Landscape fitness: integrating density, familial networks and population dynamics for the conservation of boreal woodland caribou

Landscape fitness: integrating density, familial networks and population dynamics for the conservation of boreal woodland caribou

Dissertation Thesis

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[1] `https://people.mpi-sws.org/~turon/turon-thesis.pdf`

[2] `https://bitbucket.org/amiede/classicthesis/`

[3] `https://github.com/Tufte-LaTeX/tufte-latex`

I never ask 'why' to myself. I ask 'how'.
If I feel like I can do it, that for me is
enough motivation.
—Børge Ousland

Abstract

Variation in habitat quality and disturbance levels can strongly influence a species' distribution, leading to spatial variation in population density and influencing population dynamics. It is therefore critical to understand how density can lead to variability in demographic responses for effective conservation and recovery of species. My dissertation illustrates how density and spatial familial networks can be integrated together to gain a better understanding of the influence of density on population dynamics of boreal caribou. First, I created an analytical framework to assess results from empirical studies to inform spatially-explicit capture-recapture sampling design, using both simulated and empirical data from noninvasive genetic sampling of several boreal caribou populations in Alberta, Canada, which varied in range size and estimated population density. Analysis of the empirical data indicated that reduced sampling intensity had a greater impact on density estimates in smaller ranges, and the best sampling designs did not differ with estimated population density but differed between large and small population ranges. Secondly, I used parent-offspring relationships to construct familial networks of boreal caribou in Saskatchewan, Canada to inform recovery efforts. Using network measures, I assessed the contribution of individual caribou to the population with several centrality measures and then determined which measures were best suited to inform on the population demographic structure. I found substantial differences in the centrality of individuals in different local areas, highlighting the importance of analyzing familial networks at different spatial scales. The network revealed that boreal caribou in Saskatchewan form a complex, interconnected familial network. These results identified individuals presenting different fitness levels, short- and long-distance dispersing ability across the range, and can be used in support of population monitoring and recovery efforts. Finally, I used a spatial capture-recapture analytical framework with covariates to estimate spatial density of boreal woodland caribou across the Saskatchewan Boreal Plains, and then reconstructed parent-offspring relationships to create a familial network of caribou and determined whether spatial density influenced sex-specific network centrality, dispersal distance, individual reproductive success, and the pregnancy status of females. I show that caribou density greatly varied across the landscape and was primarily affected by landscape composition and fragmentation, and density had sex-specific influences on dispersal distance, reproductive success, and network centrality. The high density areas reflected good-quality caribou habitat, and the decreased dispersal rates and female reproductive output suggest that these remnant patches of habitat may be influencing demographic responses of caribou.

Keywords

Anthropogenic disturbance; boreal caribou; density; familial networks; graph theory; landscape change; pedigree; population parameters; *Rangifer tarandus caribou*; spatial analysis; spatial capture-recapture

Preface

My dissertation has been written in manuscript format. Chapter 1 and Chapter 2 have both been published in Ecology and Evolution, and Chapter 3 has been submitted to the Journal of Animal Ecology. My research has been done in collaboration with others, and therefore the plural "we" and "our" have been used in my dissertation. The full citation of each publication has been included on the title page of each respective chapter.

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Part I

INTRODUCTION

1

Introduction

Although the recovery strategy and definition of critical habitat for boreal caribou is based on population-level assessments (Environment Canada 2012), spatially-explicit information is essential to inform action plans. Under Canada's *Species at Risk Act*, critical habitat is defined as the portion of a species' habitat that is "necessary for the survival or recovery of the species" (*Species at Risk Act* [SARA], S.C. 2002, c 29). One of the primary criteria used in identifying critical habitat is species persistence, usually evaluated through comparison to an acceptable threshold extinction risk or species abundance (Camaclang et al. 2014; Rosenfeld and Hatfield 2006). Often when there is no spatially-explicit assessments of population viability over time, minimum viable population size estimates are used to determine threshold values (Shaffer 1981; Traill et al. 2007; Camaclang et al. 2014). Robust and accurate abundance estimates are critical for the monitoring and recovery of species, yet most abundance estimates are aspatial and the spatial nature of animal habitat use is generally neglected. Therefore, spatially-explicit data is critical for recovery of endangered species.

