC	51.059	118.206	Wild	2490-57702
BCR021	Frisby Ridge Rd Revelstoke, BC	51.141	118.209	Wild	2490-57703
BCR022	Frisby Ridge Rd Revelstoke, BC	51.059	118.223	Wild	2490-57704
BCR023	Frisby Ridge Rd Revelstoke, BC	51.062	118.224	Wild	2490-57705
BCR024	Frisby Ridge Rd Revelstoke, BC	51.062	118.224	Wild	2490-57706
BCR025	Frisby Ridge Rd Revelstoke, BC	51.062	118.224	Wild	2490-57707
BCR026	Frisby Ridge Rd Revelstoke, BC	51.065	118.226	Wild	2490-57708
BCR027	Frisby Ridge Rd Revelstoke, BC	51.063	118.232	Wild	2490-57709
BCR028	Frisby Ridge Rd Revelstoke, BC	51.063	118.232	Wild	2490-57710
BCR029	Frisby Ridge Rd Revelstoke, BC	51.049	118.229	Wild	2490-57711
BCR030	Frisby Ridge Rd Revelstoke, BC	51.049	118.229	Wild	2490-57712
BCR031	Frisby Ridge Rd Revelstoke, BC	51.052	118.226	Wild	2490-57713
BCR032	Frisby Ridge Rd Revelstoke, BC	51.056	118.225	Wild	2490-57714
BCR033	West Bridge, Revelstoke BC	51.003	118.218	Wild	2500-94928
BCR034	Machete Island 2, Revelstoke, BC	50.971	118.202	Wild	2500-94930
BCR035	Westside RD 2, Revelstoke BC	51.013	118.237	Wild	2500-94931

BCR036	Westside RD 2, Revelstoke BC	51.013	118.237	Wild	2500-94932
BCR037	Bridge Creek, Revelstoke BC	50.994	118.172	Wild	2500-94933
BCR038	Westside RD 1, Revelstoke BC	51.004	118.228	Wild	2500-94937
BCR039	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48305
BCR040	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48306
BCR041	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48307
BCR042	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48308
BCR043	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48309
BCR044	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48310
BCR045	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48311
BCR046	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48312
BCR047	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48313
BCR048	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48314
BCR049	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48315
BCR050	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48316
BCR051	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48317
BCR052	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48318
BCR053	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48319
BCR054	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48320
CAB001	Olds, AB	51.792	114.286	Wild	3111-48301
CAB002	Olds, AB	51.806	114.593	Wild	2520-38802
CAB003	Olds, AB	51.806	114.593	Wild	2520 39803
CAB004	Olds, AB	51.807	114.593	Wild	2520-39804
CAB005	Innisfail, AB	54.032	113.962	Wild	2520-39805
CAB006	Innisfail, AB	54.032	113.962	Wild	2520-39806
CAB007	Innisfail, AB	54.032	113.962	Wild	2520-39807
CAB008	Innisfail, AB	54.032	113.962	Wild	2520-39808
CAB009	Innisfail, AB	54.032	113.962	Wild	2520-39809
CAB010	Innisfail, AB	54.032	113.962	Wild	2520-39810
CAB011	Innisfail, AB	54.032	113.962	Wild	2520-39811
CAB012	Innisfail, AB	54.032	113.962	Wild	2520-39812

CAB013	Innisfail, AB	54.024	110.982	Wild	2520-39813
CAB014	Buck Lake, AB	54.972	115.605	Wild	2520-39814
CAB015	Buck Lake, AB	54.972	115.605	Wild	2520-39815
CAB016	Buck Lake, AB	54.972	115.605	Wild	2520-39816
CAB017	Buck Lake, AB	54.972	115.605	Wild	2520-39817
CAB018	Buck Lake, AB	54.972	115.605	Wild	2520-39818
CAB019	Buck Lake, AB	54.972	115.605	Wild	2520-39819
CAB020	Buck Lake, AB	54.972	115.605	Wild	2520-39820
CAB021	Hinton, AB	53.400	117.579	Wild	2520-39822
CAB022	Hinton, AB	53.387	117.590	Wild	2520-39823
CAB023	Edmonton, AB	53.530	113.554	Wild	2520-39826
CAB024	Edmonton, AB	53.530	113.554	Wild	2520-39827
CAB025	Edmonton, AB	53.483	113.555	Wild	2520-39828
CAB026	Edmonton, AB	53.481	113.424	Wild	2520-39829
CAB027	Edson, AB	53.629	116.802	Wild	2520-39830
CAB028	Mt. Robson, BC	53.029	119.239	Wild	2520-39838
CAB029	Mt. Robson, BC	53.020	119.222	Wild	2520-39839
CAB030	Whistlers Campground, Jasper NP, CAB	52.849	118.080	Wild	2500-94961
CBC001	Smithers, BC	54.785	127.151	Wild	2520-39893
CBC002	Smithers, BC	54.785	127.151	Wild	2529-39882
CBC003	Smithers, BC	54.785	127.151	Wild	2520-39883
CBC004	Smithers, BC	54.785	127.151	Wild	2520-29884
CBC005	Smithers, BC	54.785	127.151	Wild	2520-39885
CBC006	Smithers, BC	54.785	127.151	Wild	2520-39886
CBC007	Smithers, BC	54.785	127.151	Wild	2520-39887
CBC008	Smithers, BC	54.785	127.151	Wild	2520-39888
CBC009	Smithers, BC	54.785	127.151	Wild	2520-39889
CBC010	Smithers, BC	54.785	127.151	Wild	2520-39890
CBC011	Smithers, BC	54.785	127.151	Wild	2520-39891
CBC012	Smithers, BC	54.785	127.151	Wild	2520-39892
CBC013	Smithers, BC	54.785	127.151	Wild	2520-39898

CBC014	Smithers, BC	54.785	127.151	Wild	2520-39894
CBC015	Smithers, BC	54.785	127.151	Wild	2520-39899
CBC016	Smithers, BC	54.785	127.151	Wild	2520-39900
CBC017	Smithers, BC	54.785	127.151	Wild	2490-57761
CBC018	Smithers, BC	54.785	127.151	Wild	2490-57762
CBC019	Smithers, BC	54.785	127.151	Wild	2490-57763
CBC020	Smithers, BC	54.785	127.151	Wild	2490-57764
CBC021	Smithers, BC	54.785	127.151	Wild	2490-57765
CBC022	Smithers, BC	54.785	127.151	Wild	2490-57766
CBC023	Smithers, BC	54.785	127.151	Wild	2490-57767
CBC024	Smithers, BC	54.785	127.151	Wild	2490-57768
CBC025	3928 Mountainview Ave, Thornhill BC	54.506	128.543	Wild	2500-94901
CBC026	Ferry Island, BC	54.512	128.574	Wild	2500-94902
CBC027	Stockner's Residence; Kispiox BC	55.468	127.735	Wild	2500-94903
CBC028	Stockner's Residence; Kispiox BC	55.468	127.735	Wild	2500-94904
CBC029	Tyee Lake, Telkwa BC	54.707	127.040	Wild	2500-94906
CBC030	Tyee Lake, Telkwa BC	54.707	127.040	Wild	2500-94907
CBC031	Tyee Lake, Telkwa BC	54.707	127.040	Wild	2500-94908
CBC032	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94915
CBC033	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94916
CBC034	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94917
CBC035	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94918
CBC036	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94919
CBC037	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94920
CBC038	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94909
CBC039	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94910
CBC040	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94911
CBC041	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94912
CBC042	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94913
CBC043	4567 Tyee Lake Rd., Telkwa BC	54.725	127.036	Wild	2500-94914
CID001	Ponderosa State Park - Meadow Marsh, McCall, ID	40.626	105.223	Wild	2540-22967

CID002	Day Use Road, Ponderosa State Park, McCall, ID	39.996	105.270	Wild	2540-22968
CID003	Day Use Road, Ponderosa State Park, McCall, ID	39.996	105.270	Wild	2540-22969
CID004	N. Payette River, McCall, ID	39.908	105.608	Wild	2540-22970
CID005	N. Payette River, McCall, ID	39.811	105.530	Wild	2540-22971
CID006	North Payette River, McCall, ID	39.811	105.530	Wild	2540-22972
CID007	North Payette River, McCall, ID	39.842	105.522	Wild	2540-22973
CID008	New Meadows, Blue Bunch Road, ID	39.783	105.392	Wild	2540-22974
CID009	New Meadows, Blue Bunch Road, ID	39.775	105.376	Wild	2540-22975
CID010	Payette River by bridge, McCall, ID	39.770	105.402	Wild	2540-22976
CID011	Payette River by bridge, McCall, ID	39.784	105.398	Wild	2540-22977
CID012	Payette River by pedestrian bridge, ID	39.842	105.524	Wild	2540-22978
CID013	Little Payette Lake, McCall, ID	39.851	105.482	Wild	2540-22979
CID014	Little Payette Lake, McCall, ID	39.779	105.369	Wild	2540-22980
CID015	Little Payette Lake, McCall, ID	40.042	105.501	Wild	2540-22981
CID016	Little Payette Lake, McCall, ID	40.632	105.186	Wild	2540-22982
CID017	Little Payette Lake, McCall, ID	40.632	105.186	Wild	2540-22983
CID018	Little Payette Lake, McCall, ID	40.632	105.186	Wild	2540-22984
CID019	Little Payette Lake, McCall, ID	40.632	105.186	Wild	2540-22985
CID020	Little Payette Lake, McCall, ID	40.632	105.186	Wild	2540-22986
CID021	Aspen Stand by Pedestrian Bridge, McCall, ID	37.350	127.036	Wild	2540-22987
CO001	Rist Canyon, CO	40.626	105.223	Wild	2540-23101
CO002	Boulder (Jone's), CO	39.996	105.270	Wild	2540-23102
CO003	Boulder (Jone's), CO	39.996	105.270	Wild	2540-23103
CO004	Rollands Pass Road (FS 149), CO	39.908	105.608	Wild	2540-23104
CO005	Central City (graveyard), CO	39.811	105.530	Wild	2540-23105
CO006	Central City (graveyard), CO	39.811	105.530	Wild	bcch 20
CO007	Pickle Gulch, CO	39.842	105.522	Wild	2540-23106
CO008	N of Cottonwood (Stuart Wheeler), CO	39.783	105.392	Wild	2540-23107
CO009	N of Cottonwood (Trent and Cidy Miller), CO	39.775	105.376	Wild	2540-23108
CO010	N odfCottonwood (Larry Turner), CO	39.770	105.402	Wild	2540-23109
CO011	Cottonwood (Molly and David Nevin), CO	39.784	105.398	Wild	2540-23110

CO012	Pickle Gulch campground, CO	39.842	105.524	Wild	2540-23111
CO013	N of Central City (HWY 119), CO	39.851	105.482	Wild	2540-23112
CO014	N of Central City (LIZ), CO	39.779	105.369	Wild	2540-23113
CO015	N of Central City (LIZ), CO	40.042	105.501	Wild	2540-23114
CO016	Fort Collins, CO	40.632	105.186	Wild	2540-23115
CO017	Fort Collins, CO	40.632	105.186	Wild	2540-23116
CO018	Fort Collins, CO	40.632	105.186	Wild	2540-23117
CO019	Fort Collins, CO	40.632	105.186	Wild	2540-23118
CO020	Fort Collins, CO	40.632	105.186	Wild	2540-23119
CO021	Hawk Hill, Durango, CO	37.350	107.858	Wild	2540-22953
COR001	Toledo, OR 510 Strdevant DR.	44.633	123.921	Wild	2540-23001
COR002	Toledo, OR 510 Strdevant DR.	44.633	123.921	Wild	2540-23002
ID001	1037 Showalter Rd, Moscow ID	46.774	116.862	Wild	bcch1
ID002	1358 4 Mile Rd, Moscow, ID	46.840	116.965	Wild	2540-23054
ID003	1358 4 Mile Rd, Moscow, ID	46.840	116.965	Wild	2540-23055
ID004	6341 Thirteenhundred Rd, Coeur d'Alene ID	47.621	116.799	Wild	2540-23056
ID005	6341 Thirteenhundred Rd, Coeur d'Alene ID	47.621	116.799	Wild	2540-23057
ID006	6341 Thirteenhundred Rd, Coeur d'Alene ID	47.621	116.799	Wild	2540-23058
ID007	6341 Thirteenhundred Rd, Coeur d'Alene ID	47.621	116.799	Wild	2540-23059
ID008	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23060
ID009	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23061
ID010	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23062
ID011	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23063
ID012	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23064
ID013	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23065
ID014	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23066
ID015	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23067
ID016	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23068
ID017	2136 Roop Rd Cocolalla, ID	48.132	116.661	Wild	2540-23069
ID018	Garfield Recreation Area, Sandpoint, ID	48.276	116.553	Wild	2540-23070
ID019	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22955

ID020	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22956
ID021	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22957
ID022	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22958
ID023	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22959
ID024	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22960
ID025	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22961
ID026	2162 Roop Rd, Cocolalla, ID	48.133	116.655	Wild	2540-22962
ID027	Roop Road, Cocolalla, ID	-		Wild	2540-22963
ID028	Roop Road, Cocolalla, ID	-		Wild	2540-22964
ID029	Roop Road, Cocolalla, ID	-		Wild	2540-22965
ID030	Roop Road, Cocolalla, ID	-		Wild	2540-22966
IL001	Tinley Park, Cook Co, IL	41.573	87.784	FMC	351136-S90-007
IL002	Palos Park, Cook Co, IL	41.667	87.830	FMC	351137-S90-008
IL003	Chicago, Lincoln Park Zoo, Cook Co, IL	41.878	87.630	FMC	434418-LPZ-171
IL004	Glen Ellyn, DuPage Co, IL	41.878	88.067	FMC	435597-WWH-343
IL005	Wheaton, DuPage Co, IL	41.868	88.107	FMC	435598-WWH-266
IL006	Lisle, DuPage Co, IL	41.801	88.075	FMC	435599-WWH-258
IL007	Lake Forest, Lake Co, IL	42.259	87.841	FMC	436104-S02-082
IL008	Glen Ellyn, DuPage Co, IL	41.878	88.067	FMC	440305-WWH-565
IL009	Warrenville, DuPage Co, IL	41.818	88.173	FMC	440306-WWH-535
IL010	Warrenville, DuPage Co, IL	41.818	88.173	FMC	440308-WWH-541
IL011	West Chicago, DuPage Co, IL	41.885	88.204	FMC	443459-WWH-736
IL012	Oak Brook Terrace, Butterfield and McArthur, DuPage Co, IL	41.850	87.965	FMC	449034-WWH-850
IL013	Lake Forest, Shaw Woods, Lake Co, IL	40.633	89.399	FMC	460034-S08-920
IL014	need info	41.853	88.092	FMC	WWH-2637-WWH-2637
LAB01	Birch Island Road, Happy Valley-Goose Bay, Lab	53.291	60.318	Wild	2500-94857
LAB02	25 Palliser Crescent, Happy Valley-Goose Bay, Lab	53.302	60.317	Wild	2500-94858
LAB03	416 Hamilton River Road, Happy Valley-Goose Bay, Lab	53.315	60.382	Wild	2500-94863
LAB04	Blind Hill' Road, Happy Valley-Goose Bay, Lab	53.376	60.427	Wild	2500-94871
LAB05	Birch Island Road, Happy Valley-Goose Bay, Lab	53.295	60.311	Wild	2500-94879
LETH001	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57738

LETH002	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57739
LETH003	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57740
LETH004	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57741
LETH005	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57742
LETH006	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57743
LETH007	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57744
LETH008	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57745
LETH009	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57746
LETH010	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57747
LETH011	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57748
LETH012	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57749
LETH013	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57750
LETH014	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57751
LETH015	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57752
LETH016	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57753
LETH017	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57754
LETH018	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57755
LETH019	Helen Schuler Nature Centre, Lethbridge AB	49.694	112.863	Wild	2490-57757
MB01	Aggassiz, MB (RMNP vicinity)	50.778	99.641	CWS	3510-63171
MB02	Aggassiz, MB (RMNP vicinity)	50.778	99.652	CWS	3510-63176
MB03	Aggassiz, MB (RMNP vicinity)	50.772	99.661	CWS	2060-41988
MB04	Edward's Creek, MB (RMNP vicinity)	51.023	100.039	CWS	2060-41989
MB05	Ostenfeld, SE MB	49.783	96.502	CWS	2060-41368
MB06	Edward's Creek, MB (RMNP vicinity)	50.999	100.065	CWS	3510-63164
MB07	Edward's Creek, MB (RMNP vicinity)	51.012	100.072	CWS	3510-63169
MB08	Dawson Road, SE MB	49.649	96.242	CWS	2060-41365
MB09	Edward's Creek, MB (RMNP vicinity)	50.990	100.066	CWS	2060-41953
MB10	Edward's Creek, MB (RMNP vicinity)	51.011	100.069	CWS	3510-63189
MB11	Vermillion Creek, MB (RMNP vicinity)	50.972	100.266	CWS	2060-41966
MI001	Rapid River, Delta Co., Michigan	45.704	86.936	UMICH	240966
MI002	Whitefish Pt Bird Observatory, Vermillion Fld Sta, Chippewa Co.,	46.763	85.151	UMICH	240978

	Michigan				
MI003	Rapid River, Delta Co., Michigan	45.704	86.936	UMICH	240965
MI004	Dearborn, Univ Mich Dearborn, Wayne Co., Michigan	42.317	83.232	UMICH	240960
MI005	Commerce Twp., 2000 Marble Ct, Oakland Co., Michigan	42.564	83.464	UMICH	240716
MI006	Hancock, Houghton Co., Michigan	47.130	88.600	UMICH	240890
MI007	Waterloo Twp, Sec 24, Jackson Co., Michigan	42.382	84.138	UMICH	240793
MI008	Dexter, 2 mi NW, Washtenaw Co., Michigan	42.359	83.916	UMICH	240595
MI009	Joyfield Twp, T25N, R15W, SW part, Benzie Co., Michigan	44.538	86.131	UMICH	239393
MI010	Sands Twp, Marquette Co., Michigan	46.300	87.415	UMICH	239368
MI011	Sylvan Twp, Hayes Rd, Washtenaw Co., Michigan	42.261	84.113	UMICH	238975
MI012	Ann Arbor, Washtenaw Co., Michigan	42.271	83.726	UMICH	238705
MI013	Whitefish Point, Chippewa Co., Michigan	46.766	84.965	UMICH	238245
MI014	Albee Twp., T10N, R5E, Sec. 36, Saginaw Co., Michigan	43.228	83.825	UMICH	238223
MI015	Colfax Twp., T15N, R 9W, Sec. 12, Mecosta Co., Michigan	43.706	85.335	UMICH	238189
MI016	Austin Twp., Sec 32, NE 1/4 of NW 1/4, Mecosta Co., Michigan	43.567	85.416	UMICH	238188
MI017	Austin Twp., sec.32, NE1/4 of NW1/4, Mecosta Co., Michigan	43.567	85.416	UMICH	238186
MI018	Austin Twp., sec.32, NE1/4 of NW1/4, Mecosta Co., Michigan	43.567	85.416	UMICH	238185
MI019	Ontonagon, Ontonagon Co., Michigan	46.872	89.315	UMICH	238163
MI020	Ontonagon, Ontonagon Co., Michigan	46.872	89.315	UMICH	238162
MI021	Rapid River, Delta Co., Michigan	45.926	86.967	UMICH	238160
MI022	Barbeau, Chippewa Co., Michigan	46.289	84.281	UMICH	236450
MI023	Sheridan Twp., Mecosta Co., Michigan	43.683	85.147	UMICH	236031
MI024	Colfax Twp., Sec. 12, E 1/2 of NE 1/4 of NW 1/4, Mecosta Co., Michigan	43.712	85.337	UMICH	235624
MI025	Colfax Twp., Sec. 12, E 1/2 of NE 1/4 of NW 1/4, Mecosta Co., Michigan	43.712	85.337	UMICH	235622
MI026	Colfax Twp., Sec. 12, E 1/2 of NE 1/4 of NW 1/4, Mecosta Co., Michigan	43.712	85.337	UMICH	235621
MI027	Ann Arbor, Washtenaw Co., Michigan, Captive	42.271	83.726	UMICH	234775
MI028	Webster Twp, Huron River Drive near Mast, Washtenaw Co., Michigan	42.342	83.879	UMICH	227554
MI029	Plymouth, Wayne Co., Michigan	42.371	83.470	UMICH	227013
MI030	Ypsilanti, Prospect Road, Washtenaw Co., Michigan	42.286	83.604	UMICH	227012
MI031	Whitefish Point Bird Obs., Vermillion Field Sta., Chippewa Co., MI	46.762	85.151	UMICH	239485
MI032	Pavilion Twp, Sec 31, Pitsfield Banding Station, Kalamazoo Co., MI	42.172	85.516	UMICH	-6284

MI033	Fenton, Genesee Co., MI	42.797	83.707	UMICH	225937
MI034	Monterey, Highland (C near W border), Virginia	42.367	83.467	UMICH	225938
MO01	Saint Louis, MO	38.574	90.594	Wild	2540-23156
MO02	12432 Cape Cod Dr, St Louis, MO	38.681	90.457	Wild	2540-23157
MO03	Grand pass conservation area, MO	39.308	93.328	Wild	2580-47064
MO04	Grand pass conservation area, MO	39.308	93.328	Wild	2580-47099
MO05	Grand pass conservation area, MO	39.308	93.328	Wild	2580-47276
MO06	Grand pass conservation area, MO	39.308	93.328	Wild	2580-47280
MO07	Ashland, state road Y, MO	38.759	92.144	Wild	2540-23158
MO08	Ashland, state road Y, MO	38.759	92.144	Wild	2540-23159
MO09	University of Missouri research area, MO	38.757	92.201	Wild	2540-23160
MO10	University of Missouri research area, MO	38.757	92.201	Wild	2540-23161
MO11	University of Missouri research area, MO	38.757	92.201	Wild	2540-23162
MT001	Helena National Forest, Helena, MT	46.483	111.848	Wild	2540-22891
MT002	Helena National Forest, Helena, MT	46.483	111.848	Wild	2540-22892
MT003	Helena National Forest, Helena, MT	46.482	111.843	Wild	2540-22893
MT004	Helena National Forest, Helena, MT	46.482	111.843	Wild	2540-22894
MT005	Helena National Forest, Helena, MT	46.482	111.843	Wild	2540-22895
MT006	Orofino, Helena, MT	46.554	112.067	Wild	2530-19201
MT007	Orofino, Helena, MT	46.524	112.112	Wild	2530-19209
MT008	Road to Park Lake, Helena, MT	46.468	112.159	Wild	2530-19219
MT009	Road to Park Lake, Helena, MT	46.468	112.159	Wild	2530-19220
MT010	Orofino, Helena, MT	46.562	112.065	Wild	2530-19221
MT011	Orofino, Helena, MT	46.562	112.065	Wild	2530-19224
MT012	Orofino, Helena, MT	46.562	112.065	Wild	2530-19225
MT013	Road to Park Lake, Helena, MT	46.524	112.112	Wild	2530-19226
MT014	Road to Park Lake, Helena, MT	46.524	112.112	Wild	2530-19228
MT015	Road to Park Lake, Helena, MT	46.524	112.112	Wild	2530-19229
MT016	Road to Park Lake, Helena, MT	46.524	112.112	Wild	2530-19230
MT017	Road to Park Lake, Helena, MT	46.522	112.118	Wild	2530-19231
MT018	Road to Park Lake, Helena, MT	46.522	112.118	Wild	2530-19232

MT019	Road to Park Lake, Helena, MT	46.522	112.118	Wild	2530-19233
MT020	Twin Peaks Rd, Helena, MT	46.751	112.228	Wild	2530-19234
MT021	Twin Peaks Rd, Helena, MT	46.751	112.228	Wild	2530-19235
MT022	Twin Peaks Rd, Helena, MT	46.751	112.228	Wild	2530-19236
MT023	Montana City, near Helena, MT	46.532	111.990	Wild	2530-19239
MT024	Hitching Post Rd, Bozeman, MT	45.628	111.027	Wild	2530-19241
MT025	Hitching Post Rd, Bozeman, MT	45.628	111.027	Wild	2530-19242
MT026	Hitching Post Rd, Bozeman, MT	45.628	111.027	Wild	2530-19243
MT027	Bridger Woods Rd, Bozeman, MT	45.694	110.905	Wild	2530-19244
MT028	Bridger Woods Rd, Bozeman, MT	45.694	110.905	Wild	2530-19246
MT029	Bridger Woods Rd, Bozeman, MT	45.694	110.905	Wild	2530-19247
NC01	Purchase Knob, NC	35.586	83.073	Wild	2540-23155
NC02	North Carolina	35.620	79.064	NCM	catalog#15205
NC03	North Carolina	35.303	82.896	NCM	catalog#15207
NC04	North Carolina	-		NCM	catalog#15227
NC05	North Carolina	35.219	82.778	NCM	catalog#15248
NEOR001	Morgan Lake, OR	45.301	118.136	Wild	2540-23028
NEOR002	Catherine Creek St. park, OR	45.152	117.742	Wild	2540-23031
NEOR003	Catherine Creek St. park, OR	45.152	117.742	Wild	2540-23032
NEOR004	Bird Track Springs Trail, OR	45.303	118.308	Wild	2540-23034
NEOR005	Bird Track Springs Trail, OR	45.303	118.308	Wild	2540-23035
NEOR006	Bird Track Springs Trail, OR	45.303	118.308	Wild	2540-23036
NEOR007	Bird Track Springs Trail, OR	45.303	118.308	Wild	2540-23037
NEOR008	Bird Track Springs Trail, OR	45.303	118.308	Wild	2540-23038
NEOR009	Hilgard junction state park, OR	45.343	118.239	Wild	2540-23040
NEOR010	Red Bridge State park, OR	45.290	118.333	Wild	2540-23041
NEOR011	Red Bridge State park, OR	45.290	118.333	Wild	2540-23042
NEOR012	Hilgard junction state park, OR	45.343	118.239	Wild	2540-23043
NEOR013	Bird Track Springs Trail, OR	45.303	118.308	Wild	2540-23033
NEOR014	Hilgard junction state park, OR	45.343	118.239	Wild	2540-23039
NEOR015	Hilgard junction state park, OR	45.343	118.239	Wild	2540-23044

NL001	Richard Squires PP, NL	49.347	57.335	Wild	2490-57579
NL002	Richard Squires PP, NL	49.347	57.335	Wild	2490-57582
NL003	Richard Squires PP, NL	49.347	57.335	Wild	2490-57585
NL004	Richard Squires PP, NL	49.347	57.335	Wild	2490-57586
NL005	Richard Squires PP, NL	49.347	57.335	Wild	2490-57587
NL006	Barachois PP, NL	48.454	58.433	Wild	2490-57588
NL007	Barachois PP, NL	48.454	58.433	Wild	2490-57589
NL008	Barachois PP, NL	48.454	58.433	Wild	2490-57590
NL009	Barachois PP, NL	48.454	58.433	Wild	2490-57591
NL010	Barachois PP, NL	48.454	58.433	Wild	2490-57593
NL011	Passadena, NL	49.014	57.598	Wild	2490-57594
NL012	Passadena, NL	49.014	57.598	Wild	2490-57595
NL013	Passadena, NL	49.014	57.598	Wild	2490-57599
NL014	Passadena, NL	49.014	57.598	Wild	2490-57600
NL015	Passadena, NL	49.014	57.598	Wild	2490-57604
NL016	Passadena, NL	49.014	57.598	Wild	2490-57606
NL017	Passadena, NL	49.014	57.598	Wild	2490-57610
NL018	Passadena, NL	49.014	57.598	Wild	2490-57611
NL019	Deer Lake, NL	49.175	57.424	Wild	2490-57612
NL020	Deer Lake, NL	49.175	57.424	Wild	2490-57613
NL021	Terra Nova NP (SW Brook), NL	48.520	53.967	Wild	2490-57621
NL022	Terra Nova NP (SW Brook), NL	48.520	53.967	Wild	2490-57622
NL023	Terra Nova NP (SW Brook), NL	48.520	53.967	Wild	2490-57623
NL024	Terra Nova NP (Newman), NL	48.520	53.967	Wild	2490-57626
NL025	Terra Nova NP (Malady Head), NL	48.520	53.967	Wild	2490-57627
NL026	Terra Nova NP (Malady Head), NL	48.520	53.967	Wild	2490-57628
NL027	Terra Nova NP (Malady Head), NL	48.520	53.967	Wild	2490-57629
NL028	Terra Nova NP (Malady Head), NL	48.520	53.967	Wild	2490-57631
NL029	Campground, Sir Richard Squires PP, NL	49.350	57.167	Wild	2500-94842
NL030	Lomond Campground, Gros Morne NP, NL	49.459	57.760	Wild	2500-94850
NL031	Lomond Campground, Gros Morne NP, NL	49.459	57.760	Wild	2500-94852

NL032	Shallow Bay Campground, Gros Morne NP, NL	49.939	57.760	Wild	2500-94854
NL033	Berry Hill Pond/Bog, Gros Morne NP, NL	49.625	57.928	Wild	2500-94855
NL034	Killdevil Camp, Gros Morne NP, NL	49.454	57.756	Wild	2500-94885
NL035	Killdevil Camp, Gros Morne NP, NL	49.454	57.756	Wild	2500-94886
NM001	Pulloff 1/3 mile from Chimisa Trailhead, Santa Fe NF, NM	35.728	105.869	Wild	2580-49301
NM002	Pulloff 1/3 mile from Chimisa Trailhead, Santa Fe NF, NM	35.728	105.869	Wild	2580-49302
NM003	Randall Davey Audubon Center, Santa Fe, NM	35.690	105.888	Wild	2580-49303
NM004	Randall Davey Audubon Center, Santa Fe, NM	35.690	105.888	Wild	2580-49304
NM005	Mile 6, Hyde Park Road, Santa Fe NF, NM	35.728	105.878	Wild	2580-49305
NM006	Santa Fe Canyon Preserve, The Nature Conservancy, Santa Fe, NM	35.689	105.892	Wild	2580-49306
NM007	Pajarito Village, NM	-		MSB	MSB21348
NM008	Pajarito Village, NM	-		MSB	MSB24161
NM009	Pajarito Village, NM	-		MSB	MSB24162
NM010	Pajarito Village, NM	-		MSB	MSB24163
NM011	Rio Grande Nature Center, Albuquerque, NM	-		MSB	MSB28982
NSNB001	Margaretsville, NS	45.095	65.597	Wild	2490-57501
NSNB002	Margaretsville, NS	45.095	65.597	Wild	2490-57511
NSNB003	Margaretsville, NS	45.095	65.597	Wild	2490-57503
NSNB004	Margaretsville, NS	45.095	65.597	Wild	2490-57512
NSNB005	Margaretsville, NS	45.095	65.597	Wild	2490-57505
NSNB006	Margaretsville, NS	45.095	65.597	Wild	2490-57506
NSNB007	Margaretsville, NS	45.095	65.597	Wild	2490-57507
NSNB008	Margaretsville, NS	45.095	65.597	Wild	2490-57508
NSNB009	Margaretsville, NS	45.095	65.597	Wild	2490-57509
NSNB010	Margaretsville, NS	45.095	65.597	Wild	2490-57510
NSNB011	Economy Lake, NS	45.095	65.597	Wild	2490-57561
NSNB012	Margaretsville, NS	45.095	65.597	Wild	2490-57513
NSNB013	Margaretsville, NS	45.095	65.597	Wild	2490-57514
NSNB014	Margaretsville, NS	45.095	65.597	Wild	2490-57515
NSNB015	Margaretsville, NS	45.095	65.597	Wild	2490-57516
NSNB016	Margaretsville, NS	45.095	65.597	Wild	2490-57517

NSNB017	Margaretsville, NS	45.095	65.597	Wild	2490-57518
NSNB018	Margaretsville, NS	45.095	65.597	Wild	2490-57519
NSNB019	Margaretsville, NS	45.095	65.597	Wild	2490-57520
NSNB020	Margaretsville, NS	45.095	65.597	Wild	2490-57521
NSNB021	Margaretsville, NS	45.095	65.597	Wild	2490-57522
NSNB022	Margaretsville, NS	45.095	65.597	Wild	2490-57523
NSNB023	Mt Hanley, NS	44.754	65.131	Wild	2490-57524
NSNB024	Mt Hanley, NS	44.754	65.131	Wild	2490-57525
NSNB025	Mt Hanley, NS	44.754	65.131	Wild	2490-57526
NSNB026	Mt Hanley, NS	44.754	65.131	Wild	2490-57527
NSNB027	Mt Hanley, NS	44.754	65.131	Wild	2490-57528
NSNB028	Mt Hanley, NS	44.754	65.131	Wild	2490-57529
NSNB029	Mt Hanley, NS	44.754	65.131	Wild	2490-57530
NSNB030	Mt Hanley, NS	44.754	65.131	Wild	2490-57531
NSNB032	Margaretsville, NS	45.095	65.597	Wild	2490-57504
NSNB033	Mt Hanley, NS	44.754	65.131	Wild	2490-57532
NSNB034	Mt Hanley, NS	44.754	65.131	Wild	2490-57533
NSNB035	Margaretsville, NS	45.095	65.597	Wild	2490-57534
NSNB036	Margaretsville, NS	45.095	65.597	Wild	2490-57535
NSNB037	Mt Hanley, NS	44.754	65.131	Wild	2490-57536
NSNB038	Mt Hanley, NS	44.754	65.131	Wild	2490-57537
NSNB039	Middleton, NS	44.754	65.131	Wild	2490-57538
NSNB040	Middleton, NS	44.754	65.131	Wild	2490-57539
NSNB041	Middleton, NS	44.754	65.131	Wild	2490-57540
NSNB042	Middleton, NS	44.754	65.131	Wild	2490-57541
NSNB043	Middleton, NS	44.754	65.131	Wild	2490-57542
NSNB044	Alysford, NS	45.029	64.838	Wild	2490-57543
NSNB045	Alysford, NS	45.029	64.838	Wild	2490-57544
NSNB046	Alysford, NS	45.029	64.838	Wild	2490-57545
NSNB048	Alysford, NS	45.029	64.838	Wild	2490-57547
NSNB049	Alysford, NS	45.029	64.838	Wild	2490-57548

NSNB050	Middleton, NS	44.961	65.067	Wild	2490-57549
NSNB051	Alysford, NS	45.029	64.838	Wild	2490-57550
NSNB052	Alysford, NS	45.029	64.838	Wild	2490-57551
NSNB053	Alysford, NS	45.029	64.838	Wild	2490-57552
NSNB054	Alysford, NS	45.029	64.838	Wild	2490-57553
NSNB055	Alysford, NS	45.029	64.838	Wild	2490-57554
NSNB056	Alysford, NS	45.029	64.838	Wild	2490-57555
NSNB057	Economy Lake, NS	45.385	63.911	Wild	2490-57562
NSNB058	Economy Lake, NS	45.385	63.911	Wild	2490-57563
NSNB059	Economy Lake, NS	45.385	63.911	Wild	2490-57564
NSNB060	Fundy NP, NB	45.615	65.036	USNM	2490-57565
NSNB061	Fundy NP, NB	45.615	65.036	USNM	2490-57566
NSNB062	Fundy NP, NB	45.615	65.036	USNM	2490-57567
NSNB063	Fundy NP, NB	45.615	65.036	USNM	2490-57571
NSNB064	Cape North, NS	46.888	60.530	Wild	2490-57574
NSNB065	Cape North, NS	46.888	60.530	Wild	2490-57575
NSNB066	Cape North, NS	46.888	60.530	Wild	2490-57576
NSNB067	Antigonish, NS	45.622	61.994	Wild	2490-57577
NSNB068	Fundy Headquarters Campground, Fundy NP, NB	45.598	64.951	USNM	2500-94801
NSNB069	Fundy Headquarters Campground, Fundy NP, NB	45.598	64.951	USNM	2500-94802
NSNB070	Two Neck Road, Quispamsis, NB	45.479	65.919	USNM	2500-94803
NSNB071	Two Neck Road, Quispamsis, NB	45.479	65.919	USNM	2500-94804
NSNB072	Two Neck Road, Quispamsis, NB	45.479	65.919	Wild	2500-94805
NSNB073	Two Neck Road, Quispamsis, NB	45.479	65.919	USNM	2500-94806
NSNB074	Two Neck Road, Quispamsis, NB	45.479	65.919	USNM	2500-94807
NSNB075	Two Neck Road, Quispamsis, NB	45.479	65.919	USNM	2500-94808
NSNB076	Two Neck Road, Quispamsis, NB	45.479	65.919	USNM	2500-94809
NSNB077	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94810
NSNB078	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94811
NSNB079	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94812
NSNB080	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94813

NSNB081	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94814
NSNB082	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94815
NSNB083	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94816
NSNB084	47 Silas Lewis Road, Second North River, NB	46.063	65.049	Wild	2500-94817
NSNB085	47 Silas Lewis Road, Second North River, NB	46.063	65.049	USNM	2500-94818
NSNB086	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94820
NSNB087	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94821
NSNB088	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94823
NSNB089	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94824
NSNB090	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94825
NSNB091	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94826
NSNB092	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94822
NSNB093	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94827
NSNB094	70 Browns Place Road, Middle Musquodoboit, NS	45.035	63.085	Wild	2500-94828
NSNB095	218 Fraser Road, East Hants, NS	45.107	63.638	Wild	2500-94830
NSNB096	218 Fraser Road, East Hants, NS	45.107	63.638	Wild	2500-94831
NSNB097	218 Fraser Road, East Hants, NS	45.107	63.638	Wild	2500-94832
NSNB098	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94833
NSNB099	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94834
NSNB100	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94835
NSNB101	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94836
NSNB102	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94837
NSNB103	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94838
NSNB104	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94840
NSNB105	1814 Fairmont Road, Antigonish, NS	45.716	61.942	Wild	2500-94841
NSNB106	Blueberry Burn', Musquodoboit Valley, NS	45.014	63.028	Wild	2500-94887
NSNB107	Pepper's Property, Musquodoboit Valley, NS	45.015	63.034	Wild	2500-94889
NSNB108	Pepper's Property, Musquodoboit Valley, NS	45.015	63.034	Wild	2500-94890
NSNB109	Reid's Road, Middle Musquodoboit, NS	45.014	63.049	Wild	2500-94891
NSNB110	Reid's Road, Middle Musquodoboit, NS	45.014	63.049	Wild	2500-94892
NSNB111	Clay Slump Trail, Restigouche Rd, near St. Quentin, NB	47.491	67.223	Wild	2500-94962

NSNB112	Acadian Timber Road A1, near Mt Carleton PP, NB	47.432	66.995	Wild	2500-94963
NSNB113	Acadian Timber Road A1, near Mt Carleton PP, NB	47.432	66.995	Wild	2500-94964
NWBC001	Telegraph Creek, BC	58.401	131.212	Wild	2520-39865
NWBC002	Telegraph Creek, BC	58.401	131.212	Wild	2520-39866
NWBC003	Telegraph Creek, BC	57.909	131.224	Wild	2520-39867
NWBC004	Telegraph Creek, BC	57.909	131.224	Wild	2520-39868
NWBC005	Dease Lake, BC	58.507	130.023	Wild	2520-39874
NWBC006	Dease Lake, BC	58.430	129.987	Wild	2520-39875
NWBC007	Dease Lake, BC	58.430	129.987	Wild	2520-39876
NWBC008	Dease Lake, BC	58.430	129.987	Wild	2520-39877
NWBC009	Dease Lake, BC	58.430	129.987	Wild	2520-39878
NWBC010	Dease Lake, BC	58.430	129.987	Wild	2520-39879
NWBC011	Dease Lake, BC	58.430	129.987	Wild	2520-39880
NWBC012	Dease Lake, BC	58.430	129.987	Wild	2520-39881
NWBC013	Telegraph Creek, BC	57.913	131.210	Wild	2520-39859
NWBC014	Telegraph Creek, BC	57.913	131.210	Wild	2520-39860
NWBC015	Telegraph Creek, BC	57.913	131.210	Wild	2520-39861
NWBC016	Telegraph Creek, BC	57.913	131.210	Wild	2520-39862
NWBC017	Telegraph Creek, BC	57.913	131.210	Wild	2520-39863
ON001	QUBS near Kingston ON	44.567	76.317	QUBS	11-2005
ON002	QUBS near Kingston ON	44.567	76.317	QUBS	112-2005
ON003	QUBS near Kingston ON	44.567	76.317	QUBS	116-2005
ON004	QUBS near Kingston ON	44.567	76.317	QUBS	119-2005
ON005	QUBS near Kingston ON	44.567	76.317	QUBS	120-2005
ON006	QUBS near Kingston ON	44.567	76.317	QUBS	121-2005
ON007	QUBS near Kingston ON	44.567	76.317	QUBS	123-2005
ON008	QUBS near Kingston ON	44.567	76.317	QUBS	124-2005
ON009	QUBS near Kingston ON	44.567	76.317	QUBS	126-2005
ON010	QUBS near Kingston ON	44.567	76.317	QUBS	127-2005
ON011	QUBS near Kingston ON	44.567	76.317	QUBS	128-2005
ON012	QUBS near Kingston ON	44.567	76.317	QUBS	129-2005

ON013	QUBS near Kingston ON	44.567	76.317	QUBS	131-2005
ON014	QUBS near Kingston ON	44.567	76.317	QUBS	133-2005
ON015	QUBS near Kingston ON	44.567	76.317	QUBS	137-2005
ON016	QUBS near Kingston ON	44.567	76.317	QUBS	145-2005
ON017	QUBS near Kingston ON	44.567	76.317	QUBS	147-2005
ON018	QUBS near Kingston ON	44.567	76.317	QUBS	172-2005
ON019	QUBS near Kingston ON	44.567	76.317	QUBS	173-2005
ON020	QUBS near Kingston ON	44.567	76.317	QUBS	51-2005
ON021	QUBS near Kingston ON	44.567	76.317	QUBS	88-2005
ON022	QUBS near Kingston ON	44.567	76.317	QUBS	89-2005
ON023	QUBS near Kingston ON	44.567	76.317	QUBS	BBRS125-2005
ON024	QUBS near Kingston ON	44.567	76.317	QUBS	BGRS163-2005
ON025	QUBS near Kingston ON	44.567	76.317	QUBS	GPGS167-2005
ON026	QUBS near Kingston ON	44.567	76.317	QUBS	MBRS169-2005
ON027	QUBS near Kingston ON	44.567	76.317	QUBS	MGPS171-2005
ON028	QUBS near Kingston ON	44.567	76.317	QUBS	MRPS166-2005
ON029	QUBS near Kingston ON	44.567	76.317	QUBS	PGBS170-2005
ON030	QUBS near Kingston ON	44.567	76.317	QUBS	PGMS160-2005
ON31	Rainy River, ON	48.708	94.441	CWS	2060-41375
ON33	Rainy River, ON	48.708	94.441	CWS	2060-41376
ON34	Rainy River, ON	48.708	94.441	CWS	2060-41377
SAB001	West Castle, AB	49.345	114.415	Wild	2490-57633
SAB002	West Castle, AB	49.345	114.415	Wild	2490-57634
SAB003	West Castle, AB	49.345	114.415	Wild	2490-57635
SAB004	West Castle, AB	49.345	114.415	Wild	2490-57636
SAB005	West Castle, AB	49.345	114.415	Wild	2490-57637
SAB006	West Castle, AB	49.345	114.415	Wild	2490-57638
SAB007	West Castle, AB	49.345	114.415	Wild	2490-57639
SAB008	West Castle, AB	49.345	114.415	Wild	2490-57646
SAB009	West Castle, AB	49.345	114.415	Wild	2490-57647
SAB010	West Castle, AB	49.345	114.415	Wild	2490-57649

SAB011	West Castle, AB	49.345	114.415	Wild	2490-57650
SAB012	West Castle, AB	49.345	114.415	Wild	2490-57651
SAB013	West Castle, AB	49.345	114.415	Wild	2490-57652
SAB014	West Castle, AB	49.345	114.415	Wild	2490-57653
SAB015	West Castle, AB	49.345	114.415	Wild	2490-57654
SAB016	West Castle, AB	49.345	114.415	Wild	2490-57655
SAB017	West Castle, AB	49.345	114.415	Wild	2490-57656
SAB018	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57659
SAB019	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57660
SAB020	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57661
SAB021	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57662
SAB022	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57663
SAB023	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57664
SAB024	Field station cabin, AB	49.349	114.411	Wild	2490-57673
SAB025	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57677
SAB026	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57678
SAB027	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57679
SAB028	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57680
SAB029	North Lost Creek Rd, AB	49.472	114.463	Wild	2490-57682
SAB030	North Lost Creek Rd, AB	49.472	114.463	Wild	2490-57683
SAB031	Hwy 6, Waterton, S AB	49.106	113.821	Wild	2490-57715
SAB032	Hwy 6, Waterton, S AB	49.106	113.821	Wild	2490-57716
SAB033	Hwy 6, Waterton, S AB	49.106	113.821	Wild	2490-57717
SAB034	Hwy 6, Waterton, S AB	49.106	113.821	Wild	2490-57718
SAB035	Crandall Lake Campground, Waterton, S AB	49.097	113.955	Wild	2490-57719
SAB036	Crandall Lake Campground, Waterton, S AB	49.097	113.955	Wild	2490-57721
SAB037	Hwy 6, Waterton, S AB	49.084	113.802	Wild	2490-57722
SAB038	Hwy 6, Waterton, S AB	49.084	113.802	Wild	2490-57723
SAB039	Hwy 6, Waterton, S AB	49.084	113.802	Wild	2490-57724
SAB040	Hwy 6, Waterton, S AB	49.076	113.791	Wild	2490-57725
SAB041	Hwy 6, Waterton, S AB	49.076	113.791	Wild	2490-57726

SAB042	Belly River Campground, Waterton, S AB	49.022	113.687	Wild	2490-57727
SAB043	Belly River Campground, Waterton, S AB	49.022	113.687	Wild	bcch 43
SAB044	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57728
SAB045	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57729
SAB046	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57730
SAB047	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57731
SAB048	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57732
SAB049	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57733
SAB050	Marquis Hole Picnic Area, Waterton, S AB	49.069	113.856	Wild	2490-57734
SAB051	Marquis Hole, Waterton, S AB	49.069	113.856	Wild	2490-57737
SAB052	Belly River Campground Waterton, AB	49.023	113.687	Wild	A
SD001	"No Vehicles" Trail, Needles Highway, Custer State Park, SD	43.796	103.442	Wild	2540-22937
SD002	"Sapsucker Enclosure", 87 & 16 Junction, Custer State Park, SD	43.759	103.484	Wild	2540-22938
SD003	"Sapsucker Enclosure", 87 & 16 Junction, Custer State Park, SD	43.759	103.484	Wild	2540-22939
SD004	Hole in the Wall Picnic Area, Custer State Park, SD	43.811	103.456	Wild	2540-22940
SD005	Transistor Pulloff, Needles Highway, Custer State Park, SD	43.779	103.449	Wild	2540-22941
SD006	Transistor Pulloff, Needles Highway, Custer State Park, SD	43.779	103.449	Wild	2540-22942
SD007	Low Powerline Wetland, Needles Highway, Custer State Park, SD	43.776	103.453	Wild	2540-22943
SD008	Low Powerline Wetland, Needles Highway, Custer State Park, SD	43.776	103.453	Wild	2540-22944
SD009	Center Lake Campground, Custer State Park, SD	43.808	103.422	Wild	2540-22945
SD010	Chipmunk Corner, Needles Highway, Custer State Park, SD	43.808	103.422	Wild	2540-22946
SD011	Chipmunk Corner, Needles Highway, Custer State Park, SD	43.808	103.422	Wild	2540-22947
SD012	Chipmunk Corner, Needles Highway, Custer State Park, SD	43.808	103.422	Wild	2540-22948
SD013	Chipmunk Corner, Needles Highway, Custer State Park, SD	43.808	103.422	Wild	2540-22949
SD014	Sylvan Lake Day Use Area, Custer State Park, SD	43.846	103.559	Wild	2540-22950
SD015	Center Lake Campground, Custer State Park, SD	43.808	103.422	Wild	2540-22951
SD016	Center Lake Campground, Custer State Park, SD	43.808	103.422	Wild	2540-22952
SD017	"Sapsucker Enclosure", 87 & 16 Junction, Custer State Park, SD	43.759	103.484	Wild	2540-22954
SK01	Narrows Campground, Campsite 67, Prince Albert NP, SK	53.982	106.292	Wild	2500-94893
SK02	Narrows Campground, Campsite 67, Prince Albert NP, SK	53.982	106.292	Wild	2500-94894
SK03	Narrows Campground, Campsite 67, Prince Albert NP, SK	53.982	106.292	Wild	2500-94895