1.1 DENSITY

When the distribution of a species is dependent on habitat type and availability, or landscape disturbance impacts a species, obtaining accurate demographic data is crucial for successful conservation of wild species. Abundance is the most commonly used quantitative population metric in endangered species recovery plans and is the key population parameter underlying extinction risk (Shaffer 1981; Lande 1993; Campbell et al. 2002), but population size has no spatial component, and the spatial area to which this abundance estimate applies to is unknown (Efford et al. 2009). Population density is a fundamental demographic parameter and is integral to population regulation (Clutton-Brock et al. 1985), density dependence (Gaillard et al. 2000), and predator response to prey (Nilsson 2001). Density can also influence demographic population parameters, such as individual reproductive fitness (e.g. Webber and Vander Wal 2018; Bonenfant et al. 2009; Clutton-Brock et al. 1997; Coulson et al. 2000; Gaillard et al. 2000; McLoughlin et al. 2006), dispersal (Matthysen 2005; Ronce 2007; Travis et al. 1999), and kinship (De Bona et al. 2019; Hamilton and May 1977), making population density a critical component of monitoring and recovery of threatened and endangered species. However, obtaining accurate density estimates for wild populations can be difficult, particularly for species that occur at low densities, are cryptic, or exhibit elusive behaviour that makes capture difficult (Kéry et al. 2011; Pollock et al. 2006). Often, these issues are further exacerbated by inaccessible habitat (Kéry et al. 2011; McCain and Childs 2008). Noninvasive genetic sampling can alleviate a lot of these challenges, by constructing individual capture histories from DNA collected via feces, hair, feathers, or other noninvasively collected samples (Waits and Paetkau 2005; Lampa et al. 2013). Noninvasive techniques avoid physical capture of individuals, reducing disruption and stress to the animals, and often results in a higher capture success rate than traditional capture-mark-recapture (CMR) methods (Prugh et al. 2005; Waits and Paetkau 2005; Lampa et al. 2013).

CMR models have been a primary method for estimating demographic population parameters and abundance of populations for decades (Williams et al. 2002), but CMR cannot estimate density directly. Density is a spatial population parameter, and crude density estimates have been calculated by dividing the abundance estimate by the area assumed to be estimated by the population ($Density = Abundance/Area$); this may be an adequate method when the population of interest occupies a defined area such as an island, and every member of the population has an equal risk of capture, but these assumptions are almost always violated (Efford et al. 2009). Most study populations are likely to be ill-defined subsets of the larger population of interest that extends beyond the sampling area, and crude density estimates can be inaccurate, since the effective sampling area is not truly known, and study sites are generally chosen based on a priori knowledge of high density or occupancy use, leading to study sites having consistently higher density estimates than non-study areas (Efford et al. 2009; Smallwood and Schonewald 1996; Smallwood 1997; Gaston et al. 1999). Abundance estimates from CMR models are also limited in that they cannot explicitly model for heterogeneity in the landscape; species will selectively use habitat types differently, and landscape disturbance can also affect habitat use and population density (Lamb et al. 2018; Morrell et al. 2021; Srivathsa et al. 2021).

Spatial capture-recapture (SCR) models were first introduced in the early 2000s as a novel approach for inferring animal density based on CMR data (Borchers and Efford 2008; Royle and Young 2008). SCR was an important advancement in capture-recapture methods as it acknowledged that both ecological processes and observation processes are inherently spatial (Royle et al. 2013). SCR models are becoming a new standard in abundance estimation, as they are robust to small sample sizes and can accommodate low capture probabilities (Borchers and Efford 2008; Efford et al. 2009; Ivan et al. 2013; Royle et al. 2013). By including the spatial locations of sampled individuals directly into SCR analyses, these models resolve issues around the effective trapping area and geographic closure of populations, common issues in CMR studies (Efford and Fewster 2013; Royle et al. 2013). Covariates can be incorporated directly into SCR models to examine the combined effects of multiple landscape variables on population density (Royle et al. 2013), and these can be used to identify potential limiting factors affecting population density.