SK04	South Bay, Prince Albert NP, SK	53.899	106.159	Wild	2500-94898
SK05	South Bay, Prince Albert NP, SK	53.899	106.159	Wild	2500-94899
SK06	South Bay, Prince Albert NP, SK	53.899	106.159	Wild	D1
SK07	South Bay, Prince Albert NP, SK	53.899	106.159	Wild	2500-94900
SK08	South Bay, Prince Albert NP, SK	53.899	106.159	Wild	2500-94898
SK09	57 Trail, Prince Albert NP, SK	53.945	106.228	Wild	2490-57777
SK10	57 Trail, Prince Albert NP, SK	53.945	106.228	Wild	2490-57778
SK11	57 Trail, Prince Albert NP, SK	53.945	106.228	Wild	2490-57779
SK12	Fisher Trail, Prince Albert NP, SK	53.923	106.067	Wild	2490-57780
SK13	Fisher Trail, Prince Albert NP, SK	53.923	106.067	Wild	2490-57781
SK14	Fisher Trail, Prince Albert NP, SK	53.923	106.067	Wild	2490-57782
SK15	Fisher Trail, Prince Albert NP, SK	53.923	106.067	Wild	2490-57783
SK16	Treebeard Trail, Prince Albert NP, SK	53.973	106.290	Wild	2490-57784
SK17	Narrows Campground, Campsite 82, Prince Albert NP, SK	53.981	106.294	Wild	2500-94942
SK18	Narrows Campground, Campsite 82, Prince Albert NP, SK	53.981	106.294	Wild	2500-94943
SK19	Fisher Trail, Prince Albert NP, SK	53.923	106.067	Wild	2490-57785
SK20	Narrows Campground, Campsite 74, Prince Albert NP, SK	53.981	106.294	Wild	2500-94894
SK21	Narrows Campground, Campsite 74, Prince Albert NP, SK	53.981	106.294	Wild	2500-94946
SK22	Freight Trail, 'D' entrance, Prince Albert NP, SK	53.707	106.054	Wild	2490-57787
SK23	Freight Trail, 'D' entrance, Prince Albert NP, SK	53.707	106.054	Wild	2490-57788
SK24	Trippes Beach, Prince Albert NP, SK	53.908	106.182	Wild	2500-94957
SK25	Trippes Beach, Prince Albert NP, SK	53.908	106.182	Wild	2500-94958
SK26	Red Deer Trail Blue Loop, Prince Albert NP, SK	53.940	106.060	Wild	2490-57790
SK27	Mud Creek Trail, Prince Albert NP, SK	53.898	106.164	Wild	2490-57791
SK28	Mud Creek Trail, Prince Albert NP, SK	53.898	106.164	Wild	2490-57792
SK29	Mud Creek Trail, Prince Albert NP, SK	53.898	106.164	Wild	2490-57793
SK30	Mud Creek Trail, Prince Albert NP, SK	53.898	106.164	Wild	2490-57794
SK31	Red Deer Trail Blue Loop, Prince Albert NP, SK	53.940	106.060	Wild	2490-57795
SK32	Red Deer Trail Blue Loop, Prince Albert NP, SK	53.940	106.060	Wild	2490-57796
SK33	Red Deer Trail Blue Loop, Prince Albert NP, SK	53.945	106.077	Wild	2490-57797
SOR001	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2510-51352

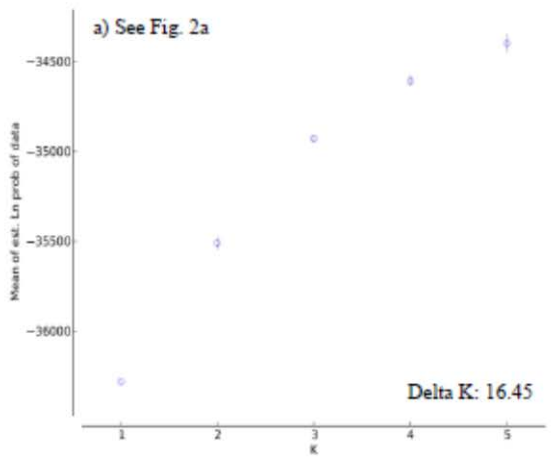
SOR002	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2540-23045
SOR003	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2510-19834
SOR004	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2540-23046
SOR005	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2540-23047
SOR006	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2440-87440
SOR007	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2510-52793
SOR008	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2540-23048
SOR009	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2560-67576
SOR010	North Mountain Nature Center, Ashland, OR	42.201	122.685	Wild	2460-25547
SOR011	Central Point, Medford, OR	42.367	122.885	Wild	2540-23049
SOR012	Central Point, Medford, OR	42.367	122.885	Wild	2540-23050
SOR013	Central Point, Medford, OR	42.367	122.885	Wild	2540-23051
SOR014	Central Point, Medford, OR	42.367	122.885	Wild	2540-23052
SOR015	Central Point, Medford, OR	42.367	122.885	Wild	2540-23053
UT001	NE Huntsville (Reservoir), UT	41.290	111.583	Wild	2540-23120
UT002	Magpie campground, UT	41.256	111.666	Wild	2540-23121
UT003	Magpie campground, UT	41.256	111.666	Wild	2540-23122
UT004	W of Woodruff (Cache Forestry Rd.), UT	41.436	111.480	Wild	2540-23123
UT005	W of Woodruff (Cache Forestry Rd.), UT	41.436	111.480	Wild	2540-23124
UT006	Boots campground, UT	41.294	111.658	Wild	2540-23125
UT007	Boots campground, UT	41.294	111.658	Wild	2540-23126
UT008	Boots campground, UT	41.294	111.658	Wild	2540-23127
UT009	Boots campground, UT	41.294	111.658	Wild	2540-23128
UT010	Snowbasin Road, UT	41.226	111.851	Wild	2540-23129
UT011	Snowbasin Road, UT	41.226	111.851	Wild	2540-23130
UT012	Snowbasin Road, UT	41.226	111.851	Wild	2540-23131
UT013	Snowbasin Road, UT	41.226	111.851	Wild	2540-23132
UT014	Snowbasin Road, UT	41.226	111.851	Wild	2540-23133
UT015	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23134
UT016	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23135
UT017	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23136

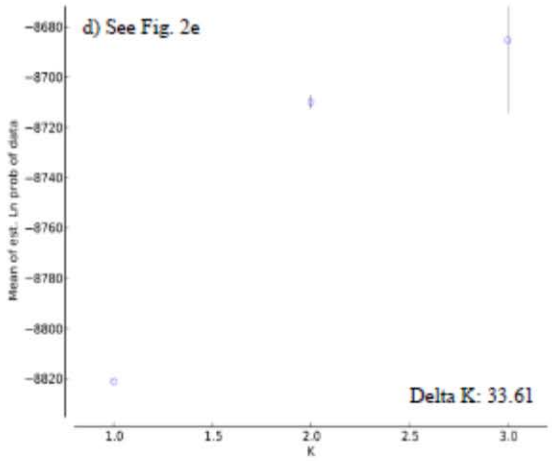
UT018	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23137
UT019	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23138
UT020	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23139
UT021	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23140
UT022	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23141
UT023	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23142
UT024	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23143
UT025	Snow Basin Rd., UT	41.280	110.654	Wild	2540-23144
UT026	Jefferson Hunt, Campground, Huntsville UT	41.249	111.769	Wild	2540-23145
UT027	Jefferson Hunt, Campground, Huntsville UT	41.249	111.769	Wild	2540-23146
UT028	3 Mile Creek, UT	41.453	111.851	Wild	2540-23147
UT029	Hwy 226, Ogden, UT	41.227	111.835	Wild	2540-23148
UT030	Hwy 226, Ogden, UT	41.227	111.835	Wild	2540-23149
WA001	206 23 Ave SE Puyallup, WA	47.169	122.291	Wild	2540-23003
WA002	206 23 Ave SE Puyallup, WA	47.169	122.291	Wild	2540-23004
WA003	206 23 Ave SE Puyallup, WA	47.169	122.291	Wild	2540-23005
WA004	206 23 Ave SE Puyallup, WA	47.169	122.291	Wild	2540-23006
WA005	Auburn 2535 26 St, WA	47.286	122.195	Wild	2540-23007
WA006	Auburn 2535 26 St, WA	47.286	122.195	Wild	2540-23008
WA007	Lake Tapps 16318 37St. Cr. E., WA	47.223	122.213	Wild	2540-23009
WA008	Lake Tapps 16318 37St. Cr. E., WA	47.223	122.213	Wild	2540-23010
WA009	Puyallup, WA	47.113	122.213	Wild	2540-23011
WA010	Lake Tapps 16318 37St. Cr. E., WA	47.223	122.213	Wild	2540-23012
WA011	Puyallup 12009 64th Ave E., WA	47.147	122.344	Wild	2540-23013
WA012	Seattle. Forest Park 15815 34th Ave NE, WA	47.743	122.293	Wild	2550-23014
WA013	Seattle South othello St.	47.536	122.263	Wild	2540-23015
WA014	Seattle South othello St.	47.536	122.263	Wild	2540-23016
WA015	Seattle South othello St.	47.536	122.263	Wild	2540-23017
WA016	Seattle South othello St.	47.536	122.263	Wild	2540-23018
WA017	Seattle South othello St.	47.536	122.263	Wild	2540-23019
WA018	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23020

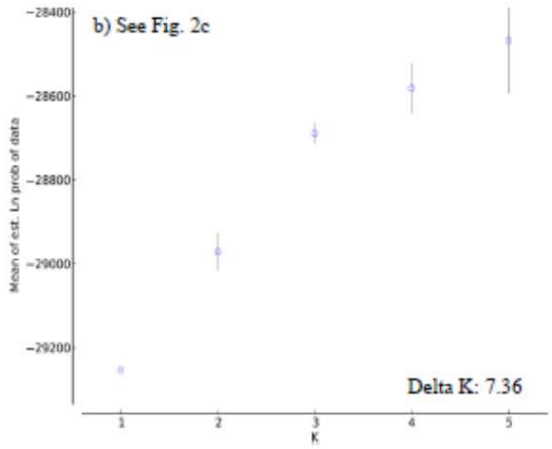
WA019	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23021
WA020	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23022
WA021	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23023
WA022	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23024
WA023	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23025
WA024	Seattle Shoreline Ashworth Ave.	47.764	122.341	Wild	2540-23026
WA025	Seattle 7018 Maltby RD	47.804	122.139	Wild	2540-23027
WA026	Washington	46.972	120.810	NCM	catalog#19641
WA027	Washington	46.972	120.810	NCM	catalog#19642 tissue#B08984
WV01	Monterey, Highland (C near W border), Virginia	38.586	79.637	USNM	voucher#587440 tissue#B09005
WV02	Reddish Knob, Augusta (C near W border), Virginia	38.455	79.252	USNM	voucher#587441 tissue#B12081
WV03	Ryder Gap, Bath (C near W border), Virginia	38.185	79.921	USNM	voucher#601417 tissue#B12110
WV04	Warm Springs, Bath (C near W border), Virginia	38.149	79.765	USNM	voucher#601401 tissue#B13208
WV05	Trout Dale, Grayson (SW), Virginia	36.670	81.487	USNM	voucher#601580 tissue#B13216
WV06	Atkins, Smyth (SW), Virginia	36.835	81.371	USNM	voucher#601622 tissue#B17025
WV07	Dryden, 1.4 mi NE, at Powell River, near Rt. 621, Lee (SW), Virginia	36.800	82.904	USNM	voucher#633890 tissue#B17028
WV08	Dryden, 1.4 mi NE, at Powell River, near Rt. 621, Lee (SW), Virginia	36.800	82.904	USNM	voucher#633893 tissue#B17033
WV09	Dryden, 1.4 mi NE, at Powell River, near Rt. 621, Lee (SW), Virginia	36.800	82.904	USNM	voucher#633918 tissue#B17866
WV10	Monterey, Highland (C near W border), Virginia	38.583	79.637	USNM	voucher#634200 tissue#B17867
WV11	Monterey, Highland (C near W border), Virginia	38.583	79.637	USNM	voucher#634201 tissue#B08865
WV12	Paddy Knob, Pocahontas (clusters with Bath), West Virginia	38.268	79.793	USNM	voucher#586253 tissue#B08870
WV13	Paddy Knob, Pocahontas (clusters with Bath), West Virginia	38.268	79.793	USNM	voucher#586255

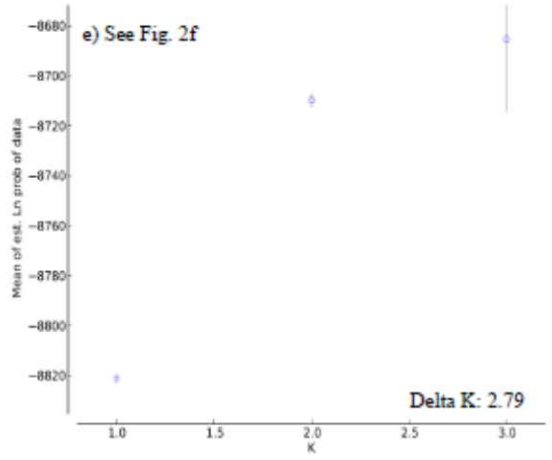
Appendix 1.2. Repeat type (if known), primer sequence, allele size range (bp), number of alleles (***Na***) and $MgCl_2$ concentration for each microsatellite locus used to genotype black-capped chickadee individuals.

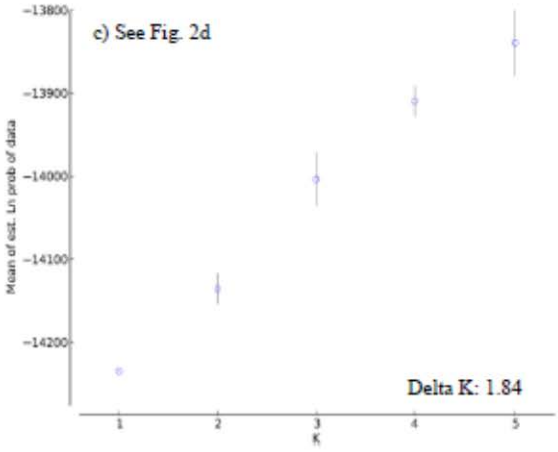
Locus	Repeat type	Sequence (5' to 3')	Size range (bp)	*Na*	$MgCl_2$ (mM)	Reference
PAT MP 2-14F		GAACAGATAAAGCCAAATTAC	139-177	24	2	Otter *et al.*, 1998
PAT MP 2-14R		TAGTGAATGCTTGATTTCTTTG				
PAT MP 2-43F		ACAGGTAGTCAGAAATGGAAAG	145-257	37	1.5	Otter *et al.*, 1998
PAT MP 2-43R		GTATCCAGAGTCTTTGCTGATG				
Escu6F		CATAGTGATGCCCTGCTAGG	114-172	20	1.5	Hanotte *et al.*, 1994
Escu6R		GCAAGTGCTCCTTAATATTTGG				
Titgata02F	$(GATA)_{12}$	ATTGCTTGATATTTGAAAGCATA	204-320	20	2	Wang *et al.*, 2005
Titgata02R		TTGTCTTTTGGGTTGCCTGA				
Titgata39F	$(GATA)_{10}$	CATGTATTTTCCAAAAGTAAATAT	228-262	18	2	Wang *et al.*, 2005
Titgata39R		CTGCTATTCTGCAAACTTGTGG				
CcaTgu11F		TGCTTAGGAAATAGGAAGCACA	210-218	5	2	Olano-Marin *et al.*, 2010
CcaTgu11R		CTGCAACTTAAGCARRGTTATGA				
PmanTAGAn71F	$(TAGG)_6(TAGA)_{11}$	TCAGCCTCCAAGGAAAACAG	157-195	11	2.5	Saladin *et al.*, 2003
PmanTAGAn71R		GCATAAGCAACACCATGCAG				
PmanTAGAn45F	$(TGA)_{10}$	CCCCTGGCTCTTTCATATCC	232-392	28	2	Saladin *et al.*, 2003
PmanTAGAn45R		GACAGGTGTTGGCACAAGG				
Ase18F	$(GT)_{12}$	ATCCAGTCTTCGCAAAAGCC	188-224	10	2.5	Richardson *et al.*, 2000
Ase18R		TGCCCCAGAGGGAAGAAG				
Cuμ28F	$(CA)_{12}$	GAGGCACAGAAATGTGAATT	180-192	7	2.5	Gibbs *et al.*, 1999
Cuμ28R		TAAGTAGAAGGACTTGATGGCT				
Ppi2F		CACAGACCATTCGAAGCAGA	322-488	46	2.5	Martinez *et al.*, 1999
Ppi2R		GCTCCGATGGTGAATGAAGT				

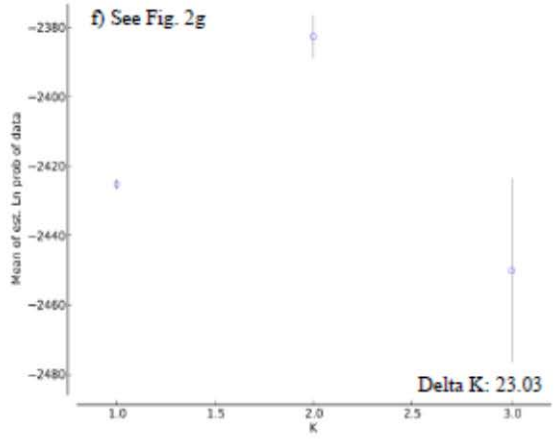

a) See Fig. 2a
Mean of est. Ln prob of data
−34500
−35000
−35500
−36000
Delta K: 16.45
1
2
3
4
5
K

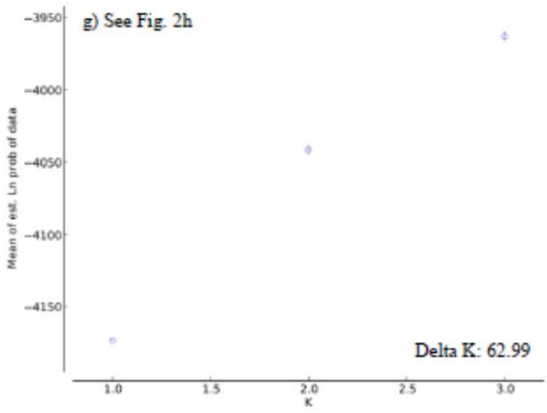

d) See Fig. 2e
Mean of est. Ln prob of data
−8680
−8700
−8720
−8740
−8760
−8780
−8800
−8820
Delta K: 33.61
1.0
1.5
2.0
2.5
3.0
K


b) See Fig. 2c
Mean of est. Ln prob of data
−28400
−28600
−28800
−29000
−29200
Delta K: 7.36
1
2
3
4
5
K

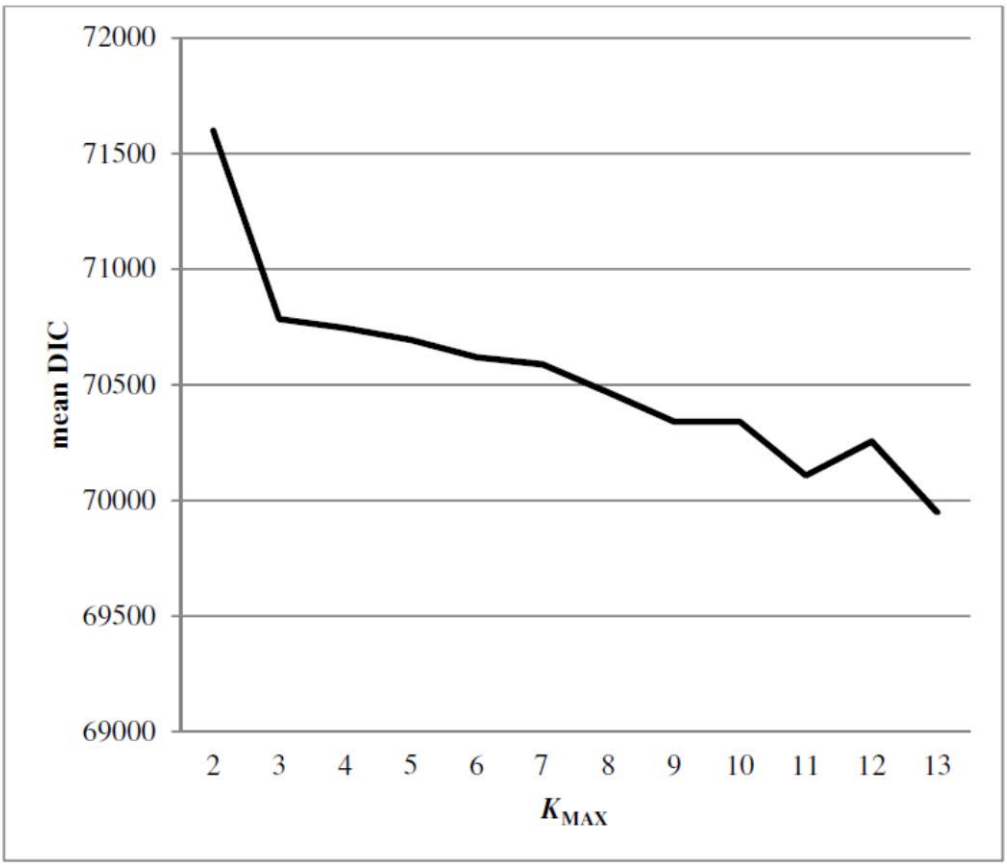

e) See Fig. 2f
Mean of est. Ln prob of data
−8680
−8700
−8720
−8740
−8760
−8780
−8800
−8820
Delta K: 2.79
1.0
1.5
2.0
2.5
3.0
K


c) See Fig. 2d
Mean of est. Ln prob of data
−13800
−13900
−14000
−14100
−14200
Delta K: 1.84
1
2
3
4
5
K

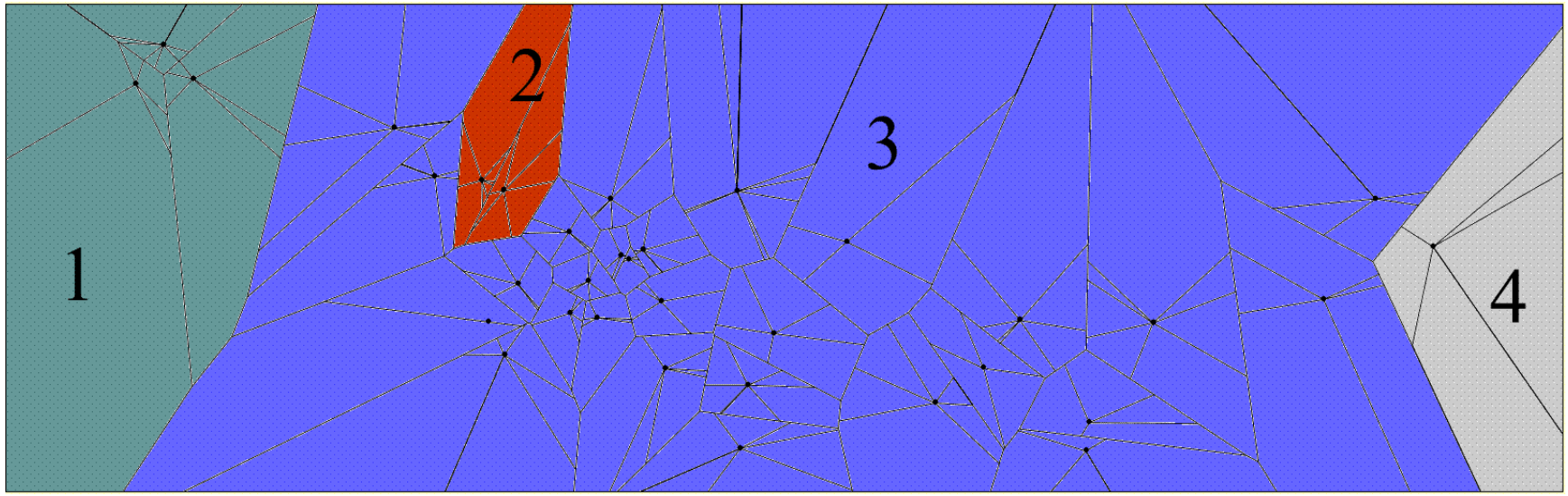

f) See Fig. 2g
Mean of est. Ln prob of data
−2380
−2400
−2420
−2440
−2460
−2480
Delta K: 23.03
1.0
1.5
2.0
2.5
3.0
K



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_{MAX} (2 – 13) following 50,000 burn in sweeps and 100,000 McMC sweeps, under the CAR model and ψ 0.6, conducted in the program TESS v.2.3.



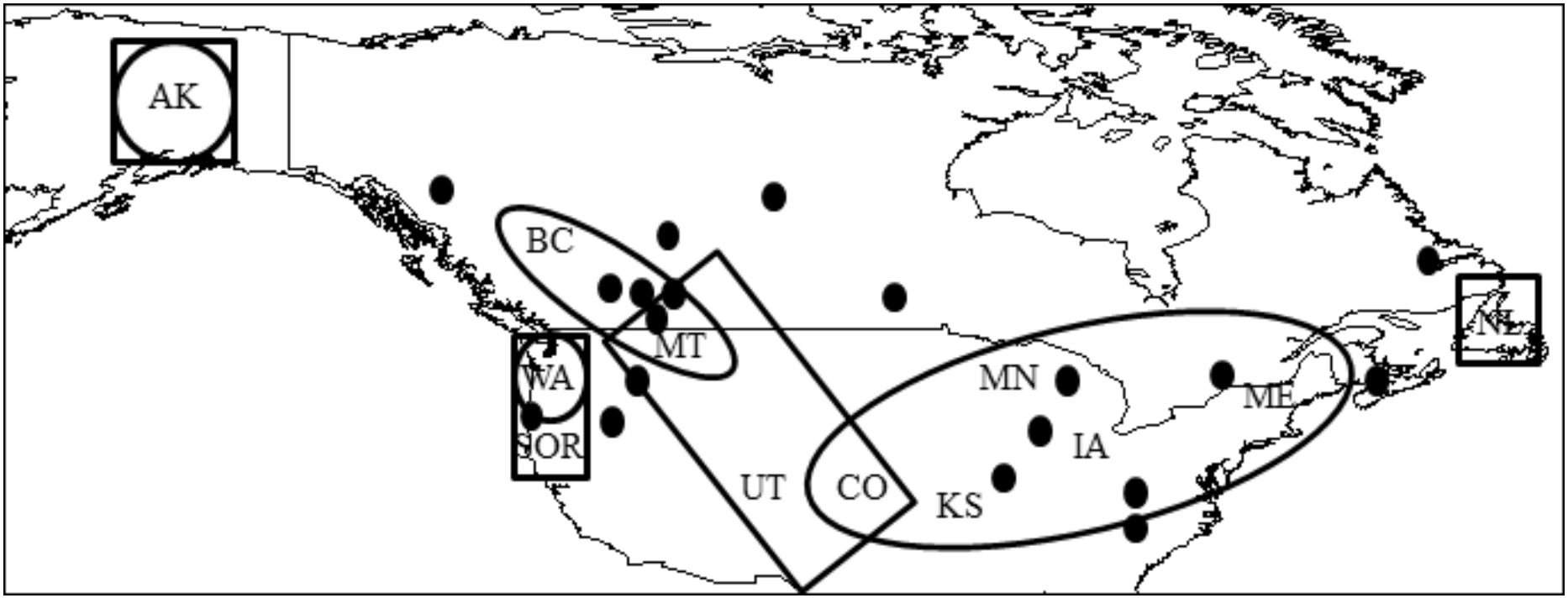
Appendix 1.5. Clusters as determined by TESS v2.3.

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 (α = 0.008). Populations with n < 5 were removed from the analysis.

	AKA	AKF	AKW	NWBC	NBC	FtStJ	PG	BCR	CAB	LETH	SAB1	SAB2	MB	SK	WA	SOR	NEOR	CID	ID	MT	SD	UT	CO	NM	IL	MI	MO	ON	NSNB	WV	NL
AKA	*	0.006	0.003	0.099	0.100	0.211	0.316	0.128	0.144	0.192	0.135	0.123	0.152	0.145	0.183	0.173	0.193	0.140	0.142	0.101	0.149	0.126	0.121	0.157	0.222	0.142	0.144	0.150	0.139	0.177	0.171
AKF	**0.011**	*	0.010	0.106	0.089	0.206	0.294	0.126	0.126	0.146	0.131	0.119	0.145	0.135	0.188	0.170	0.195	0.118	0.130	0.096	0.165	0.092	0.143	0.164	0.174	0.146	0.129	0.122	0.126	0.180	0.166
AKW	0.005	**0.016**	*	0.107	0.090	0.182	0.283	0.131	0.150	0.180	0.139	0.110	0.132	0.100	0.201	0.178	0.205	0.112	0.162	0.093	0.184	0.122	0.138	0.200	0.169	0.125	0.175	0.146	0.124	0.170	0.173
NWBC	**0.059**	**0.063**	**0.079**	*	0.033	0.075	0.251	0.030	0.048	0.077	0.041	0.034	0.041	0.047	0.098	0.207	0.141	0.062	0.048	0.030	0.085	0.071	0.076	0.103	0.102	0.036	0.060	0.062	0.057	0.081	0.080
NBC	**0.055**	**0.056**	**0.062**	**0.022**	*	0.046	0.224	0.040	0.019	0.065	0.016	0.019	0.011	0.029	0.060	0.130	0.090	0.025	0.055	0.046	0.069	0.076	0.093	0.147	0.074	0.018	0.047	0.029	0.029	0.065	0.070
FtStJ	**0.113**	**0.108**	**0.114**	**0.083**	**0.081**	*	0.149	0.053	0.025	0.090	0.031	0.038	0.021	0.056	0.112	0.194	0.140	0.059	0.080	0.066	0.147	0.136	0.120	0.182	0.084	0.038	0.078	0.044	0.041	0.071	0.125
PG	**0.118**	**0.131**	**0.148**	**0.088**	**0.086**	**0.019**	*	0.168	0.202	0.276	0.192	0.110	0.169	0.187	0.191	0.203	0.154	0.220	0.219	0.211	0.220	0.261	0.250	0.248	0.201	0.182	0.278	0.174	0.157	0.129	0.221
BCR	**0.067**	**0.080**	**0.076**	0.003	**0.020**	**0.093**	**0.092**	*	0.029	0.074	0.038	0.030	0.038	0.059	0.066	0.153	0.109	0.061	0.037	0.031	0.095	0.107	0.085	0.121	0.101	0.038	0.067	0.035	0.046	0.107	0.117
CAB	**0.058**	**0.054**	**0.072**	0.011	**0.015**	**0.074**	**0.079**	**0.017**	*	0.056	0.009	0.007	0.009	0.025	0.058	0.131	0.095	0.062	0.048	0.035	0.092	0.085	0.075	0.133	0.066	0.030	0.026	0.032	0.031	0.064	0.114
LETH	**0.066**	**0.049**	**0.060**	**0.029**	**0.017**	**0.077**	**0.099**	**0.028**	0.004	*	0.056	0.046	0.033	0.059	0.119	0.221	0.158	0.056	0.035	0.075	0.141	0.094	0.094	0.162	0.111	0.095	0.055	0.064	0.064	0.126	0.083
SAB1	**0.063**	**0.065**	**0.073**	0.007	-0.001	**0.082**	**0.109**	0.009	-0.002	-0.001	*	0.009	0.003	0.042	0.044	0.145	0.092	0.035	0.040	0.038	0.085	0.088	0.077	0.109	0.083	0.040	0.065	0.042	0.037	0.065	0.110
SAB2	**0.065**	**0.060**	**0.066**	0.010	0.008	**0.066**	**0.075**	0.012	0.001	-0.006	-0.003	*	0.003	0.024	0.042	0.136	0.098	0.043	0.023	0.022	0.063	0.061	0.095	0.115	0.047	0.022	0.009	0.014	0.020	0.042	0.069
MB	**0.070**	**0.063**	**0.073**	0.024	0.007	**0.075**	**0.102**	**0.024**	0.004	-0.011	-0.013	-0.009	*	0.022	0.037	0.109	0.082	0.057	0.036	0.005	0.039	0.074	0.102	0.096	0.047	0.033	0.064	0.020	0.002	0.030	0.039
SK	**0.054**	**0.040**	**0.057**	**0.016**	0.008	**0.075**	**0.102**	**0.020**	**0.013**	0.009	**0.018**	**0.015**	**0.021**	*	0.069	0.109	0.090	0.061	0.077	0.042	0.096	0.134	0.097	0.126	0.065	0.042	0.093	0.050	0.036	0.051	0.101
WA	**0.067**	**0.087**	**0.093**	**0.043**	**0.026**	**0.111**	**0.108**	**0.025**	**0.026**	**0.038**	**0.022**	**0.042**	**0.034**	**0.040**	*	0.057	0.073	0.064	0.037	0.068	0.078	0.149	0.157	0.141	0.132	0.113	0.113	0.118	0.098	0.108	0.134
SOR	**0.021**	0.007	**0.034**	**0.051**	**0.029**	**0.095**	**0.106**	**0.037**	0.019	**0.024**	**0.047**	**0.029**	**0.048**	0.008	0.020	*	0.158	0.176	0.136	0.131	0.157	0.189	0.172	0.170	0.263	0.178	0.144	0.183	0.170	0.135	0.228
NEOR	**0.089**	**0.094**	**0.124**	**0.079**	**0.060**	**0.134**	**0.112**	**0.091**	**0.074**	**0.091**	**0.087**	**0.092**	**0.086**	**0.087**	**0.056**	**0.067**	*	0.105	0.115	0.068	0.121	0.149	0.208	0.183	0.151	0.110	0.191	0.127	0.101	0.071	0.124
CID	**0.044**	**0.077**	**0.063**	**0.034**	**0.033**	**0.094**	**0.105**	**0.017**	**0.041**	**0.049**	**0.045**	**0.034**	**0.052**	**0.036**	**0.039**	0.016	**0.093**	*	0.021	0.053	0.106	0.101	0.066	0.088	0.057	0.030	0.082	0.052	0.047	0.073	0.068
ID	**0.058**	**0.084**	**0.088**	**0.021**	**0.032**	**0.095**	**0.089**	**0.020**	**0.028**	**0.039**	**0.030**	**0.025**	**0.032**	**0.039**	**0.028**	**0.034**	**0.067**	0.005	*	0.034	0.083	0.088	0.064	0.118	0.104	0.067	0.019	0.055	0.046	0.098	0.087
MT	**0.070**	**0.083**	**0.076**	0.008	**0.014**	**0.082**	**0.083**	0.000	**0.013**	**0.017**	0.005	0.006	0.006	**0.027**	**0.028**	**0.050**	**0.073**	**0.024**	**0.017**	*	0.064	0.018	0.080	0.101	0.107	0.043	0.059	0.070	0.051	0.093	0.093
SD	**0.064**	**0.069**	**0.085**	**0.026**	**0.017**	**0.086**	**0.075**	**0.022**	**0.031**	**0.034**	**0.020**	0.015	**0.029**	**0.025**	**0.027**	**0.042**	**0.062**	**0.036**	**0.029**	**0.019**	*	0.122	0.117	0.089	0.151	0.132	0.114	0.115	0.096	0.123	0.128
UT	**0.071**	**0.056**	**0.067**	**0.028**	**0.021**	**0.081**	**0.080**	**0.038**	**0.022**	**0.019**	**0.021**	**0.016**	**0.018**	**0.038**	**0.066**	**0.055**	**0.086**	**0.063**	**0.058**	**0.018**	**0.037**	*	0.118	0.130	0.173	0.080	0.057	0.079	0.062	0.099	0.134
CO	**0.060**	**0.071**	**0.070**	**0.020**	**0.035**	**0.091**	**0.088**	**0.030**	**0.038**	**0.037**	**0.037**	**0.030**	**0.039**	**0.019**	**0.058**	**0.041**	**0.098**	0.013	**0.027**	**0.024**	**0.022**	**0.046**	*	0.072	0.111	0.119	0.103	0.131	0.112	0.130	0.184
NM	**0.082**	**0.110**	**0.118**	**0.056**	**0.081**	**0.139**	**0.131**	**0.057**	**0.082**	**0.083**	**0.073**	**0.074**	**0.091**	**0.081**	**0.073**	**0.078**	**0.107**	**0.042**	**0.053**	**0.066**	**0.048**	**0.094**	**0.027**	*	0.190	0.127	0.185	0.145	0.122	0.164	0.184
IL	**0.074**	**0.069**	**0.086**	**0.053**	**0.047**	**0.072**	**0.108**	**0.070**	**0.036**	**0.034**	**0.053**	**0.039**	**0.031**	**0.051**	**0.088**	**0.062**	**0.133**	**0.057**	**0.066**	**0.053**	**0.061**	**0.046**	**0.035**	**0.116**	*	0.027	0.096	0.049	0.059	0.044	0.199
MI	**0.051**	**0.055**	**0.044**	0.011	0.007	**0.057**	**0.068**	**0.015**	0.005	0.003	0.002	0.002	-0.002	**0.022**	**0.048**	**0.035**	**0.088**	**0.022**	**0.027**	0.002	**0.033**	**0.014**	**0.019**	**0.079**	0.006	*	0.028	0.003	0.020	0.010	0.088
MO	**0.064**	**0.065**	**0.069**	0.014	0.013	**0.065**	**0.084**	**0.027**	0.006	0.015	**0.019**	0.005	0.011	0.016	**0.055**	**0.033**	**0.109**	**0.041**	**0.036**	**0.021**	**0.047**	0.010	**0.034**	**0.098**	**0.029**	-0.003	*	0.012	0.045	0.050	0.132
ON	**0.074**	**0.058**	**0.074**	**0.033**	**0.020**	**0.068**	**0.096**	**0.034**	0.008	0.000	**0.013**	-0.002	-0.005	**0.022**	**0.063**	**0.053**	**0.120**	**0.055**	**0.046**	**0.027**	**0.041**	**0.018**	**0.051**	**0.109**	**0.031**	0.005	0.001	*	0.009	0.016	0.097
NSNB	**0.060**	**0.057**	**0.062**	**0.022**	**0.007**	**0.077**	**0.092**	**0.020**	0.007	0.003	0.006	0.001	-0.006	**0.017**	**0.044**	**0.031**	**0.085**	**0.040**	**0.032**	**0.010**	**0.031**	**0.013**	**0.035**	**0.089**	**0.036**	-0.006	0.006	0.002	*	0.037	0.078
WV	**0.049**	**0.037**	**0.059**	0.019	0.005	**0.042**	**0.072**	**0.028**	0.007	0.001	0.011	-0.003	-0.014	0.009	**0.057**	0.025	**0.081**	**0.037**	**0.030**	0.016	0.014	0.015	0.012	**0.090**	0.005	0.006	-0.004	-0.010	0.001	*	0.120
NL	**0.090**	**0.096**	**0.102**	**0.027**	**0.025**	**0.102**	**0.108**	**0.029**	**0.033**	**0.031**	**0.022**	**0.028**	0.013	**0.040**	**0.046**	**0.062**	**0.065**	**0.068**	**0.034**	**0.017**	**0.038**	**0.048**	**0.049**	**0.107**	**0.104**	**0.042**	**0.048**	**0.054**	**0.024**	**0.048**	*

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	FtStJ	PG	BCR	CAB	LETH	SAB1	SAB2	MB	SK	WA	SOR	NEOR	CID	ID	MT	SD	UT	CO	NM	IL	MI	MO	ON	NSNB	WV	NL
AKA	0.000																														
AKF	0.014	0.000																													
AKW	0.031	0.043	0.000																												
NWBC	0.185	0.162	0.192	0.000																											
NBC	0.186	0.161	0.206	0.060	0.000																										
FtStJ	0.320	0.294	0.308	0.167	0.155	0.000																									
PG	0.847	0.839	0.723	0.811	0.771	0.670	0.000																								
BCR	0.232	0.238	0.237	0.082	0.098	0.175	0.696	0.000																							
CAB	0.219	0.188	0.233	0.068	0.040	0.132	0.749	0.071	0.000																						
LETH	0.286	0.227	0.289	0.132	0.109	0.208	0.810	0.157	0.112	0.000																					
SAB1	0.237	0.199	0.239	0.072	0.048	0.140	0.755	0.102	0.036	0.118	0.000																				
SAB2	0.358	0.339	0.352	0.189	0.147	0.190	0.696	0.178	0.154	0.208	0.131	0.000																			
MB	0.298	0.255	0.303	0.096	0.069	0.124	0.824	0.114	0.043	0.103	0.015	0.139	0.000																		
SK	0.258	0.207	0.228	0.083	0.048	0.148	0.703	0.098	0.042	0.116	0.076	0.171	0.074	0.000																	
WA	0.318	0.306	0.331	0.196	0.119	0.247	0.700	0.149	0.118	0.213	0.113	0.205	0.137	0.142	0.000																
SOR	0.408	0.367	0.401	0.369	0.275	0.352	0.652	0.300	0.260	0.384	0.265	0.331	0.294	0.265	0.134	0.000															
NEOR	0.367	0.355	0.382	0.313	0.263	0.355	0.626	0.272	0.231	0.357	0.265	0.332	0.339	0.290	0.186	0.244	0.000														
CID	0.250	0.228	0.251	0.081	0.104	0.191	0.778	0.125	0.130	0.124	0.123	0.242	0.152	0.120	0.180	0.333	0.347	0.000													
ID	0.242	0.224	0.274	0.075	0.095	0.186	0.778	0.093	0.085	0.129	0.088	0.191	0.094	0.137	0.119	0.258	0.239	0.041	0.000												
MT	0.220	0.205	0.213	0.051	0.064	0.176	0.767	0.086	0.055	0.152	0.074	0.193	0.035	0.089	0.156	0.329	0.284	0.115	0.093	0.000											
SD	0.347	0.316	0.372	0.156	0.160	0.265	0.808	0.206	0.184	0.248	0.182	0.256	0.112	0.177	0.199	0.335	0.370	0.192	0.172	0.151	0.000										
UT	0.207	0.170	0.200	0.114	0.107	0.237	0.749	0.163	0.120	0.184	0.149	0.224	0.141	0.176	0.234	0.319	0.299	0.199	0.171	0.048	0.181	0.000									
CO	0.248	0.242	0.269	0.136	0.172	0.220	0.828	0.181	0.167	0.208	0.156	0.289	0.178	0.195	0.281	0.399	0.429	0.141	0.144	0.160	0.223	0.186	0.000								
NM	0.299	0.307	0.346	0.186	0.244	0.320	0.818	0.201	0.246	0.304	0.230	0.336	0.208	0.230	0.291	0.379	0.440	0.184	0.201	0.207	0.182	0.235	0.164	0.000							
IL	0.373	0.309	0.323	0.177	0.172	0.176	0.603	0.202	0.115	0.217	0.139	0.207	0.156	0.119	0.235	0.324	0.305	0.158	0.188	0.185	0.264	0.240	0.251	0.319	0.000						
MI	0.237	0.226	0.219	0.076	0.061	0.128	0.666	0.051	0.048	0.142	0.086	0.154	0.086	0.059	0.176	0.290	0.267	0.096	0.111	0.081	0.203	0.118	0.198	0.240	0.076	0.000					
MO	0.243	0.200	0.272	0.087	0.050	0.156	0.802	0.141	0.057	0.105	0.096	0.165	0.112	0.132	0.183	0.298	0.296	0.138	0.057	0.112	0.221	0.116	0.184	0.308	0.167	0.072	0.000				
ON	0.246	0.204	0.237	0.100	0.074	0.131	0.686	0.060	0.047	0.112	0.078	0.165	0.058	0.068	0.178	0.282	0.289	0.122	0.105	0.101	0.203	0.111	0.208	0.254	0.100	-0.001	0.053	0.000			
NSNB	0.232	0.197	0.221	0.074	0.048	0.141	0.688	0.064	0.037	0.088	0.055	0.154	0.021	0.051	0.150	0.265	0.251	0.104	0.075	0.062	0.153	0.099	0.170	0.218	0.110	0.022	0.049	0.017	0.000		
WV	0.328	0.295	0.300	0.190	0.164	0.189	0.561	0.177	0.136	0.268	0.139	0.153	0.161	0.172	0.181	0.180	0.182	0.217	0.155	0.219	0.269	0.186	0.291	0.310	0.101	0.061	0.124	0.084	0.112	0.000	
NL	0.286	0.258	0.307	0.114	0.112	0.252	0.772	0.163	0.169	0.116	0.163	0.206	0.125	0.153	0.226	0.379	0.322	0.168	0.142	0.144	0.209	0.185	0.278	0.316	0.317	0.131	0.143	0.147	0.101	0.251	0.000



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).