1.2 DISTURBANCE

Landscape disturbance can be a major driver of population density patterns. Disturbances alter the state of an ecosystem, and are key drivers of spatial and temporal heterogeneity (Turner 2010; Bond and Keeley 2005). Anthropogenic disturbances lead to habitat loss, fragmentation and alteration of many ecosystems, and anthropogenic disturbances have surpassed natural disturbances in the boreal forest as the primary source of disturbance (Cyr et al. 2009; Benítez-López et al. 2010). Roads and other linear features are known to have negative impacts on wildlife and ecosystems, and can lead to habitat loss, barrier effects, isolation of populations, road mortality, and increased human access (Benítez-López et al. 2010; Forman and Alexander 1998; Trombulak and Frissell 2000). Construction of roads and linear features such as seismic lines leads to the creation of open spaces in previously closed forests, which can fragment populations or lead to avoidance of habitat edges (Vos and Chardon 1998; Ortega and Capen 1999; Bolger et al. 1997). The conversion of forests through logging and fire can affect species through the alteration of forest composition (Bond and Keeley 2005), resulting in a greater abundance of competing species (Geary et al. 2020) and increased predation (Singer et al. 1997; Lendrum et al. 2018). Disturbance can also lead to changes in space use and behaviour of species (Schaefer and Pruitt 1991; Spitz et al. 2018; Loosen et al. 2021), such as avoiding areas of human activity and infrastructure (Schaefer and Mahoney 2007; Loosen et al. 2021; Rogala et al. 2011), and avoiding certain habitats (e.g. Spitz et al. 2018; May et al. 2006). Increased fragmentation from anthropogenic disturbances can lead to reduced connectivity between populations, which can affect dispersal success (Clergeau and Burel 1997), migration and metapopulation persistence (Hanski and Gilpin 1991), and can increase the loss of genetic diversity through genetic drift (Hedrick 2005; Epps et al. 2005; Allendorf and Luikart 2007). Reduced genetic diversity can lead to increased likelihood of population extinction rates through inbreeding depression (Couvet 2002; Fredrickson et al. 2007; Charlesworth and Charlesworth 1987), loss of adaptive evolutionary potential (Fraser and Bernatchez 2001), and the accumulation of deleterious mutations (Couvet 2002; Keller 2002).

For species that depend on mature and old-growth forests, the effects of habitat alteration can be severe. The abundance of many species, including red squirrels (*Tamiasciurus hudsonicus*), flying squirrels (*Glaucomys sabrinus*), hares (*Lepus* spp.), bats (*Chiroptera* spp.), mustelids (Mustelidae), canids (Canidae), and boreal caribou (*Rangifer tarandus caribou*) generally decrease following fire or forest harvest (Fisher and Wilkinson 2005). Old-growth forests are defined by the presence of old trees and associated plants, animals and ecosystem processes; they are forests that are no longer dominated by species that dominated the post-fire canopy (Bergeron and Fenton 2012; Wirth et al. 2009; Kneeshaw and Gauthier 2003). After a forest fire, old-growth forests return to young seral stage forests with regenerating trees, shrubs and grasses, which are good-quality habitat for many ungulate species, such as moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), black-tailed deer (*O. hemionus*), and elk (*Cervus elaphus*). Caribou feed primarily on lichen, which is often destroyed in burns, resulting in a lack of lichen for winter forage in young seral forests (Schaefer and Pruitt 1991; Morneau and Payette 1989). For caribou, forestry has a similar effect on forest stand structure as fire; caribou tend to use clear cuts less than other boreal habitat types or stand ages, as lichen is no longer found in adequate amounts (Mahoney and Virgl 2003; Smith et al. 2000; Rettie and Messier 2000). Caribou are positively associated with old-growth forests, as lichen mat thickness steadily increases as stands progress from new burns to old-growth forests (Arseneault et al. 1997). These effects are long-lasting; it can take forest stands a century or more to reach the old-growth stage after a fire or harvest (Fisher and Wilkinson 2005). Integrating spatial habitat and disturbance covariates with density estimation methods can provide a method to investigate potential limiting factors to boreal caribou population density.