Pop	ID	Location	Lat (°N)	Long (°W)	Source	Band/ Museum ID
BCR	BCR001	Revelstoke, BC	50.981	118.182	Wild	2490-57684
BCR	BCR002	Revelstoke, BC	50.981	118.182	Wild	2490-57685
BCR	BCR003	Revelstoke, BC	50.983	118.179	Wild	bcch 3
BCR	BCR004	Mt Revelstoke Ski Chalet, BC	51.007	118.191	Wild	2490-57686
BCR	BCR005	Mt Revelstoke Ski Chalet, BC	51.007	118.191	Wild	2490-57687
BCR	BCR006	Mt Revelstoke Ski Chalet, BC	51.014	118.203	Wild	2490-57688
BCR	BCR007	Mt Revelstoke Ski Chalet, BC	51.014	118.203	Wild	2490-57689
BCR	BCR008	Mt Revelstoke Ski Chalet, BC	51.006	118.182	Wild	2490-57690
BCR	BCR009	Revelstoke field, BC	50.982	118.180	Wild	2490-57691
BCR	BCR010	Revelstoke Resort, BC	50.970	118.172	Wild	2490-57692
BCR	BCR011	Revelstoke Resort, BC	50.970	118.174	Wild	2490-57693
BCR	BCR012	Begbie Falls Revelstoke, BC	50.944	118.205	Wild	2490-57694
BCR	BCR013	Mount MacPherson Revelstoke, BC	50.942	118.223	Wild	2490-57695
BCR	BCR014	9 mile Revelstoke, BC	50.897	118.114	Wild	2490-57696
BCR	BCR015	Smokey Bear Revelstoke, BC	50.989	118.278	Wild	2490-57697
BCR	BCR016	Frisby Rd Revelstoke, BC	51.066	118.194	Wild	2490-57698
BCR	BCR017	Frisby Rd Revelstoke, BC	51.066	118.194	Wild	2490-57699
BCR	BCR018	Frisby Rd Revelstoke, BC	51.052	118.219	Wild	2490-57700
BCR	BCR019	Frisby Ridge Rd Revelstoke, BC	51.059	118.206	Wild	2490-57701
BCR	BCR020	Frisby Ridge Rd Revelstoke, BC	51.059	118.206	Wild	2490-57702
BCR	BCR021	Frisby Ridge Rd Revelstoke, BC	51.141	118.209	Wild	2490-57703
BCR	BCR022	Frisby Ridge Rd Revelstoke, BC	51.059	118.223	Wild	2490-57704
BCR	BCR023	Frisby Ridge Rd Revelstoke, BC	51.062	118.224	Wild	2490-57705
BCR	BCR024	Frisby Ridge Rd Revelstoke, BC	51.062	118.224	Wild	2490-57706
BCR	BCR025	Frisby Ridge Rd Revelstoke, BC	51.062	118.224	Wild	2490-57707
BCR	BCR026	Frisby Ridge Rd Revelstoke, BC	51.065	118.226	Wild	2490-57708

BCR	BCR027	Frisby Ridge Rd Revelstoke, BC	51.063	118.232	Wild	2490-57709
BCR	BCR028	Frisby Ridge Rd Revelstoke, BC	51.063	118.232	Wild	2490-57710
BCR	BCR029	Frisby Ridge Rd Revelstoke, BC	51.049	118.229	Wild	2490-57711
BCR	BCR030	Frisby Ridge Rd Revelstoke, BC	51.049	118.229	Wild	2490-57712
BCR	BCR031	Frisby Ridge Rd Revelstoke, BC	51.052	118.226	Wild	2490-57713
BCR	BCR032	Frisby Ridge Rd Revelstoke, BC	51.056	118.225	Wild	2490-57714
BCR	BCR033	West Bridge, Revelstoke, BC	51.003	118.218	Wild	2500-94928
BCR	BCR034	Machete Island 2, Revelstoke, BC	50.971	118.202	Wild	2500-94930
BCR	BCR035	Westside RD 2, Revelstoke, BC	51.013	118.237	Wild	2500-94931
BCR	BCR036	Westside RD 2, Revelstoke, BC	51.013	118.237	Wild	2500-94932
BCR	BCR037	Bridge Creek, Revelstoke, BC	50.994	118.172	Wild	2500-94933
BCR	BCR038	Westside RD 1, Revelstoke, BC	51.004	118.228	Wild	2500-94937
BCR	BCR039	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48305
BCR	BCR040	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48306
BCR	BCR041	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48307
BCR	BCR042	Williamson Lake, Revelstoke, BC	50.970	118.175	Wild	3111-48308
BCR	BCR043	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48309
BCR	BCR044	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48310
BCR	BCR045	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48311
BCR	BCR046	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48312
BCR	BCR047	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48313
BCR	BCR048	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48314
BCR	BCR049	Begbie Dyke, Revelstoke, BC	50.996	118.315	Wild	3111-48315
BCR	BCR050	Revelstoke City Park, BC	50.984	118.198	Wild	3111-48316
BCR	BCR051	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48317
BCR	BCR052	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48318
BCR	BCR053	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48319
BCR	BCR054	Westside Road, Revelstoke, BC	51.004	118.228	Wild	3111-48320
NBC	CBC001	Smithers, BC	54.785	127.151	Wild	2520-39893
NBC	CBC002	Smithers, BC	54.785	127.151	Wild	2529-39882

NBC	CBC003	Smithers, BC	54.785	127.151	Wild	2520-39883
NBC	CBC004	Smithers, BC	54.785	127.151	Wild	2520-29884
NBC	CBC005	Smithers, BC	54.785	127.151	Wild	2520-39885
NBC	CBC006	Smithers, BC	54.785	127.151	Wild	2520-39886
NBC	CBC007	Smithers, BC	54.785	127.151	Wild	2520-39887
NBC	CBC008	Smithers, BC	54.785	127.151	Wild	2520-39888
NBC	CBC009	Smithers, BC	54.785	127.151	Wild	2520-39889
NBC	CBC010	Smithers, BC	54.785	127.151	Wild	2520-39890
NBC	CBC011	Smithers, BC	54.785	127.151	Wild	2520-39891
NBC	CBC012	Smithers, BC	54.785	127.151	Wild	2520-39892
NBC	CBC013	Smithers, BC	54.785	127.151	Wild	2520-39898
NBC	CBC014	Smithers, BC	54.785	127.151	Wild	2520-39894
NBC	CBC015	Smithers, BC	54.785	127.151	Wild	2520-39899
NBC	CBC016	Smithers, BC	54.785	127.151	Wild	2520-39900
NBC	CBC017	Smithers, BC	54.785	127.151	Wild	2490-57761
NBC	CBC018	Smithers, BC	54.785	127.151	Wild	2490-57762
NBC	CBC019	Smithers, BC	54.785	127.151	Wild	2490-57763
NBC	CBC020	Smithers, BC	54.785	127.151	Wild	2490-57764
NBC	CBC021	Smithers, BC	54.785	127.151	Wild	2490-57765
NBC	CBC022	Smithers, BC	54.785	127.151	Wild	2490-57766
NBC	CBC023	Smithers, BC	54.785	127.151	Wild	2490-57767
NBC	CBC024	Smithers, BC	54.785	127.151	Wild	2490-57768
NBC	CBC025	3928 Mountainview Ave, Thornhill, BC	54.506	128.543	Wild	2500-94901
NBC	CBC026	Ferry Island, BC	54.512	128.574	Wild	2500-94902
NBC	CBC027	Stockner's Residence; Kispiox, BC	55.468	127.735	Wild	2500-94903
NBC	CBC028	Stockner's Residence; Kispiox, BC	55.468	127.735	Wild	2500-94904
NBC	CBC029	Tyee Lake, Telkwa, BC	54.707	127.040	Wild	2500-94906
NBC	CBC030	Tyee Lake, Telkwa, BC	54.707	127.040	Wild	2500-94907
NBC	CBC031	Tyee Lake, Telkwa, BC	54.707	127.040	Wild	2500-94908
NBC	CBC032	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94915

NBC	CBC033	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94916
NBC	CBC034	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94917
NBC	CBC035	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94918
NBC	CBC036	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94919
NBC	CBC037	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94920
NBC	CBC038	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94909
NBC	CBC039	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94910
NBC	CBC040	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94911
NBC	CBC041	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94912
NBC	CBC042	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94913
NBC	CBC043	4567 Tyee Lake Rd., Telkwa, BC	54.725	127.036	Wild	2500-94914
CLU	CBC-CLU131	Cluculz Lake- Brookside camp, BC	53.913	123.593	Wild	2560-28981
CLU	CBC-CLU132	Cluculz Lake- Brookside camp, BC	53.913	123.593	Wild	2560-28982
CLU	CBC-CLU133	Cluculz Lake - West Meier Road, BC	53.875	123.638	Wild	2560-28983
CLU	CBC-CLU134	Cluculz Lake - West Meier Road, BC	53.875	123.638	Wild	2560-28984
CLU	CBC-CLU135	Cluculz Lake - West Meier Road, BC	53.875	123.638	Wild	2560-28985
CLU	CBC-CLU136	Cluculz Lake - West Meier Road, BC	53.875	123.638	Wild	2560-28986
CLU	CBC-CLU137	Finmore Rd - Cluculz Lake, BC	53.940	123.580	Wild	2560-28987
CLU	CBC-CLU138	Finmore Rd - Cluculz Lake, BC	53.950	123.573	Wild	2560-28988
CLU	CBC-CLU139	Cobb Lake, Cluculz, BC	53.962	123.557	Wild	2560-28989
CLU	CBC-CLU140	Cobb Lake Road, Cluculz, BC	53.962	123.557	Wild	2560-28990
CLU	CBC-CLU141	Cobb Lake Road, Cluculz, BC	53.962	123.557	Wild	2560-28991
CLU	CBC-CLU142	Cobb Lake Road, Cluculz, BC	53.962	123.566	Wild	2560-28992
CLU	CBC-CLU143	Finmore Rd - Cluculz Lake, BC	53.935	123.576	Wild	2560-28993
CLU	CBC-CLU144	Beverly Lake Forest Road, Cluculz, BC	53.923	123.575	Wild	2560-28994
CLU	CBC-CLU145	Tapping Road, Cluculz, BC	53.885	123.573	Wild	2560-28995
CLU	CBC-CLU146	Tapping Road, Cluculz, BC	53.885	123.573	Wild	2560-28996
CLU	CBC-CLU147	Tapping Road, Cluculz, BC	53.890	123.521	Wild	2560-28997
CLU	CBC-CLU148	Lloyd Road, Cluculz, BC	53.868	123.494	Wild	2560-28998
CLU	CBC-CLU149	Lloyd Road, Cluculz, BC	53.875	123.502	Wild	2560-29000

CLU	CBC-CLU150	Lloyd Road, Cluculz, BC	53.875	123.502	Wild	3111-48304
FF	CBC-FF120	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28970
FF	CBC-FF121	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28971
FF	CBC-FF122	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28972
FF	CBC-FF123	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28973
FF	CBC-FF124	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28974
FF	CBC-FF125	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28975
FF	CBC-FF126	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28976
FF	CBC-FF127	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28977
FF	CBC-FF128	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28978
FF	CBC-FF129	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28979
FF	CBC-FF130	Lily Lake Road - Fort Fraser, BC	53.963	124.533	Wild	2560-28980
FrL	CBC-FrL062	17224 Colleymount Rd, Francois Lake, BC	54.040	125.991	Wild	2560-28912
FrL	CBC-FrL063	17224 Colleymount Rd, Francois Lake, BC	54.040	125.991	Wild	2560-28913
FrL	CBC-FrL064	Colleymount Road, Francois Lake, BC	54.040	125.987	Wild	2560-28914
FrL	CBC-FrL065	Colleymount Road, Francois Lake, BC	54.040	125.987	Wild	2560-28915
FrL	CBC-FrL066	Colleymount Road, Francois Lake, BC	54.040	125.987	Wild	2560-28916
FrL	CBC-FrL067	Colleymount Road, Francois Lake, BC	54.040	125.987	Wild	2560-28917
FrL	CBC-FrL068	Colleymount Road, Francois Lake, BC	54.040	125.987	Wild	2560-28918
FrL	CBC-FrL069	30867 Collymount Road, Francois Lake, BC	54.019	125.184	Wild	2560-28919
FrL	CBC-FrL070	30867 Collymount Road, Francois Lake, BC	54.019	125.184	Wild	2560-28920
FrL	CBC-FrL071	30867 Collymount Road, Francois Lake, BC	54.019	125.184	Wild	2560-28921
FrL	CBC-FrL072	30867 Collymount Road, Francois Lake, BC	54.019	125.184	Wild	2560-28922
FrL	CBC-FrL073	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28923
FrL	CBC-FrL074	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28924
FrL	CBC-FrL075	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28925
FrL	CBC-FrL076	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28926
FrL	CBC-FrL077	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28927
FrL	CBC-FrL078	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28928
FrL	CBC-FrL079	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28929

FrL	CBC-FrL080	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28930
FrL	CBC-FrL081	Collymount Road, Francois Lake, BC	54.005	126.265	Wild	2560-28931
FtStJ2	CBC-FSJ 044	Necoslie Road, Fort St James, BC	54.416	124.220	Wild	2500-94994
FtStJ2	CBC-FSJ 045	Necoslie Road, Fort St James, BC	54.416	124.220	Wild	2500-94995
FtStJ2	CBC-FSJ 046	Necoslie Road, Fort St James, BC	54.416	124.220	Wild	2500-94996
FtStJ2	CBC-FSJ 047	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2500-94997
FtStJ2	CBC-FSJ 048	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2500-94998
FtStJ2	CBC-FSJ 049	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2500-94999
FtStJ2	CBC-FSJ 050	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2500-95000
FtStJ2	CBC-FSJ 051	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2560-28901
FtStJ2	CBC-FSJ 052	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2560-28902
FtStJ2	CBC-FSJ 053	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2560-28903
FtStJ2	CBC-FSJ 054	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2560-28904
FtStJ2	CBC-FSJ 055	4494 Sowchea Road, Fort St James, BC	54.427	124.314	Wild	2560-28905
FtStJ2	CBC-FSJ 056	Hanley, Fort St James, BC	54.402	124.287	Wild	2560-28906
FtStJ2	CBC-FSJ 057	4712 Sowchea Road, Fort St James, BC	54.426	124.317	Wild	2560-28907
FtStJ2	CBC-FSJ 058	4712 Sowchea Road, Fort St James, BC	54.426	124.317	Wild	2560-28908
FtStJ2	CBC-FSJ 059	4712 Sowchea Road, Fort St James, BC	54.426	124.317	Wild	2560-28909
FtStJ2	CBC-FSJ 060	4712 Sowchea Road, Fort St James, BC	54.426	124.317	Wild	2560-28910
FtStJ2	CBC-FSJ 061	4712 Sowchea Road, Fort St James, BC	54.426	124.317	Wild	2560-28911
HAZ	CBC-HAZ082	Kispiox Salmon River Rd, BC	55.281	127.669	Wild	2560-28932
HAZ	CBC-HAZ083	Kispiox Salmon River Rd, BC	55.281	127.669	Wild	2560-28933
HAZ	CBC-HAZ084	New Hazelton College St., BC	55.251	128.453	Wild	2560-28934
HAZ	CBC-HAZ085	New Hazelton College St., BC	55.251	128.453	Wild	2560-28935
HAZ	CBC-HAZ086	New Hazelton College St., BC	55.251	128.453	Wild	2560-28936
HAZ	CBC-HAZ087	New Hazelton College St., BC	55.251	128.453	Wild	2560-28937
HAZ	CBC-HAZ088	New Hazelton College St., BC	55.251	128.453	Wild	2560-28938
HAZ	CBC-HAZ089	New Hazelton College St., BC	55.251	128.453	Wild	2560-28939
HAZ	CBC-HAZ090	New Hazelton College St., BC	55.251	128.453	Wild	2560-28940
HAZ	CBC-HAZ091	New Hazelton College St., BC	55.251	128.453	Wild	2560-28941

HAZ	CBC-HAZ092	New Hazelton College St., BC	55.251	128.453	Wild	2560-28942
HAZ	CBC-HAZ093	New Hazelton College St., BC	55.251	128.453	Wild	2560-28943
HAZ	CBC-HAZ094	New Hazelton College St., BC	55.251	128.453	Wild	2560-28944
HAZ	CBC-HAZ095	New Hazelton College St., BC	55.251	128.453	Wild	2560-28945
HAZ	CBC-HAZ096	New Hazelton College St., BC	55.251	128.453	Wild	2560-28946
HAZ	CBC-HAZ097	New Hazelton College St., BC	55.251	128.453	Wild	2560-28947
HAZ	CBC-HAZ098	New Hazelton College St., BC	55.251	128.453	Wild	2560-28948
HAZ	CBC-HAZ099	Swannell Dr, New Hazelton, BC	55.264	127.652	Wild	2560-28949
HAZ	CBC-HAZ100	Swannell Dr, New Hazelton, BC	55.264	127.652	Wild	2560-28950
HAZ	CBC-HAZ101	Swannell Dr, New Hazelton, BC	55.264	127.652	Wild	2560-28951
HOU	CBC-HOU102	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28952
HOU	CBC-HOU103	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28953
HOU	CBC-HOU104	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28954
HOU	CBC-HOU105	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28955
HOU	CBC-HOU106	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28956
HOU	CBC-HOU107	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28957
HOU	CBC-HOU108	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28958
HOU	CBC-HOU109	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28959
HOU	CBC-HOU110	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28960
HOU	CBC-HOU111	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28961
HOU	CBC-HOU112	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28962
HOU	CBC-HOU113	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28963
HOU	CBC-HOU114	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28964
HOU	CBC-HOU115	Houston - Duck Pond, BC	54.391	126.656	Wild	2560-28967
HOU	CBC-HOU116	Houston - Duck Pond, BC	54.391	126.656	Wild	2560-28966
HOU	CBC-HOU117	Houston - Duck Pond, BC	54.391	126.656	Wild	2560-28965
HOU	CBC-HOU118	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28968
HOU	CBC-HOU119	Houston - Shady Campground, BC	54.416	126.633	Wild	2560-28969
KEL	KEL001	Mission Creek, Kelowna, BC	49.867	119.439	Wild	2590-61272
KEL	KEL002	Mission Creek, Kelowna, BC	49.867	119.439	Wild	2590-61273

KEL	KEL003	Mission Creek, Kelowna, BC	49.867	119.439	Wild	2590-61274
KEL	KEL004	Mill Creek, Kelowna, BC	49.972	119.364	Wild	2590-61275
KEL	KEL005	Mill Creek, Kelowna, BC	49.972	119.364	Wild	2590-61276
KEL	KEL006	Mill Creek, Kelowna, BC	49.972	119.364	Wild	2590-61277
KEL	KEL007	Mill Creek, Kelowna, BC	49.972	119.364	Wild	2590-61278
KEL	KEL008	Mission Creek, Kelowna BC	49.876	119.430	Wild	2710-78331
NWBC	NWBC001	Telegraph Creek, BC	58.401	131.212	Wild	2520-39865
NWBC	NWBC002	Telegraph Creek, BC	58.401	131.212	Wild	2520-39866
NWBC	NWBC003	Telegraph Creek, BC	57.909	131.224	Wild	2520-39867
NWBC	NWBC004	Telegraph Creek, BC	57.909	131.224	Wild	2520-39868
NWBC	NWBC005	Dease Lake, BC	58.507	130.023	Wild	2520-39874
NWBC	NWBC006	Dease Lake, BC	58.430	129.987	Wild	2520-39875
NWBC	NWBC007	Dease Lake, BC	58.430	129.987	Wild	2520-39876
NWBC	NWBC008	Dease Lake, BC	58.430	129.987	Wild	2520-39877
NWBC	NWBC009	Dease Lake, BC	58.430	129.987	Wild	2520-39878
NWBC	NWBC010	Dease Lake, BC	58.430	129.987	Wild	2520-39879
NWBC	NWBC011	Dease Lake, BC	58.430	129.987	Wild	2520-39880
NWBC	NWBC012	Dease Lake, BC	58.430	129.987	Wild	2520-39881
NWBC	NWBC013	Telegraph Creek, BC	57.913	131.210	Wild	2520-39859
NWBC	NWBC014	Telegraph Creek, BC	57.913	131.210	Wild	2520-39860
NWBC	NWBC015	Telegraph Creek, BC	57.913	131.210	Wild	2520-39861
NWBC	NWBC016	Telegraph Creek, BC	57.913	131.210	Wild	2520-39862
NWBC	NWBC017	Telegraph Creek, BC	57.913	131.210	Wild	2520-39863
VAN	VAN001	Jericho Park, Vancouver	49.267	123.195	Wild	2590-61239
VAN	VAN002	Jericho Park, Vancouver	49.271	123.199	Wild	2590-61240
VAN	VAN003	Stanley park, Vancouver, BC	49.294	123.143	Wild	2590-61241
VAN	VAN004	Stanley park, Vancouver, BC	49.294	123.143	Wild	Not Banded #1
VAN	VAN005	Stanley park, Vancouver	49.294	123.143	Wild	2590-61242
VAN	VAN006	Memorial South, Vancouver	49.230	123.0863	Wild	2590-61243
VAN	VAN007	Memorial South, Vancouver, BC	49.230	123.086	Wild	2590-61244

VAN	VAN008	Memorial South, Vancouver	49.230	123.086	Wild	2590-61245
VAN	VAN009	Pacific Spirit, Vancouver, BC	49.270	123.237	Wild	Not Banded #2
VAN	VAN010	Pacific Spirit, Vancouver, BC	49.270	123.237	Wild	2590-61246
VAN	VAN011	Pacific Spirit, Vancouver, BC	49.270	123.237	Wild	2590-61247
VAN	VAN012	Pacific Spirit, Vancouver, BC	49.270	123.237	Wild	2590-61248
VAN	VAN013	Queen Elizabeth, Vancouver, BC	49.241	123.116	Wild	2590-61249
VAN	VAN014	Queen Elizabeth, Vancouver, BC	49.241	123.116	Wild	2590-61250
VAN	VAN015	Queen Elizabeth, Vancouver, BC	49.243	123.113	Wild	2590-61251
VAN	VAN016	Queen Elizabeth, Vancouver, BC	49.243	123.113	Wild	2590-61252 #1
VAN	VAN017	Burnaby Lake, Vancouver, BC	49.240	122.952	Wild	2590-61252 #2
VAN	VAN018	Burnaby Lake, Vancouver, BC	49.240	122.952	Wild	2590-61254
VAN	VAN019	Burnaby Lake, Vancouver, BC	49.240	122.952	Wild	2590-61255
VAN	VAN020	Burnaby Lake, Vancouver, BC	49.244	122.937	Wild	2590-61256
VAN	VAN021	Burnaby Lake, Vancouver, BC	49.244	122.937	Wild	2590-61257
VAN	VAN022	Burnaby Lake, Vancouver, BC	49.245	122.939	Wild	2590-61258/59
VAN	VAN023	Burnaby Lake, Vancouver, BC	49.245	122.939	Wild	2590-61260
VAN	VAN024	Trout Lake, Vancouver, BC	49.256	123.061	Wild	2590-61261
VAN	VAN025	Trout Lake, Vancouver, BC	49.256	123.061	Wild	2590-61262
VAN	VAN026	Centre, Vancouver, BC	49.226	123.021	Wild	2590-61263
VAN	VAN027	Centre, Vancouver, BC	49.226	123.021	Wild	2590-61264
VAN	VAN028	Centre, Vancouver, BC	49.226	123.021	Wild	2590-61265
VAN	VAN029	Centre, Vancouver, BC	49.226	123.021	Wild	2590-61266
VAN	VAN030	Centre, Vancouver, BC	49.227	123.014	Wild	2590-61267
VAN	VAN031	Centre, Vancouver, BC	49.227	123.014	Wild	2590-61268
VAN	VAN032	Centre, Vancouver, BC	49.226	123.016	Wild	2590-61269
VAN	VAN033	Centre, Vancouver, BC	49.226	123.016	Wild	2590-61270
FtStJ1	BC-MI-037	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75681
FtStJ1	BC-MI-038	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75926
FtStJ1	BC-MI-039	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75727
FtStJ1	BC-MI-040	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75703

FtStJ1	BC-MI-041	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36368
FtStJ1	BC-MI-042	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-76006
FtStJ1	BC-MI-043	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36334
FtStJ1	BC-MI-044	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75916
FtStJ1	BC-MI-045	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75732
FtStJ1	BC-MI-046	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36327
FtStJ1	BC-MI-047	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75921
FtStJ1	BC-MI-048	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75920
FtStJ1	BC-MI-049	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75919
FtStJ1	BC-MI-050	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36308
FtStJ1	BC-MI-051	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36307
FtStJ1	BC-MI-052	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36329
FtStJ1	BC-MI-053	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36302
FtStJ1	BC-MI-054	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75908
FtStJ1	BC-MI-055	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75729
FtStJ1	BC-MI-056	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36309
FtStJ1	BC-MI-057	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36339
FtStJ1	BC-MI-058	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36349
FtStJ1	BC-MI-059	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36354
FtStJ1	BC-MI-060	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36340
FtStJ1	BC-MI-061	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75924
FtStJ1	BC-MI-062	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36301
FtStJ1	BC-MI-063	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75911
FtStJ1	BC-MI-064	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36342
FtStJ1	BC-MI-065	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75933
FtStJ1	BC-MI-066	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-76009
FtStJ1	BC-MI-067	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75939
FtStJ1	BC-MI-068	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-76082
FtStJ1	BC-MI-069	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75938
FtStJ1	BC-MI-070	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75931