1.3 INDIVIDUAL-LEVEL DEMOGRAPHIC PARAMETERS

Habitat fragmentation and loss of habitat result in the isolation of populations, and in the long-term reduces genetic variation, increases extinction probability of populations due to reduced fitness and inbreeding, reduces reproductive success, and increases susceptibility to disease (Singh et al. 2017; Wright et al. 2007; Amos and Balmford 2001; Spielman et al. 2004). The loss of genetic variability due to reduced movements of individuals as a result of ecological and biological factors inhibiting individual movement has been documented in many highly vagile and long-ranging species, including pumas (*Puma concolor*, Ernest et al. 2003; Johnson et al. 2010), jaguars (*Panthera onca*, Haag et al. 2010), grizzly bears (*Ursus arctos*, Miller and Waits 2003), Eurasian lynx (*Lynx lynx*, Spong and Hellborg 2002), and several wolf species (*Canis* spp., Fredrickson et al. 2007; Gottelli et al. 2012; Hedrick et al. 2014). As most species are not driven to extinction before being adversely affected by genetic factors such as reduced reproductive fitness, lowered evolutionary potential, and elevated extinction risk (Spielman et al. 2004), knowledge of the fine-scale spatial structuring, genetic variation of a population, as well as individual fitness levels are needed for conserving endangered species.

Evolutionary and ecological changes of populations are generated from the variation in individual performance, or the fitness of an individual (Allendorf and Luikart 2007; Coulson et al. 2005). The contribution of offspring produced by an individual contributes to both the subsequent genetic composition of a population, as well as the numerical contribution to the growth of a population (Coulson et al. 2005; Shaw et al. 2008). Theoretically, fitness has been considered a long-term measure of relative performance of an individual in a population, and has typically been estimated by measuring the lifetime reproductive success of individuals (Coulson et al. 2005; Clutton-Brock et al. 1988). Individual fitness is comprised of the probability of surviving to reproductive age, reproductive life span, average fecundity per year, and the number of an individual's offspring that survive to reproductive maturity (Clutton-Brock et al. 1988). Individuals often display considerable heterogeneity in fitness levels within a population (Hamel et al. 2009; McFarlane et al. 2018). Genetic parentage analysis allows for familial relationships between individuals to be identified without direct behavioural observations (Moore et al. 2015; Jones and Wang 2010; Stadele and Vigilant 2016). Reconstructing familial pedigrees can inform on many demographic parameters, such as individual fitness, sexual selection, social structure, dispersal, and abundance (Creel et al. 2003; Lucena-Perez et al. 2018; Gobush et al. 2009; McFarlane et al. 2018; DeWoody 2005; Norman et al. 2019). Parentage information from direct field observation is often limited to females, but noninvasive genetic studies using molecular markers (such as microsatellites) are a powerful tool for inferring paternity in elusive or cryptic species (Bellemain et al. 2005; Hettinga et al. 2012; Eggert et al. 2003).

Graph-theoretic network approaches have been used for population genetic analyses, including assessing population genetic structure (Dyer and Nason 2004), investigating sex-specific dispersal and network structure in landscape genetics (Bertrand et al. 2017), and for analyzing spatial genetic variation across a species' range (Fortuna et al. 2009). Network analyses are flexible and powerful methods for investigating the complex networks of interconnections between individuals within and between populations (Wasserman and Faust 1994). Networks are represented as nodes [individuals, populations, habitat patches, etc.) and edges (representing a level of connection between the nodes, Urban2001). Network-based measures are commonly used to quantify the direct and indirect connections between nodes, with numerous measures capturing distinct aspects of the network. Used together, graph theory and pedigree reconstruction could highlight the interconnectedness of individuals (Escoda et al. 2019; Morrison 2016), differences in reproductive success (McFarlane et al. 2018), and ultimately inform on population demographic structure.

Pedigree data collected from noninvasive genetic surveys is inherently spatial, as the location of where the individual was sampled can be used as a basis for spatial network analyses. By incorporating space into a familial network, spatial demographic parameters can be derived, such as dispersal distance (e.g. Melero et al. 2017; Norman et al. 2019; Fountain et al. 2017), providing detailed information on individual-based dispersal of wild populations, where dispersal data can be difficult to obtain. By creating a familial pedigree network, and measuring the spatial distance between parent-offspring dyads, a natal dispersal distance can be inferred (e.g. Norman et al. 2019; Melero et al. 2017; Norman and Spong 2015; Cope et al. 2015). Natal dispersal is the movement of individuals away from their natal source (Nathan 2005; Greenwood 1980), and has also been defined as breeding dispersal (Paradis et al. 1998), juvenile dispersal (Cotto et al. 2013), and genetically-effective dispersal (Broquet and Petit 2009). While detailed information on individual dispersal events can be obtained by tracking individuals, for boreal caribou, collaring has been limited to females (e.g. Johnson et al. 2015; Beauchesne et al. 2014). In most polygynous mammal species, males are typically the dispersing sex, while females are philopatric

(Greenwood 1980; Wolff 1997). Boreal caribou exhibit a polygynous mating system (Thomas et al. 1989), and with no studies addressing dispersal of boreal caribou, dispersal heterogeneity of individuals is unknown. Natal dispersal heterogeneity has been linked to density and group characteristics of several mammalian species, including feral horses (*Equus ferus caballus*, Marjamäki et al. 2013), African lions (*Panthera leo*, VanderWaal et al. 2009), black bears (*Ursus americanus*, Moore et al. 2014), and degus (*Octodon degus*, Quirici et al. 2010). Spatial network analysis is a powerful method for characterizing dispersal patterns in wild species, providing information of movement and breeding events at the individual level; combining these analyses with spatial density can illustrate the influence density may have on individual dispersal.

1.4 MODEL SPECIES: BOREAL WOODLAND CARIBOU

There are four existing subspecies of caribou in Canada: the Peary caribou (*Rangifer tarandus pearyi*), barren-ground caribou (*R. t. groenlandicus*), Grant's caribou (*R. t. granti*), and woodland caribou (*R. t. caribou*; Banfield 1974). Caribou exhibit considerable variability in adaptive behaviours, life-history strategies, and ecological conditions across subspecies; therefore, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) classified several geographically distinct populations of caribou into Designatable Units (DUs; COSEWIC 2011). In this dissertation, I will discuss one of these units – boreal woodland caribou.

Boreal woodland caribou (hereafter referred to as boreal caribou) are part of the Boreal Designatable Unit (DU), and are wide-ranging, found throughout the boreal forests of Canada. Populations have steadily decreased throughout most of their range. Habitat loss, habitat patch size reduction, fragmentation from land conversion and resource development, and increased predation from these landscape changes are the main causes of boreal caribou declines in Canada (Thomas and Gray 2002; Environment Canada 2011). Of the 57 identified boreal caribou ranges in Canada, 58% are not self-sustaining and current habitat conditions are very unlikely to support a self-sustaining population (Environment Canada 2011; Environment Canada 2012). Boreal caribou are listed as threatened under the federal *Species at Risk Act* due to reductions in population size of more than 30% during the past three generations (Environment Canada 2012). Boreal caribou are also listed provincially/territorially in some jurisdictions, and are listed as threatened in British Columbia, Alberta, Manitoba, Ontario, and Newfoundland and Labrador (Environment Canada 2012).