FtStJ1	BC-MI-071	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-76015
FtStJ1	BC-MI-155	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61093
FtStJ1	BC-MI-156	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61094
FtStJ1	BC-MI-157	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61096
FtStJ1	BC-MI-158	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61097
FtStJ1	BC-MI-159	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	1950-36344
FtStJ1	BC-MI-160	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61098
FtStJ1	BC-MI-161	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61099
FtStJ1	BC-MI-162	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61100
FtStJ1	BC-MI-163	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75979
FtStJ1	BC-MI-164	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75802
FtStJ1	BC-MI-165	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75803
FtStJ1	BC-MI-166	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75804
FtStJ1	BC-MI-167	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75981
FtStJ1	BC-MI-168	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2359-75980
FtStJ1	BC-MI-169	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75699
FtStJ1	BC-MI-170	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75805
FtStJ1	BC-MI-171	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75807
FtStJ1	BC-MI-172	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75808
FtStJ1	BC-MI-173	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-76030
FtStJ1	BC-MI-174	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75801
FtStJ1	BC-MI-175	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2590-61108
FtStJ1	BC-MI-177	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75857
FtStJ1	BC-MI-178	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75852
FtStJ1	BC-MI-179	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75853
FtStJ1	BC-MI-180	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75854
FtStJ1	BC-MI-184	John Prince Research Station, Ft St James, BC	54.645	124.395	UNBC	2350-75856
PG	BC-PU-01	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36098
PG	BC-PU-02	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36100
PG	BC-PU-03	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36213

PG	BC-PU-04	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36214
PG	BC-PU-05	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36217
PG	BC-PU-06	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36218
PG	BC-PU-07	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36220
PG	BC-PU-08	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36227
PG	BC-PU-09	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36228
PG	BC-PU-10	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36229
PG	BC-PU-11	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36240
PG	BC-PU-12	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36252
PG	BC-PU-13	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36257
PG	BC-PU-14	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36263
PG	BC-PU-15	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36264
PG	BC-PU-16	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36157
PG	BC-PU-17	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36164
PG	BC-PU-18	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36177
PG	BC-PU-19	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36223
PG	BC-PU-20	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36294
PG	BC-PU-21	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36295
PG	BC-PU-22	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36296
PG	BC-PU-23	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36298
PG	BC-PU-24	UNBC, Prince George, BC	53.894	122.829	UNBC	1950-36300
PG	BC-PU-25	UNBC, Prince George, BC	53.894	122.829	UNBC	2350-75601
PG	BC-PU-26	UNBC, Prince George, BC	53.894	122.829	UNBC	2350-75602
PG	BC-PU-27	UNBC, Prince George, BC	53.894	122.829	UNBC	2350-75603
PG	BC-PU-28	UNBC, Prince George, BC	53.894	122.829	UNBC	2350-75604
PG	BC-PU-29	UNBC, Prince George, BC	53.894	122.829	UNBC	2350-75605
PG	BC-PU-30	UNBC, Prince George, BC	53.894	122.829	UNBC	2350-75606
SAB1	SAB001	West Castle, AB	49.345	114.415	Wild	2490-57633
SAB1	SAB002	West Castle, AB	49.345	114.415	Wild	2490-57634
SAB1	SAB003	West Castle, AB	49.345	114.415	Wild	2490-57635

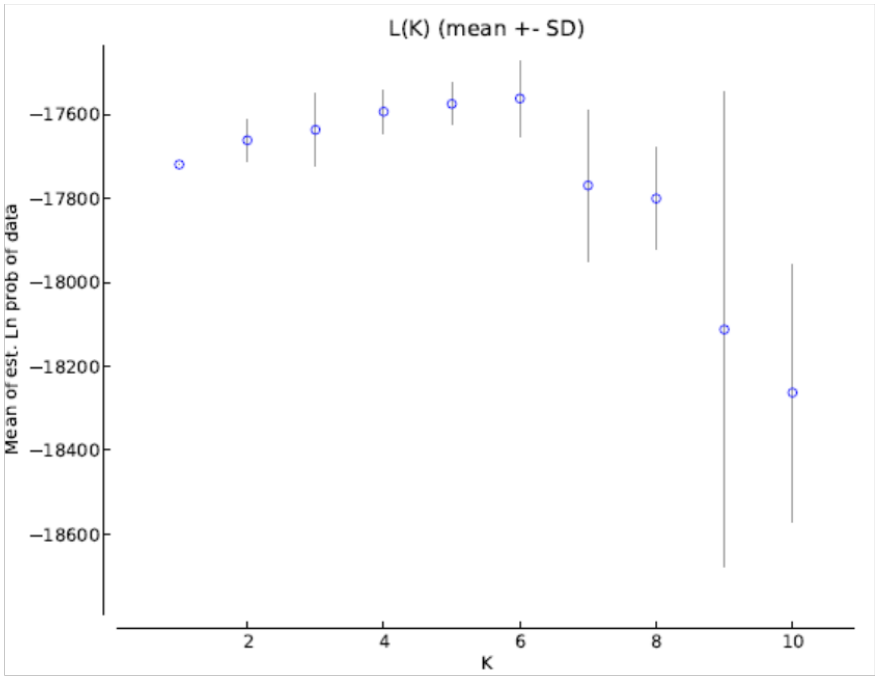
SAB1	SAB004	West Castle, AB	49.345	114.415	Wild	2490-57636
SAB1	SAB005	West Castle, AB	49.345	114.415	Wild	2490-57637
SAB1	SAB006	West Castle, AB	49.345	114.415	Wild	2490-57638
SAB1	SAB007	West Castle, AB	49.345	114.415	Wild	2490-57639
SAB1	SAB008	West Castle, AB	49.345	114.415	Wild	2490-57646
SAB1	SAB009	West Castle, AB	49.345	114.415	Wild	2490-57647
SAB1	SAB010	West Castle, AB	49.345	114.415	Wild	2490-57649
SAB1	SAB011	West Castle, AB	49.345	114.415	Wild	2490-57650
SAB1	SAB012	West Castle, AB	49.345	114.415	Wild	2490-57651
SAB1	SAB013	West Castle, AB	49.345	114.415	Wild	2490-57652
SAB1	SAB014	West Castle, AB	49.345	114.415	Wild	2490-57653
SAB1	SAB015	West Castle, AB	49.345	114.415	Wild	2490-57654
SAB1	SAB016	West Castle, AB	49.345	114.415	Wild	2490-57655
SAB1	SAB017	West Castle, AB	49.345	114.415	Wild	2490-57656
SAB1	SAB018	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57659
SAB1	SAB019	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57660
SAB1	SAB020	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57661
SAB1	SAB021	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57662
SAB1	SAB022	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57663
SAB1	SAB023	Syncline Ski Area, AB	49.391	114.340	Wild	2490-57664
SAB1	SAB024	Field station cabin, AB	49.349	114.411	Wild	2490-57673
SAB1	SAB025	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57677
SAB1	SAB026	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57678
SAB1	SAB027	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57679
SAB1	SAB028	North Lost Creek Rd, TWP 60-1, AB	49.472	114.463	Wild	2490-57680
SAB1	SAB029	North Lost Creek Rd, AB	49.472	114.463	Wild	2490-57682
SAB1	SAB030	North Lost Creek Rd, AB	49.472	114.463	Wild	2490-57683
SAB2	SAB031	Hwy 6, Waterton, AB	49.106	113.821	Wild	2490-57715
SAB2	SAB032	Hwy 6, Waterton, AB	49.106	113.821	Wild	2490-57716
SAB2	SAB033	Hwy 6, Waterton, AB	49.106	113.821	Wild	2490-57717

SAB2	SAB034	Hwy 6, Waterton, AB	49.106	113.821	Wild	2490-57718
SAB2	SAB035	Crandall Lake Campground, Waterton, AB	49.097	113.955	Wild	2490-57719
SAB2	SAB036	Crandall Lake Campground, Waterton, AB	49.097	113.955	Wild	2490-57721
SAB2	SAB037	Hwy 6, Waterton, AB	49.084	113.802	Wild	2490-57722
SAB2	SAB038	Hwy 6, Waterton, AB	49.084	113.802	Wild	2490-57723
SAB2	SAB039	Hwy 6, Waterton, AB	49.084	113.802	Wild	2490-57724
SAB2	SAB040	Hwy 6, Waterton, AB	49.076	113.791	Wild	2490-57725
SAB2	SAB041	Hwy 6, Waterton, AB	49.076	113.791	Wild	2490-57726
SAB2	SAB042	Belly River Campground, Waterton, AB	49.022	113.687	Wild	2490-57727
SAB2	SAB043	Belly River Campground, Waterton, AB	49.022	113.687	Wild	bcch 43
SAB2	SAB044	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57728
SAB2	SAB045	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57729
SAB2	SAB046	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57730
SAB2	SAB047	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57731
SAB2	SAB048	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57732
SAB2	SAB049	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57733
SAB2	SAB050	Marquis Hole Picnic Area, Waterton, AB	49.069	113.856	Wild	2490-57734
SAB2	SAB051	Marquis Hole, Waterton, AB	49.069	113.856	Wild	2490-57737
SAB2	SAB052	Belly River Campground Waterton, AB	49.023	113.687	Wild	A

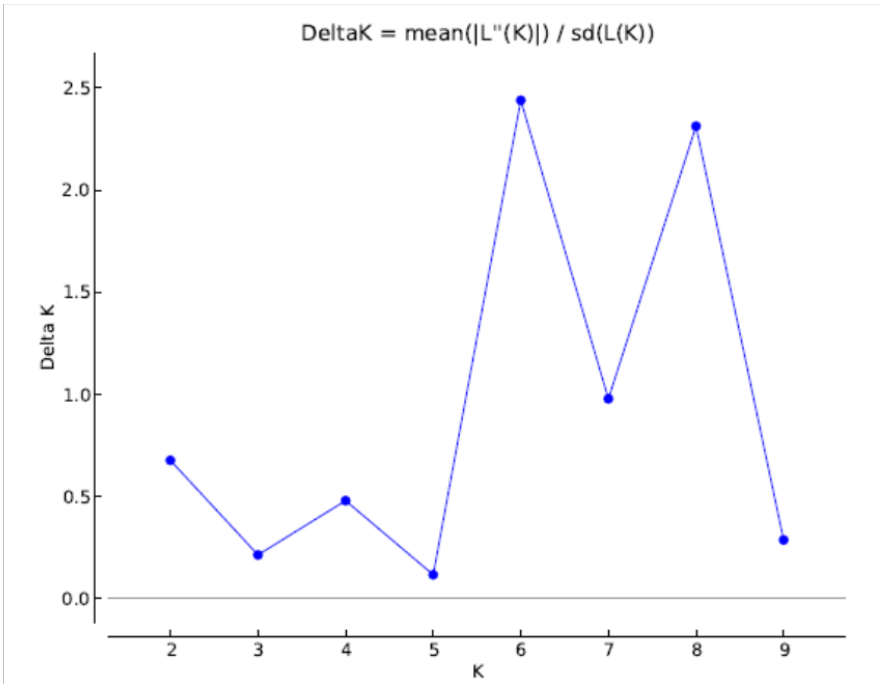
Appendix 2.2. Repeat type (if known), primer sequence, allele size range (bp), number of alleles (*Na*) and $MgCl_2$ concentration for each microsatellite locus used to genotype black-capped chickadee individuals. *indicates new primer designed during this study.

Locus	Repeat type	Sequence (5' to 3')	Size range (bp)	*Na*	$MgCl_2$ (mM)	Reference
PAT MP 2-14F	-	GAACAGATAAAGCCAAATTAC	125-167	19	2	Otter *et al.*, 1998
PAT MP 2-14R		TAGTGAATGCTTGATTTCTTTG				
PAT MP 2-43F	-	ACAGGTAGTCAGAAATGGAAAG	141-211	28	1.5	Otter *et al.*, 1998
PAT MP 2-43R		GTATCCAGAGTCTTTGCTGATG				
Escu6F	-	CATAGTGATGCCCTGCTAGG	120-248	26	1.5	Hanotte *et al.*, 1994
Escu6R		GCAAGTGCTCCTTAATATTTGG				
Titgata02F	$(GATA)_{12}$	ATTGCTTGATATTTGAAAGCATA	116-276	17	2	Wang *et al.*, 2005
Titgata02R		TTGTCTTTTGGGTTGCCTGA				
Titgata39F	$(GATA)_{10}$	CATGTATTTTCCAAAAGTAAATAT	222-258	11	2	Wang *et al.*, 2005
Titgata39R		CTGCTATTCTGCAAACTTGTGG				
CcaTgu11F	-	TGCTTAGGAAATAGGAAGCACA	212-218	4	2	Olano_Marin *et al.*, 2010
CcaTgu11R		CTGCAACTTAAGCARRGTTATGA				
PmanTAGAn71F	$(TAGG)_6(TAGA)_{11}$	TCAGCCTCCAAGGAAAACAG	157-193	10	2.5	Saladin *et al.*, 2003
PmanTAGAn71R		GCATAAGCAACACCATGCAG				
PmanTAGAn45F	$(TGA)_{10}$	CCCCTGGCTCTTTCATATCC	320-407	26	2	Saladin *et al.*, 2003
PmanTAGAn45R		GACAGGTGTTGGCACAAGG				
Ase18F	$(GT)_{12}$	ATCCAGTCTTCGCAAAAGCC	188-220	8	2.5	Richardson *et al.*, 2000
Ase18R		TGCCCCAGAGGGAAGAAG				
Cuμ28F	$(CA)_{12}$	GAGGCACAGAAATGTGAATT	182-186	3	2.5	Gibbs *et al.*, 1999
Cuμ28R		TAAGTAGAAGGACTTGATGGCT				
Ppi2F	-	CACAGACCATTCGAAGCAGA	324-488	46	2.5	Martinez *et al.*, 1999
Ppi2R		GCTCCGATGGTGAATGAAGT				
VeCr05F	$(AC)_8$	ACACACTTATGTGCATGGGCT	288-340	4	2.5	Tarvin, 2006
VeCr05R		ATATTTCAGGTATGGGTTTGGTTC				
CtC101-F	$(CATC)_8$	GTCCAGTAGGTAGGTGTGATG	232-284	12	2.5	Stenzler *et al.*, 2004
CtC101-R		TTATTTAGGTGCCAGAGAGATG				
Pij02F	$(GT)_{23}$	CACACCTACCTCATGGATCT	168-258	35	2.5	Saito *et al.*, 2005
Pij02Rnew*		CTGCATCAACTCATGTCCTG				

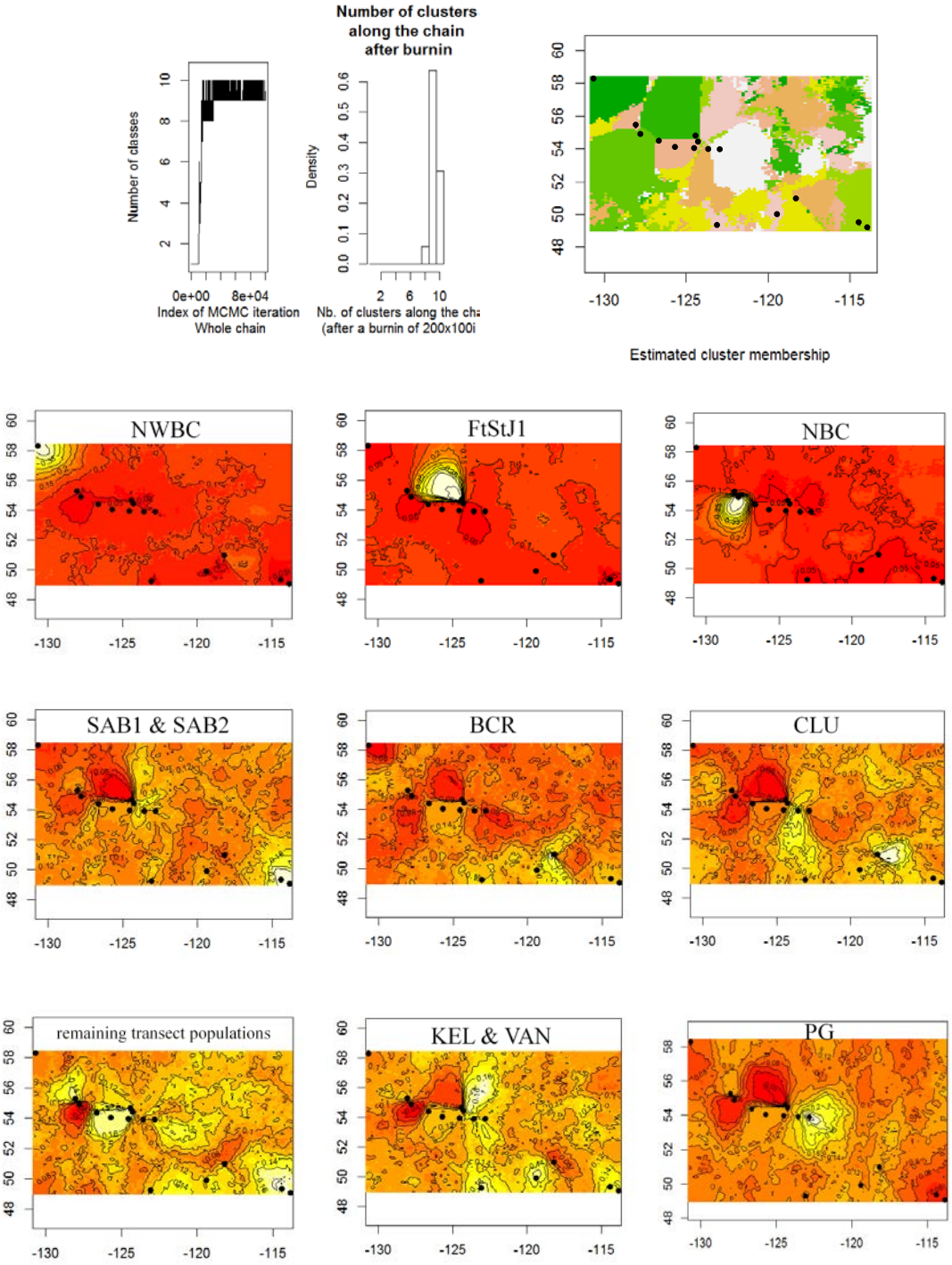
(a)



(b)



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.



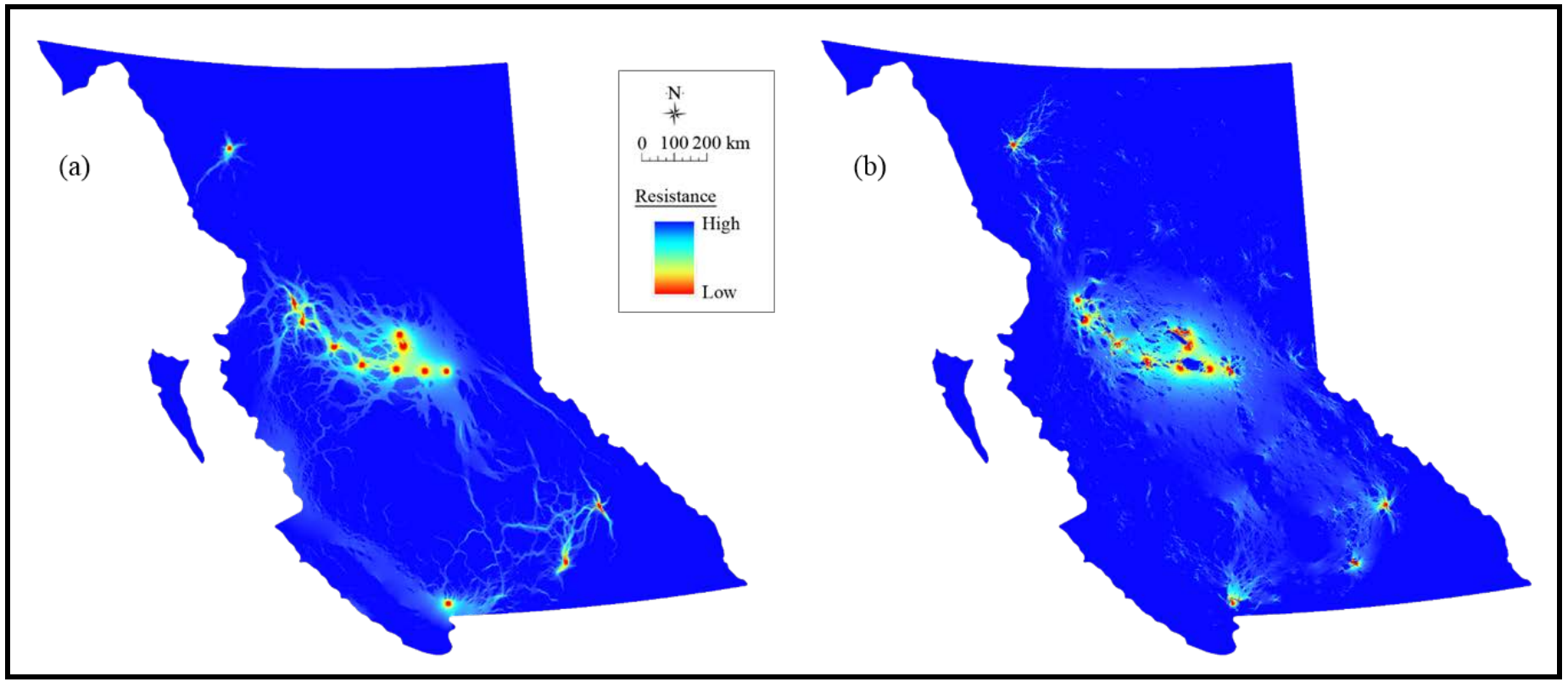
Appendix 2.4. GENELAND output including the modal number of clusters (K = 9), map of population membership, and map boundaries for each of the nine clusters inferred.

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.

	BCR	**NBC**	**CLU**	**FF**	**FrL**	**FtStJ2**	**HAZ**	**HOU**	**KEL**	**NWBC**	**VAN**	**FtStJ1**	**PG**	**SAB1**	**SAB2**
BCR	-														
NBC	**0.044**	-													
CLU	**0.052**	**0.063**	-												
FF	**0.172**	0.169	0.180	-											
FrL	**0.271**	**0.301**	0.301	0.403	-										
FtStJ2	**0.273**	**0.293**	**0.312**	0.399	0.494	-									
HAZ	**0.178**	**0.197**	0.181	0.292	**0.422**	**0.418**	-								
HOU	**0.201**	**0.196**	**0.223**	0.297	**0.434**	**0.436**	**0.360**	-							
KEL	**0.605**	**0.634**	**0.644**	**0.731**	**0.821**	0.787	**0.703**	**0.812**	-						
NWBC	**0.054**	**0.059**	**0.076**	**0.201**	**0.314**	**0.307**	**0.213**	**0.208**	**0.658**	-					
VAN	**0.536**	**0.568**	**0.588**	**0.675**	**0.764**	**0.727**	**0.676**	**0.726**	**0.983**	**0.582**	-				
FtStJ1	**0.034**	**0.042**	**0.039**	0.165	**0.287**	**0.281**	**0.177**	**0.198**	**0.622**	**0.054**	**0.550**	-			
PG	**0.108**	**0.102**	**0.107**	0.248	**0.365**	**0.376**	**0.271**	**0.251**	**0.735**	**0.112**	**0.655**	**0.096**	-		
SAB1	**0.043**	**0.045**	**0.054**	0.172	**0.294**	**0.291**	**0.192**	**0.206**	**0.646**	**0.067**	**0.579**	**0.028**	**0.115**	-	
SAB2	**0.041**	**0.041**	**0.060**	**0.173**	**0.285**	**0.291**	**0.191**	**0.201**	**0.625**	**0.066**	**0.569**	**0.041**	**0.092**	**0.036**	-

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).