Boreal caribou require large areas of undisturbed, continuous habitat, preferring mature to old-growth coniferous forests abundant with lichens, or peat lands and muskegs along with upland and hilly areas (Environment Canada 2012; Rettie and Messier 2000; Courtois et al. 2003; Stuart-Smith et al. 1997). Both natural and anthropogenic disturbances affect the spatial distribution and habitat selection of boreal caribou. Anthropogenic disturbances have had dramatic effects on the abundance and distribution of boreal caribou across Canada (Environment Canada 2012; Courtois et al. 2007; Smith et al. 2000). Although wildfire is the primary source of natural disturbances in the boreal forest (Dalerum et al. 2007; Skatter et al. 2017), anthropogenic disturbances are increasing as development in Canada's boreal forest increases, and anthropogenic sources of disturbance are the primary disturbance source in many of Canada's boreal caribou ranges (Environment Canada 2011).

1.5 THESIS OBJECTIVES

The three research chapters in this dissertation are written to stand alone as publications and each has its own specific audience and purpose. The general objective of my dissertation is to further our understanding of how the landscape affects demographic parameters of boreal caribou. The second and third chapters of my dissertation address methodological issues. In my second chapter, I identify how sampling design affects the bias and precision of spatially-explicit capture-recapture surveys, and how assessing this can aid in minimizing the effort and cost of monitoring programs, while maximizing effectiveness. In the third chapter of my dissertation, I address how population demographic structure can be inferred from individual-based familial pedigree networks, and how demographic structure varies across the landscape. Finally, in my fourth chapter, I examine a range of spatially explicit demographic parameters in a wild population of boreal caribou by determining the spatial density across the Boreal Plains of Saskatchewan, and assessing how familial networks, dispersal distances, and reproductive success were affected by density.

1.6 STUDY AREA

Extensive fecal pellet collection has occurred across the boreal caribou range in Western Canada. I focused on several boreal caribou populations within Alberta and Saskatchewan in this dissertation (Figure 1.1). In total, 9,180 fecal pellet samples were used in this dissertation, across two provinces and an area of 344,261 km^2 (15% of the boreal caribou range in Canada).

In Chapter 2, I studied seven boreal caribou populations in Alberta: Cold Lake, East Side Athabasca River [ESAR], Little Smoky, Nipisi, Red Earth, Slave Lake, and West Side Athabasca River [WSAR] (Figure 1.1). In Chapter 3, I studied boreal caribou in the Saskatchewan Boreal Plains and Saskatchewan Boreal Shield, and Chapter 4 I studied the Saskatchewan Boreal Plains (Figure 1.1).