Grouped populations	# groups	Among Groups	Among populations within groups	Within populations
BCR + remaining populations	2	2.85	-5.42	102.57
NWBC, BCR + remaining populations	3	2.83	-5.64	102.82
BCR, PG + remaining populations	3	2.8	-6.14	103.28
NWBC, BCR, PG + remaining populations	4	2.64	-5.93	103.29
PG + remaining populations	2	2.12	-5.32	103.2
FtStJ1 + remaining populations	2	2.12	-5.32	103.2
FtStJ1, PG + remaining populations	3	1.98	-5.53	103.6
NWBC + remaining populations	2	1.91	-4.88	102.97
NWBC, PG + remaining populations	3	1.03	-5	103.97
FtStJ1&SAB1 + remaining populations	2	0.38	-4.93	104.55
SAB1 + remaining populations	2	-0.01	-4.79	104.8
KEL&VAN, NWBC, BCR, PG + remaining populations	5	-2.18	-3.36	105.54
KEL&VAN, BCR, PG, NWBC, FTSJ1 + remaining populations	6	-2.37	-3.03	105.4
BCR, PG, KEL&VAN + remaining populations	4	-2.67	3.19	105.86
KEL&VAN, BCR, PG, NWBC, FtStJ1&SAB1 + remaining populations	6	-3.61	-2.02	105.63
KEL&VAN, NWBC, BCR + remaining populations	4	-3.86	-3.05	106.9
ALL populations	1	-4.79	N/A	104.79
KEL&VAN, NWBC + remaining populations	4	-9.69	-2.01	112.3
KEL&VAN + remaining populations	2	-15.71	-2.58	118.3



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.

Pop	ID	Location	Lat (°N)	Long (°W)	Source	Band/ Museum ID
WH	Whistlers Campground, Jasper NP, AB	bcchCAB030	52.8491	118.0797	Wild	2500-94961
ED	Edson, AB	bcchCAB027	53.6286	116.8019	Wild	1501-39830
HI	Hinton, AB	bcchCAB021	53.4005	117.5790	Wild	2520-39822
HI	Hinton, AB	bcchCAB022	53.3866	117.5903	Wild	2520-39823
BUC	Buck Lake, AB	bcchCAB014	52.9721	114.6046	Wild	2520-39814
BUC	Buck Lake, AB	bcchCAB015	52.9721	114.6046	Wild	2520-39815
BUC	Buck Lake, AB	bcchCAB016	52.9721	114.6046	Wild	2520-39816
BUC	Buck Lake, AB	bcchCAB017	52.9721	114.6046	Wild	2520-39817
BUC	Buck Lake, AB	bcchCAB018	52.9721	114.6046	Wild	2520-39818
BUC	Buck Lake, AB	bcchCAB019	52.9721	114.6046	Wild	2520-39819
BUC	Buck Lake, AB	bcchCAB020	52.9721	114.6046	Wild	2520-39820
NSK	Edmonton, AB	bcchCAB023	53.5296	113.5539	Wild	2520-39826
NSK	Edmonton, AB	bcchCAB024	53.5296	113.5539	Wild	2520-39827
NSK	Edmonton, AB	bcchCAB025	53.4828	113.5550	Wild	2520-39828
NSK	Edmonton, AB	bcchCAB026	53.4814	113.4238	Wild	2520-39829
NSK	Rainbow Valley Campground, Edmonton, AB	bcchCABNSASK031	53.4858	113.5560	Wild	2710-78375
NSK	Rainbow Valley Campground, Edmonton, AB	bcchCABNSASK032	53.4858	113.5560	Wild	2710-78376
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK033	53.5046	113.5595	Wild	2710-78378
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK034	53.5046	113.5595	Wild	2710-78379
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK035	53.5046	113.5595	Wild	2710-78380
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK036	53.5046	113.5595	Wild	2710-78381
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK037	53.5046	113.5595	Wild	2710-78382
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK038	53.5046	113.5595	Wild	2710-78383
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK039	53.5046	113.5595	Wild	2710-78384
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK040	53.5046	113.5595	Wild	2710-78385
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK041	53.5046	113.5595	Wild	2710-78386
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK042	53.5046	113.5595	Wild	2710-78387
NSK	Whitemud Park, Edmonton, AB	bcchCABNSASK043	53.5046	113.5595	Wild	2710-78388
NSK	Fort Edmonton Park, Edmonton, AB	bcchCABNSASK044	53.5025	113.5706	Wild	2560-14612*

NSK	Fort Edmonton Park, Edmonton, AB	bcchCABNSASK045	53.5025	113.5706	Wild	2560-14615*
NSK	Fort Edmonton Park, Edmonton, AB	bcchCABNSASK046	53.5025	113.5706	Wild	2710-78377
NSK	Fort Edmonton Park, Edmonton, AB	bcchCABNSASK047	53.5025	113.5706	Wild	2710-78389
NSK	Fort Edmonton Park, Edmonton, AB	bcchCABNSASK048	53.5025	113.5706	Wild	2710-78390
NSK	Fort Edmonton Park, Edmonton, AB	bcchCABNSASK049	53.5025	113.5706	Wild	2710-78391
OL	Olds, AB	bcchCAB001	51.7916	114.2862	Wild	3111-48301
OL	Olds, AB	bcchCAB002	51.8062	114.5933	Wild	2520-38902
OL	Olds, AB	bcchCAB003	51.8064	114.5933	Wild	2520 39803
OL	Olds, AB	bcchCAB004	51.8070	114.5933	Wild	2520-39804
IN	Innisfail, AB	bcchCAB005	52.0320	113.9624	Wild	2520-39805
IN	Innisfail, AB	bcchCAB006	52.0320	113.9624	Wild	2520-39806
IN	Innisfail, AB	bcchCAB007	52.0320	113.9624	Wild	2520-39807
IN	Innisfail, AB	bcchCAB008	52.0320	113.9624	Wild	2520-39808
IN	Innisfail, AB	bcchCAB009	52.0320	113.9624	Wild	2520-39809
IN	Innisfail, AB	bcchCAB010	52.0320	113.9624	Wild	2520-39810
IN	Innisfail, AB	bcchCAB011	52.0320	113.9624	Wild	2520-39811
IN	Innisfail, AB	bcchCAB012	52.0320	113.9624	Wild	2520-39812
IN	Innisfail, AB	bcchCAB013	52.0238	110.9824	Wild	2520-39813
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD102	52.3004	113.7853	Wild	2710-78426
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD103	52.3004	113.7853	Wild	2710-78427
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD104	52.3004	113.7853	Wild	2710-78428
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD105	52.3004	113.7853	Wild	2710-78429
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD106	52.3004	113.7853	Wild	2710-78430
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD107	52.3004	113.7853	Wild	2710-78431
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD108	52.3004	113.7853	Wild	2710-78432
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD109	52.3004	113.7853	Wild	2710-78433
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD110	52.3004	113.7853	Wild	2710-78434
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD111	52.3004	113.7853	Wild	2710-78435
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD112	52.3004	113.7853	Wild	2710-78436
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD113	52.3004	113.7853	Wild	2710-78437
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD114	52.3004	113.7853	Wild	2710-78438
RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD115	52.3004	113.7853	Wild	2710-78439

RD1	Three Mile Bend, Red Deer, (Red Deer River)	bcchSABRD116	52.3004	113.7853	Wild	2710-78440
RD1	Golf Course, Red Deer (Red Deer River)	bcchSABRD117	52.3163	113.7769	Wild	2710-78441
RD1	Golf Course, Red Deer (Red Deer River)	bcchSABRD118	52.3163	113.7769	Wild	2710-78442
RD1	Golf Course, Red Deer (Red Deer River)	bcchSABRD119	52.3163	113.7769	Wild	2710-78444
RD2	Content Bridge, HWY 21, (Red Deer River)	bcchSABRD120	52.3095	113.0785	Wild	2710-78445
RD2	Content Bridge, HWY 21, (Red Deer River)	bcchSABRD121	52.3095	113.0785	Wild	2710-78446
RD2	Content Bridge, HWY 21, (Red Deer River)	bcchSABRD122	52.3095	113.0785	Wild	2710-78447
RD2	Content Bridge, HWY 21, (Red Deer River)	bcchSABRD123	52.3095	113.0785	Wild	2710-78448
RD2	Content Bridge, HWY 21, (Red Deer River)	bcchSABRD124	52.3095	113.0785	Wild	2710-78449
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD125	52.3249	113.1673	Wild	2710-78450
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD126	52.3249	113.1673	Wild	2710-78451
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD127	52.3249	113.1673	Wild	2710-78452
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD128	52.3249	113.1673	Wild	2710-78453
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD129	52.3249	113.1673	Wild	2710-78454
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD130	52.3249	113.1673	Wild	2710-78455
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD131	52.3249	113.1673	Wild	2710-78456
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD132	52.3249	113.1673	Wild	2710-78457
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD133	52.3249	113.1673	Wild	2710-78458
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD134	52.3216	113.1599	Wild	2710-78459
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD135	52.3216	113.1599	Wild	2710-78460
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD136	52.3216	113.1599	Wild	2710-78461
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD137	52.3216	113.1599	Wild	2710-78462
RD2	Deer Valley Meadow, South of HWY 11, Red Deer River	bcchSABRD138	52.3216	113.1599	Wild	2710-78463
DR	Dinosaur Trail Drumheller, Red Deer River	bcchSABDH139	51.4673	112.7408	Wild	2710-78464
DR	Dinosaur Trail, Drumheller, Red Deer River	bcchSABDH140	51.4673	112.7408	Wild	2710-78465
DR	Dinosaur Trail, Drumheller, Red Deer River	bcchSABDH141	51.4673	112.7408	Wild	2710-78466
DR	Dinosaur Trail, Drumheller, Red Deer River	bcchSABDH142	51.4673	112.7408	Wild	2710-78467
DR	Dinosaur Trail, Drumheller, Red Deer River	bcchSABDH143	51.4673	112.7408	Wild	2710-78468
DR	Dinosaur Trail, Drumheller, Red Deer River	bcchSABDH144	51.4673	112.7408	Wild	2710-78469
DR	Dinosaur Trail, Drumheller, Red Deer River	bcchSABDH145	51.4673	112.7408	Wild	2710-78470
DR	Newcastle Trail, Drumheller, Red Deer River	bcchSABDH146	51.4638	112.7510	Wild	2710-78471
DR	Newcastle Trail, Drumheller, Red Deer River	bcchSABDH147	51.4638	112.7510	Wild	2710-78472

DR	Newcastle Trail, Drumheller, Red Deer River	bcchSABDH148	51.4638	112.7510	Wild	2710-78473
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH149	51.4516	112.6824	Wild	2710-78474
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH150	51.4516	112.6824	Wild	2710-78475
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH151	51.4516	112.6824	Wild	2710-78476
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH152	51.4516	112.6824	Wild	2710-78477
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH153	51.4516	112.6824	Wild	2710-78478
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH154	51.4516	112.6824	Wild	2710-78479
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH155	51.4516	112.6824	Wild	2710-78480
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH156	51.4516	112.6824	Wild	2710-78481
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH157	51.4516	112.6824	Wild	2710-78482
DR	Riverside Drive, Drumheller, Red Deer River	bcchSABDH158	51.4516	112.6824	Wild	2710-78483
EM	Emerson Bridge, Highway 36, Red Deer River	bcchSABEB159	50.9164	111.9007	Wild	2710-78484
EM	Emerson Bridge, Highway 36, Red Deer River	bcchSABEB160	50.9164	111.9007	Wild	2710-78485
EM	Emerson Bridge, Highway 36, Red Deer River	bcchSABEB161	50.9164	111.9007	Wild	2710-78486
EM	Emerson Bridge, Highway 36, Red Deer River	bcchSABEB162	50.9164	111.9007	Wild	2710-78487
JE	Jenner Campground, Red Deer River	bcchSABJ163	50.8440	111.1527	Wild	2710-78488
JE	Jenner Campground, Red Deer River	bcchSABJ164	50.8440	111.1527	Wild	2710-78489
BUF	Buffalo Campground, Red Deer River	bcchSABBU165	50.8494	110.6970	Wild	2710-78490
BO	Wyndham-Carseland Park, AB	bcchSABBOW181	50.8290	113.4220	Wild	2710-78333
BO	Wyndham-Carseland Park, AB	bcchSABBOW182	50.8290	113.4220	Wild	2710-78334
BO	Wyndham-Carseland Park, AB	bcchSABBOW183	50.8290	113.4220	Wild	2710-78335
BO	Wyndham-Carseland Park, AB	bcchSABBOW184	50.8290	113.4220	Wild	2710-78336
BO	Wyndham-Carseland Park, AB	bcchSABBOW185	50.8290	113.4220	Wild	2710-78337
BO	Wyndham-Carseland Park, AB	bcchSABBOW186	50.8290	113.4220	Wild	2710-78338
BO	Wyndham-Carseland Park, AB	bcchSABBOW187	50.8290	113.4220	Wild	2710-78339
BO	Wyndham-Carseland Park, AB	bcchSABBOW188	50.8290	113.4220	Wild	2710-78340
BO	Wyndham-Carseland Park, AB	bcchSABBOW189	50.8290	113.4220	Wild	2710-78341
BO	Wyndham-Carseland Park, AB	bcchSABBOW190	50.8290	113.4220	Wild	2710-78342
BO	Wyndham-Carseland Park, AB	bcchSABBOW191	50.8290	113.4220	Wild	2710-78343
BO	Wyndham-Carseland Park, AB	bcchSABBOW192	50.8290	113.4220	Wild	2710-78344
BO	Wyndham-Carseland Park, AB	bcchSABBOW193	50.8290	113.4220	Wild	2710-78345
BO	Wyndham-Carseland Park, AB	bcchSABBOW194	50.8290	113.4220	Wild	2710-78346

BO	Wyndham-Carseland Park, AB	bcchSABBOW195	50.8290	113.4220	Wild	2710-78347
BO	Wyndham-Carseland Park, AB	bcchSABBOW196	50.8290	113.4220	Wild	2710-78348
BO	Wyndham-Carseland Park, AB	bcchSABBOW197	50.8290	113.4220	Wild	2710-78349
BO	Wyndham-Carseland Park, AB	bcchSABBOW198	50.8290	113.4220	Wild	2710-78350
BO	Wyndham-Carseland Park, AB	bcchSABBOW199	50.8290	113.4220	Wild	2710-78351
BO	Wyndham-Carseland Park, AB	bcchSABBOW200	50.8290	113.4220	Wild	2710-78352
SB2	Hwy 6, Waterton, AB	bcchSAB031	49.0694	113.8561	Wild	2490-57715
SB2	Hwy 6, Waterton, AB	bcchSAB032	49.0694	113.8561	Wild	2490-57716
SB2	Hwy 6, Waterton, AB	bcchSAB033	49.0694	113.8561	Wild	2490-57717
SB2	Hwy 6, Waterton, AB	bcchSAB034	49.0694	113.8561	Wild	2490-57718
SB2	Crandall Lake Campground, Waterton, AB	bcchSAB035	49.0694	113.8561	Wild	2490-57719
SB2	Crandall Lake Campground, Waterton, AB	bcchSAB036	49.0694	113.8561	Wild	2490-57721
SB2	Hwy 6, Waterton, AB	bcchSAB037	49.0694	113.8561	Wild	2490-57722
SB2	Hwy 6, Waterton, AB	bcchSAB038	49.0694	113.8561	Wild	2490-57723
SB2	Hwy 6, Waterton, AB	bcchSAB039	49.0694	113.8561	Wild	2490-57724
SB2	Hwy 6, Waterton, AB	bcchSAB040	49.0694	113.8561	Wild	2490-57725
SB2	Hwy 6, Waterton, AB	bcchSAB041	49.0694	113.8561	Wild	2490-57726
SB2	Belly River Campground, Waterton, AB	bcchSAB042	49.0694	113.8561	Wild	2490-57727
SB2	Belly River Campground, Waterton, AB	bcchSAB043	49.0694	113.8561	Wild	bcch 43
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB044	49.0694	113.8561	Wild	2490-57728
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB045	49.0694	113.8561	Wild	2490-57729
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB046	49.0694	113.8561	Wild	2490-57730
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB047	49.0694	113.8561	Wild	2490-57731
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB048	49.0694	113.8561	Wild	2490-57732
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB049	49.0694	113.8561	Wild	2490-57733
SB2	Marquis Hole Picnic Area, Waterton, AB	bcchSAB050	49.0694	113.8561	Wild	2490-57734
SB2	Marquis Hole, Waterton, AB	bcchSAB051	49.0694	113.8561	Wild	2490-57737
SB2	Belly River Campground Waterton, AB	bcchSAB052	49.0227	113.6874	Wild	A
SB2	Belly River Campground, Waterton, AB	bcchSAB242	49.0295	113.6809	Wild	2710-78530
SB2	Belly River Campground, Waterton, AB	bcchSAB243	49.0295	113.6809	Wild	2710-78531
SB2	Belly River Campground, Waterton, AB	bcchSAB244	49.0295	113.6809	Wild	2710-78532
SB2	Belly River Campground, Waterton, AB	bcchSAB245	49.0295	113.6809	Wild	2710-78533

SB2	Crandell Lake Campground, Waterton, AB	bcchSAB246	49.0998	113.9586	Wild	2710-78534
SB2	Crandell Lake Campground, Waterton, AB	bcchSAB247	49.0998	113.9586	Wild	2710-78535
SB2	Waterton Village, Waterton, AB	bcchSAB248	49.0503	113.9157	Wild	2710-78536
DY	W of Twp Rd. 041, Drywood Creek, AB	bcchSABDRY223	49.2806	114.0227	Wild	2710-78392
DY	W of Twp Rd. 041, Drywood Creek, AB	bcchSABDRY224	49.2806	114.0227	Wild	2710-78393
DY	Bow Crow Forest, Drywood Creek, AB	bcchSABDRY225	49.2731	114.0165	Wild	2710-78394
DY	Bow Crow Forest, Drywood Creek, AB	bcchSABDRY226	49.2731	114.0165	Wild	2710-78395
DY	Beauvais Lake PP, AB	bcchSABDRY227	49.4138	114.1132	Wild	2710-78396
DY	Beauvais Lake PP, AB	bcchSABDRY228	49.4138	114.1132	Wild	2710-78397
DY	Beauvais Lake PP, AB	bcchSABDRY229	49.4138	114.1132	Wild	2710-78398
DY	Beauvais Lake PP, AB	bcchSABDRY230	49.4138	114.1132	Wild	2710-78399
DY	Range Rd 303, near Drywood Creek, AB	bcchSABDRY231	49.2808	113.9765	Wild	2710-78400
DY	North of Bow Crow Forest, near Drywood Creek, AB	bcchSABDRY232	49.2758	114.0189	Wild	2710-78521
DY	S of Range Rd. 303, near Drywood Creek, AB	bcchSABDRY233	49.2592	113.9966	Wild	2710-78522
DY	S of Range Rd. 303, near Drywood Creek, AB	bcchSABDRY234	49.2592	113.9966	Wild	2710-78523
DY	S of Range Rd. 303, near Drywood Creek, AB	bcchSABDRY235	49.2592	113.9966	Wild	BCCH_SAB658
DY	S of Range Rd. 303, near Drywood Creek, AB	bcchSABDRY236	49.2592	113.9966	Wild	2710-78524
DY	SE of Range Road 303, near Drywood Creek, AB	bcchSABDRY237	49.2506	113.9957	Wild	2710-78525
DY	SE of Range Road 303, near Drywood Creek, AB	bcchSABDRY238	49.2506	113.9957	Wild	2710-78526
DY	SE of Range Road 303, near Drywood Creek, AB	bcchSABDRY239	49.2506	113.9957	Wild	2710-78527
DY	SE of Range Road 303, near Drywood Creek, AB	bcchSABDRY240	49.2506	113.9957	Wild	2710-78528
DY	Twp Rd. 35, near Drywood Creek, AB	bcchSABDRY241	49.2324	113.9675	Wild	2710-78529
DY	Beauvais Lake PP Village, AB	bcchSABDRY251	49.4149	114.1059	Wild	2710-78539
SB1	West Castle, AB	bcchSAB001	49.3450	114.4153	Wild	2490-57633
SB1	West Castle, AB	bcchSAB002	49.3450	114.4153	Wild	2490-57634
SB1	West Castle, AB	bcchSAB003	49.3450	114.4153	Wild	2490-57635
SB1	West Castle, AB	bcchSAB004	49.3450	114.4153	Wild	2490-57636
SB1	West Castle, AB	bcchSAB005	49.3450	114.4153	Wild	2490-57637
SB1	West Castle, AB	bcchSAB006	49.3450	114.4153	Wild	2490-57638
SB1	West Castle, AB	bcchSAB007	49.3450	114.4153	Wild	2490-57639
SB1	West Castle, AB	bcchSAB008	49.3450	114.4153	Wild	2490-57646
SB1	West Castle, AB	bcchSAB009	49.3450	114.4153	Wild	2490-57647

SB1	West Castle, AB	bcchSAB010	49.3450	114.4153	Wild	2490-57649
SB1	West Castle, AB	bcchSAB011	49.3450	114.4153	Wild	2490-57650
SB1	West Castle, AB	bcchSAB012	49.3450	114.4153	Wild	2490-57651
SB1	West Castle, AB	bcchSAB013	49.3450	114.4153	Wild	2490-57652
SB1	West Castle, AB	bcchSAB014	49.3450	114.4153	Wild	2490-57653
SB1	West Castle, AB	bcchSAB015	49.3450	114.4153	Wild	2490-57654
SB1	West Castle, AB	bcchSAB016	49.3450	114.4153	Wild	2490-57655
SB1	West Castle, AB	bcchSAB017	49.3450	114.4153	Wild	2490-57656
SB1	Syncline Ski Area, AB	bcchSAB018	49.3908	114.3397	Wild	2490-57659
SB1	Syncline Ski Area, AB	bcchSAB019	49.3908	114.3397	Wild	2490-57660
SB1	Syncline Ski Area, AB	bcchSAB020	49.3908	114.3397	Wild	2490-57661
SB1	Syncline Ski Area, AB	bcchSAB021	49.3908	114.3397	Wild	2490-57662
SB1	Syncline Ski Area, AB	bcchSAB022	49.3908	114.3397	Wild	2490-57663
SB1	Syncline Ski Area, AB	bcchSAB023	49.3908	114.3397	Wild	2490-57664
SB1	Field station cabin, AB	bcchSAB024	49.3491	114.4108	Wild	2490-57673
SB1	North Lost Creek Rd, TWP 60-1, AB	bcchSAB025	49.4719	114.4625	Wild	2490-57677
SB1	North Lost Creek Rd, TWP 60-1, AB	bcchSAB026	49.4719	114.4625	Wild	2490-57678
SB1	North Lost Creek Rd, TWP 60-1, AB	bcchSAB027	49.4719	114.4625	Wild	2490-57679
SB1	North Lost Creek Rd, TWP 60-1, AB	bcchSAB028	49.4719	114.4625	Wild	2490-57680
SB1	North Lost Creek Rd, AB	bcchSAB029	49.4719	114.4625	Wild	2490-57682
SB1	North Lost Creek Rd, AB	bcchSAB030	49.4719	114.4625	Wild	2490-57683
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB53	49.5883	114.2142	Wild	2500-94973
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB54	49.5883	114.2142	Wild	2500-94970
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB55	49.5883	114.2142	Wild	2500-94966
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB56	49.5883	114.2142	Wild	2500-94975
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB57	49.5883	114.2142	Wild	2500-94980
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB58	49.5883	114.2142	Wild	2500-94983
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB59	49.5883	114.2142	Wild	2500-94990
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB60	49.5883	114.2142	Wild	2500-94991
CR	7318 Range Rd, Crownest Pass, AB	bcchSAB61	49.5883	114.2142	Wild	2500-94992
CR	7320 Range Rd, Crownest Pass, AB	bcchSABCR062	49.5757	114.2114	Wild	2710-78302
CR	7334 Range Rd, Crownest Pass, AB	bcchSABCR063	49.5757	114.2114	Wild	2710-78301

CR	7338 Range Rd, Crownest Pass, AB	bcchSABCR064	49.5757	114.2114	Wild	2710-78311
CR	7354 Range Rd, Crownest Pass, AB	bcchSABCR065	49.5757	114.2114	Wild	2710-78318
CR	Lundbreck Falls, Crowsnest River, AB	bcchSABCN201	49.5844	114.2055	Wild	2710-78353
CR	Lundbreck Falls, Crowsnest River, AB	bcchSABCN202	49.5844	114.2055	Wild	2710-78354
CR	Twp Rd. 72, Crowsnest, AB	bcchSABCN249	49.5534	114.2723	Wild	2710-78537
CR	Twp Rd 72-A, Villa Vega, Crowsnest, SAB	bcchSABCN250	49.5596	114.2528	Wild	2710-78538
CR	East Hillcrest Drive bridge, Crowsnest River	bcchSABEHB167	49.5671	114.3495	Wild	2710-78492
CR	East Hillcrest Drive bridge, Crowsnest River	bcchSABEHB168	49.5671	114.3495	Wild	2710-78493
CR	Lundbreck Falls, Crowsnest River	bcchSABEHB169	49.5934	114.1713	Wild	2710-78494
OM	S of river Rge Rd 29-2-1 (Oldman River)	bcchSABOMD080	49.5550	113.8184	Wild	2710-78401
OM	N of river Rge Rd 29-2-1 (Oldman River)	bcchSABOMD081	49.5583	113.8223	Wild	2710-78402
OM	N of river Rge Rd 28-2-3 (Oldman River below Old Man Dam)	bcchSABOMD082	49.5811	113.9058	Wild	2710-78403
OM	N of river Rge Rd 28-2-3 (Oldman River below Old Man Dam)	bcchSABOMD083	49.5811	113.9058	Wild	2710-78404
OM	N of river Rge Rd 28-2-3 (Oldman River below Old Man Dam)	bcchSABOMD084	49.5811	113.9058	Wild	2710-78405
OM	N of river Rge Rd 28-2-3 (Oldman River below Old Man Dam)	bcchSABOMD085	49.5811	113.9058	Wild	2710-78406
OM	SW of river, Summerview (Oldman River)	bcchSABOMD086	49.5815	113.8787	Wild	2710-78408
OM	NW of river, Rge Rd 29-2-1 (Oldman River)	bcchSABOMD087	49.5577	113.8278	Wild	2710-78409
OM	NW of river, Rge Rd 29-2-1 (Oldman River)	bcchSABOMD088	49.5577	113.8278	Wild	2710-78410
OM	S of river, Rge Rd 29-2-1 (Oldman River)	bcchSABOMD089	49.5811	113.9058	Wild	2710-78411
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP173	49.4295	113.4961	Wild	2710-78514
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP174	49.4295	113.4961	Wild	2710-78515
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP175	49.4295	113.4961	Wild	2710-78516
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP176	49.4295	113.4961	Wild	2710-78517
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP177	49.4295	113.4961	Wild	2710-78518
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP178	49.4295	113.4961	Wild	2710-78519
BL	Blue Trail RV Park, HWY810 bridge, Waterton River	bcchSABBTP179	49.4295	113.4961	Wild	2710-78520
GL	TWP Rd 52, Glenwood, Waterton River	bcchSABGW170	49.4019	113.5933	Wild	2710-78511
GL	TWP Rd 52, Glenwood, Waterton River	bcchSABGW171	49.4019	113.5933	Wild	2710-78512
GL	TWP Rd 52, Glenwood, Waterton River	bcchSABGW172	49.4019	113.5933	Wild	2710-78513
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM066	49.7342	113.4004	Wild	2430-38985
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM067	49.7342	113.4004	Wild	2430-38986
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM068	49.7342	113.4004	Wild	2430-38987

FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM069	49.7342	113.4004	Wild	2430-38988
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM070	49.7342	113.4004	Wild	2430-38989
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM071	49.7339	113.3973	Wild	2430-38990
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM072	49.7339	113.3973	Wild	2430-38991
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM073	49.7339	113.3973	Wild	2430-38992
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM074	49.7339	113.3973	Wild	2430-38993
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM075	49.7339	113.3973	Wild	2430-38994
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM076	49.7339	113.3973	Wild	2430-38996
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM077	49.7339	113.3973	Wild	2430-38997
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM078	49.7339	113.3973	Wild	2430-38998
FO	SW of 811 bridge, Fort Macleod	bcchSABFM079	49.7349	113.3890	Wild	2430-38999
FO	River Valley Park, Fort Macleod (811 Bridge)	bcchSABFM180	49.7339	113.3973	Wild	2430-39000
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH001	49.6939	112.8625	Wild	2490-57738
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH002	49.6939	112.8625	Wild	2490-57739
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH003	49.6939	112.8625	Wild	2490-57740
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH004	49.6939	112.8625	Wild	2490-57741
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH005	49.6939	112.8625	Wild	2490-57742
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH006	49.6939	112.8625	Wild	2490-57743
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH007	49.6939	112.8625	Wild	2490-57744
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH008	49.6939	112.8625	Wild	2490-57745
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH009	49.6939	112.8625	Wild	2490-57746
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH010	49.6939	112.8625	Wild	2490-57747
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH011	49.6939	112.8625	Wild	2490-57748
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH012	49.6939	112.8625	Wild	2490-57749
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH013	49.6939	112.8625	Wild	2490-57750
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH014	49.6939	112.8625	Wild	2490-57751
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH015	49.6939	112.8625	Wild	2490-57752
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH016	49.6939	112.8625	Wild	2490-57753
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH017	49.6939	112.8625	Wild	2490-57754
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH018	49.6939	112.8625	Wild	2490-57755
LE	Helen Schuler Nature Centre, Lethbridge AB	bcchLETH019	49.6939	112.8625	Wild	2490-57757
LE	Helen Schuler Nature Centre	bcchLETH020	49.7024	112.8599	Wild	2500-94993

LE	Helen Schuler Nature Centre	bcchLETH021	49.6957	112.8636	Wild	2430-38973
LE	Helen Schuler Nature Centre	bcchLETH022	49.6957	112.8636	Wild	2430-38974
LE	Helen Schuler Nature Centre	bcchLETH023	49.6957	112.8636	Wild	2430-38975
LE	Helen Schuler Nature Centre	bcchLETH024	49.6957	112.8636	Wild	2430-38976
LE	Helen Schuler Nature Centre	bcchLETH025	49.6957	112.8636	Wild	2430-38977
LE	Cottonwood Park, Lethbridge	bcchLETH026	49.6333	112.8816	Wild	2430-38978
LE	Cottonwood Park, Lethbridge	bcchLETH027	49.6333	112.8816	Wild	2430-38979
LE	Cottonwood Park, Lethbridge	bcchLETH028	49.6333	112.8816	Wild	2430-38980
LE	Cottonwood Park, Lethbridge	bcchLETH029	49.6333	112.8816	Wild	2430-38982
LE	Cottonwood Park, Lethbridge	bcchLETH030	49.6333	112.8816	Wild	2430-38983
LE	Cottonwood Park, Lethbridge	bcchLETH031	49.6333	112.8816	Wild	2430-38984
LE	Helen Schuler Nature Centre	bcchLETH032	49.6957	112.8636	Wild	2430-38972
LE	Helen Schuler Nature Centre	bcchLETH034	49.6957	112.8636	Wild	2710-78495
LE	Helen Schuler Nature Centre	bcchLETH035	49.6957	112.8636	Wild	2710-78496
LE	Helen Schuler Nature Centre	bcchLETH036	49.6957	112.8636	Wild	2710-78497
LE	Helen Schuler Nature Centre	bcchLETH037	49.6957	112.8636	Wild	2710-78498
LE	Helen Schuler Nature Centre	bcchLETH038	49.6957	112.8636	Wild	2710-78499
LE	Helen Schuler Nature Centre	bcchLETH039	49.6957	112.8636	Wild	2710-78500
LE	Helen Schuler Nature Centre	bcchLETH040	49.6957	112.8636	Wild	2710-78501
LE	Helen Schuler Nature Centre	bcchLETH041	49.6957	112.8636	Wild	2710-78502
LE	Helen Schuler Nature Centre	bcchLETH042	49.6957	112.8636	Wild	2710-78503
LE	Helen Schuler Nature Centre	bcchLETH043	49.6957	112.8636	Wild	2710-78504
LE	Helen Schuler Nature Centre	bcchLETH044	49.6957	112.8636	Wild	2710-78505
LE	Helen Schuler Nature Centre	bcchLETH045	49.6957	112.8636	Wild	2710-78506
LE	Helen Schuler Nature Centre	bcchLETH046	49.6957	112.8636	Wild	2710-78507
LE	Helen Schuler Nature Centre	bcchLETH047	49.6957	112.8636	Wild	2710-78508
LE	Helen Schuler Nature Centre	bcchLETH048	49.6957	112.8636	Wild	2710-78509
LE	Helen Schuler Nature Centre	bcchLETH049	49.6957	112.8636	Wild	2710-78510
LE	Cottonwood Park, Lethbridge	bcchLETH33	49.6333	112.8816	Wild	2430-38981
StM	Alex Russell (W of HW508) (St. Mary River)	bcchSABStM094	49.5904	112.8891	Wild	2710-78416
StM	Alex Russell (W of HW508) (St. Mary River)	bcchSABStM095	49.5904	112.8891	Wild	2710-78417
StM	Alex Russell (W of HW508) (St. Mary River)	bcchSABStM096	49.5904	112.8891	Wild	2710-78418

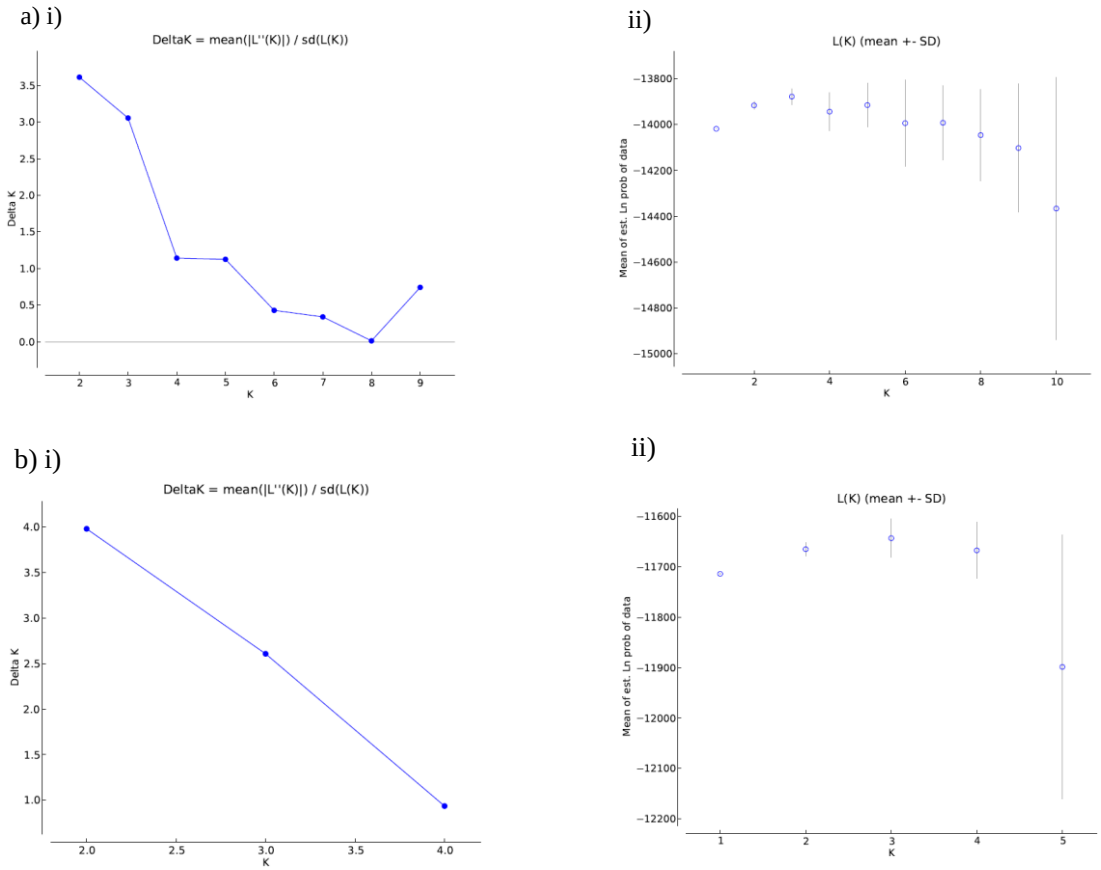
StM	Alex Russell (W of HW508) (St. Mary River)	bcchSABStM097	49.5904	112.8891	Wild	2710-78419
StM	Alex Russell (W of HW508) (St. Mary River)	bcchSABStM098	49.5866	112.8733	Wild	2710-78420
WO	Woolford Provincial Park, St. Mary River	bcchSAB_WPP099	49.1750	113.1876	Wild	2710-78421
WO	Woolford Provincial Park, St. Mary River	bcchSAB_WPP100	49.1750	113.1876	Wild	2710-78422
WO	Woolford Provincial Park, St. Mary River	bcchSAB_WPP101	49.1750	113.1876	Wild	2710-78425
TA	Municipal Park, Taber (Oldman River)	bcchSABTB090	49.8133	112.1701	Wild	2710-78412
TA	Municipal Park, Taber (Oldman River)	bcchSABTB091	49.8133	112.1701	Wild	2710-78413
TA	Municipal Park, Taber (Oldman River)	bcchSABTB092	49.8133	112.1701	Wild	2710-78414
TA	Municipal Park, Taber (Oldman River)	bcchSABTB093	49.8133	112.1701	Wild	2710-78415
FK	Forks Campground, Grassy Lake, Oldman CF	bcchSABFO166	49.9249	111.6908	Wild	2710-78491
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK203	50.0467	110.6724	Wild	2710-78355
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK204	50.0467	110.6724	Wild	2710-78356
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK205	50.0467	110.6724	Wild	2710-78357
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK206	50.0467	110.6724	Wild	2710-78358
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK207	50.0467	110.6724	Wild	2710-78359
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK208	50.0467	110.6724	Wild	2710-78360
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK209	50.0467	110.6724	Wild	2710-78361
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK210	50.0467	110.6724	Wild	2710-78362
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK211	50.0467	110.6724	Wild	2710-78363
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK212	50.0467	110.6724	Wild	2710-78364
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK213	50.0467	110.6724	Wild	2710-78365
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK214	50.0467	110.6724	Wild	2710-78366
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK215	50.0467	110.6724	Wild	2710-78367
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK216	50.0467	110.6724	Wild	2710-78368
SSK	Lions Park, Medicine Hat, AB	bcchSABSSASK217	50.0467	110.6724	Wild	2710-78369
SSK	Strathcona Park, Medicine Hat, AB	bcchSABSSASK218	50.0361	110.6522	Wild	2710-78370
SSK	Strathcona Park, Medicine Hat, AB	bcchSABSSASK219	50.0361	110.6522	Wild	2710-78371
SSK	Strathcona Park, Medicine Hat, AB	bcchSABSSASK220	50.0361	110.6522	Wild	2710-78372
SSK	Strathcona Park, Medicine Hat, AB	bcchSABSSASK221	50.0361	110.6522	Wild	2710-78373
SSK	Strathcona Park, Medicine Hat, AB	bcchSABSSASK222	50.0361	110.6522	Wild	2710-78374

Appendix 3.2. Repeat type (if known), primer sequence, allele size range (bp), number of alleles (***Na***) and $MgCl_2$ concentration for each microsatellite locus used to genotype black-capped chickadee individuals.

Locus	Repeat type	Sequence (5' to 3')	Size range (bp)	*Na*	$MgCl_2$ (mM)	Reference
PAT MP 2-14F		GAACAGATAAAGCCAAATTAC	135-173	20	2	Otter *et al.*, 1998
PAT MP 2-14R		TAGTGAATGCTTGATTTCTTTG				
PAT MP 2-43F		ACAGGTAGTCAGAAATGGAAAG	141-217	28	1.5	Otter *et al.*, 1998
PAT MP 2-43R		GTATCCAGAGTCTTTGCTGATG				
Escu6F		CATAGTGATGCCCTGCTAGG	122-248	27	1.5	Hanotte *et al.*, 1994
Escu6R		GCAAGTGCTCCTTAATATTTGG				
Titgata02F	$(GATA)_{12}$	ATTGCTTGATATTTGAAAGCATA	216-300	20	2	Wang *et al.*, 2005
Titgata02R		TTGTCTTTTGGGTTGCCTGA				
Titgata39F	$(GATA)_{10}$	CATGTATTTTCCAAAAGTAAATAT	214-266	16	2	Wang *et al.*, 2005
Titgata39R		CTGCTATTCTGCAAACTTGTGG				
CcaTgu11F		TGCTTAGGAAATAGGAAGCACA	212-218	4	2	Olano_Marin *et al.*, 2010
CcaTgu11R		CTGCAACTTAAGCARRGTTATGA				
PmanTAGAn71F	$(TAGG)_6(TAGA)_{11}$	TCAGCCTCCAAGGAAAACAG	161-195	12	2.5	Saladin *et al.*, 2003
PmanTAGAn71R		GCATAAGCAACACCATGCAG				
Ase18F	$(GT)_{12}$	ATCCAGTCTTCGCAAAAGCC	196-236	9	2.5	Richardson *et al.*, 2000
Ase18R		TGCCCCAGAGGGAAGAAG				
Cuμ28F	$(CA)_{12}$	GAGGCACAGAAATGTGAATT	180-186	4	2.5	Gibbs *et al.*, 1999
Cuμ28R		TAAGTAGAAGGACTTGATGGCT				
VeCr05F	$(AC)_8$	ACACACTTATGTGCATGGGCT	308-320	2	2.5	Tarvin, 2006
VeCr05R		ATATTTCAGGTATGGGTTTGGTTC				
CtC101-F	$(CATC)_8$	GTCCAGTAGGTAGGTGTGATG	232-392	24	2.5	Stenzler *et al.*, 2004
CtC101-R		TTATTTAGGTGCCAGAGAGATG				
Pij02F	$(GT)_{23}$	CACACCTACCTCATGGATCT	332-488	33	2.5	Saito *et al.*, 2005
Pij02Rnew		CTGCATCAACTCATGTCCTG				

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.

# Groups	Grouped populations	Among Groups	Among populations within groups	Within populations
2	SSK and remaining populations	1.57	1.80	96.63
2	DR and remaining populations	1.11	1.87	97.02
3	SSK, LE and remaining populations	1.02	1.62	97.36
4	DR, LE, SSK and remaining populations	0.79	1.65	97.53
2	DR, LE and remaining populations	0.78	1.50	97.38
2	LE and remaining populations	0.53	1.88	97.60
2	SSK, LE and remaining populations	0.33	1.91	97.76
2	BO and remaining populations	0.21	2.00	97.79



Appendix 3.4. Delta *K* (Δ*K*) and log likelihood (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 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 AIC_c = corrected Akaike's Information Criterion, Δ_i = differences in AIC_c values, w_i = AIC_c weights. Bold values indicate the best models based on AIC.

Model	F_{ST}			D_{EST}		
	AIC_c	Δ_i	w_i	AIC_c	Δ_i	w_i
Distance (through suitable habitat)	-569.9	35.9	0.00	-427.1	8.3	0.25
Elevation	-580.2	25.6	0.00	-427.5	7.9	0.24
Elevation + distance	-578.4	27.4	0.00	-431.5	3.9	0.12
Land cover	-604.6	1.2	0.21	-433.3	2.1	0.06
Land cover + distance	-603.2	2.6	0.11	-434.5	0.9	0.03
Land cover + elevation	**-605.8**	0	0.39	-434.6	0.8	0.02
Land cover + elevation + distance	-604.6	1.2	0.21	**-435.4**	0	0.00
Land cover x elevation	-601.7	4.1	0.05	-429.9	5.5	0.16
Land cover x elevation +distance	-600.7	5.1	0.03	-431.2	4.2	0.13
Distance (through suitable habitat)	-342.4	22.9	0.0	-267.8	22.3	0.00
Elevation	-350.3	15.0	0.0	-268.5	21.6	0.00
Elevation + distance	-348.5	16.8	0.0	-269.4	20.7	0.00
Land cover	-364.6	0.7	0.1	-271.6	18.5	0.00
Land cover + distance	-362.5	2.8	0.0	-271.0	19.1	0.00
Land cover + elevation	**-365.3**	0.0	0.2	-271.6	18.5	0.00
Land cover + elevation + distance	-363.5	1.8	0.1	-270.4	19.7	0.00
Hybrid-	-340.8	24.5	0.0	-262.7	27.4	0.00
Hybrid+	-340.6	24.7	0.0	-263.1	27.0	0.00
Hybrid- + distance	-340.1	25.2	0.0	-277.0	13.1	0.00
Hybrid+ + distance	-340.2	25.1	0.0	-286.4	3.7	0.10
Hybrid- + elevation	-349.3	16.0	0.0	-266.8	23.3	0.00
Hybrid+ + elevation	-349.0	16.3	0.0	-267.3	22.8	0.00
Hybrid- + elevation + distance	-346.9	18.4	0.0	-275.8	14.3	0.00
Hybrid+ + elevation + distance	-346.6	18.7	0.0	-284.3	5.8	0.04
Hybrid- + land cover	-362.4	2.9	0.0	-272.8	17.3	0.00
Hybrid+ + land cover	-362.4	2.9	0.0	-273.7	16.4	0.00
Hybrid- + land cover + distance	-360.1	5.2	0.0	-281.4	8.7	0.00
Hybrid+ + Land cover + distance	-360.1	5.2	0.0	**-290.1**	0.0	0.64
Hybrid- + elevation + land cover	-362.9	2.4	0.1	-272.0	18.1	0.00
Hybrid+ + elevation + land cover	-362.9	2.4	0.1	-273.0	17.1	0.00
Hybrid- + elevation + land cover + distance	-361.3	4.0	0.0	-278.9	11.2	0.00
Hybrid+ + elevation + land cover + distance	-361.3	4.0	0.0	-287.6	2.5	0.18
Hybrid- x elevation	-344.2	21.1	0.0	-263.5	26.6	0.00
Hybrid+ x elevation	-340.2	25.1	0.0	-263.9	26.2	0.00
Hybrid- x elevation + distance	-341.9	23.4	0.0	-265.9	24.2	0.00
Hybrid+ x elevation + distance	-343.8	21.5	0.0	-279.2	10.9	0.00
Hybrid- x elevation + land cover	-362.5	2.8	0.0	-269.3	20.8	0.00
Hybrid+ x elevation + land cover	-364.8	0.5	0.1	-273.2	16.9	0.00
Hybrid- x elevation + land cover + distance	-361.1	4.2	0.0	-269.5	20.6	0.00
Hybrid+ x elevation + land cover + distance	-362.7	2.6	0.1	-281.2	8.9	0.01
Hybrid- x land cover	-350.9	14.4	0.0	-268.9	21.2	0.00
Hybrid+ x land cover	-339.8	25.5	0.0	-262.7	27.4	0.00
Hybrid- x land cover + distance	-352.1	13.2	0.0	-266.8	23.3	0.00

Hybrid+ x land cover + distance	-342	23.3	0.0	-277.6	12.5	0.00
Hybrid- x land cover + elevation	-353.7	11.6	0.0	-269.6	20.5	0.00
Hybrid+ x land cover + elevation	-348	17.3	0.0	-266.8	23.3	0.00
Hybrid- x land cover + elevation + distance	-355	10.3	0.0	-267.5	22.6	0.00
Hybrid+ x land cover + elevation + distance	-346.3	19.0	0.0	-276.1	14.0	0.00
Hybrid- x elevation x land cover	-359.1	6.2	0.0	-280.5	9.6	0.01
Hybrid+ x elevation x land cover	-340.8	24.5	0.0	-266.5	23.6	0.00
Hybrid- x elevation x land cover + distance	-357.8	7.5	0.0	-282	8.1	0.01
Hybrid+ x elevation x land cover + distance	-342	23.3	0.0	-273.8	16.3	0.00