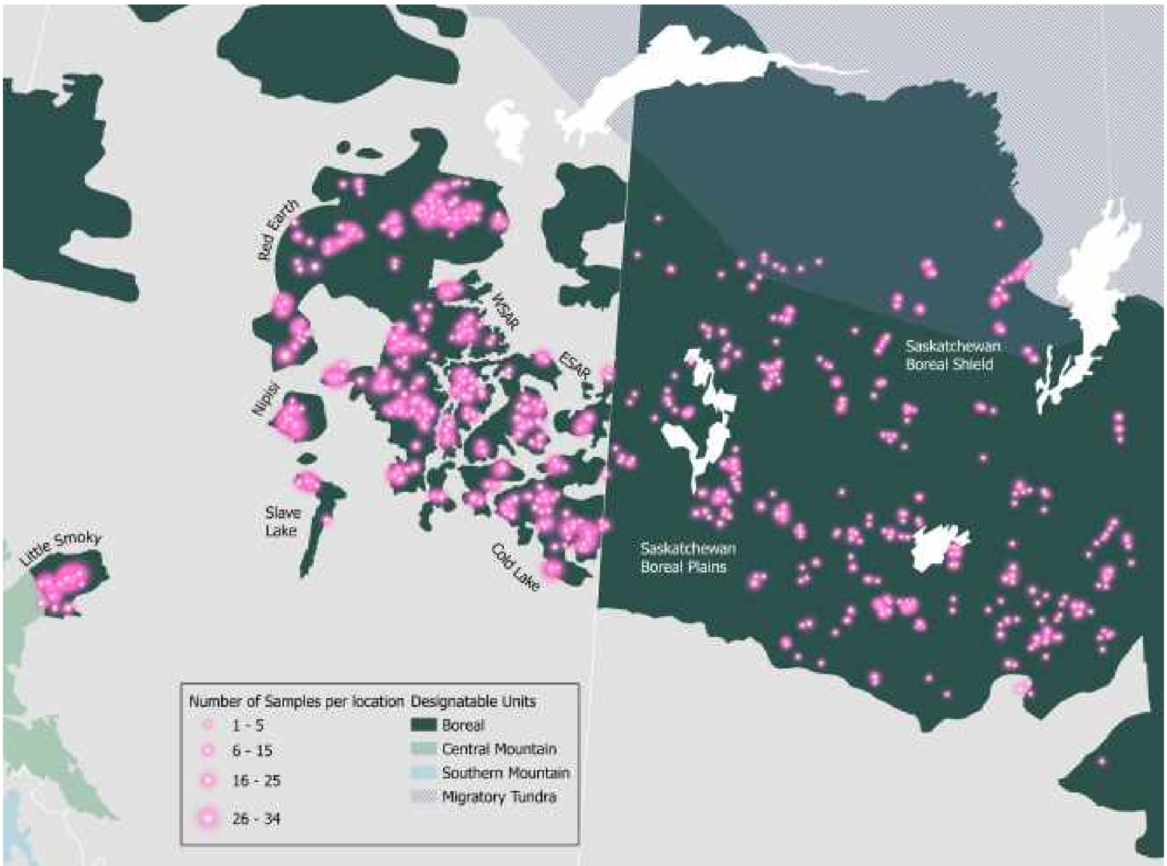

FIGURE 1.1: Boreal caribou fecal pellet samples collected and used in this dissertation.

1.7 TERMINOLOGY

Population size is one of the most fundamental demographic parameters (Lebreton et al. 1992). However, accurately estimating population size is challenging, as it is estimated as the number of individuals present in an arbitrarily designated geographic range, such as by management boundaries. In this dissertation, the use of the term "population" reflects provincial management boundaries of boreal caribou populations. In Chapter 2, I used fecal pellet data collected by the Government of Alberta. This fecal pellet collection occurred by management population, with one population completely surveyed within its population boundaries each year. As the focus of my second chapter is to estimate density using spatial capture-recapture methods and one population was surveyed per year, I needed to retain the population-specific boundaries for density estimation. In Chapters 3 and 4, I also use the term "population" to reflect the two Saskatchewan provincial management boundaries: Saskatchewan Boreal Plains and Saskatchewan Boreal Shield. The analysis for Chapters 3 and 4 are more focused on individual-level demographic analyses, and are not focused on population-specific estimates, but I continue to use the term "population" to reflect the current management boundaries of boreal caribou. My focus on estimating density reflects that population size estimates have limitations, and density inherently includes the population size in relation to space.

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Part II

ANALYSES

2

An assessment of sampling designs using SCR analyses to estimate abundance of boreal caribou

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Contributions: DH, MM, TH and SS conceived and designed the study. TH and SS lead the surveys, sample collection and shipment. SM led and implemented the analysis with contributions from MM and RS. PW coordinated DNA extraction and analysis. SM wrote the first draft of the manuscript with help from MM. All authors contributed to subsequent drafts and gave final approval for publication.

2.1 ABSTRACT

Accurately estimating abundance is a critical component of monitoring and recovery of rare and elusive species. Spatial capture–recapture (SCR) models are an increasingly popular method for robust estimation of ecological parameters. We provide an analytical framework to assess results from empirical studies to inform SCR sampling design, using both simulated and empirical data from noninvasive genetic sampling of seven boreal caribou populations (*Rangifer tarandus caribou*), which varied in range size and estimated population density. We use simulated population data with varying levels of clustered distributions to quantify the impact of nonindependence of detections on density estimates, and empirical datasets to explore the influence of varied sampling intensity on the relative bias and precision of density estimates. Simulations revealed that clustered distributions of detections did not significantly impact relative bias or precision of density estimates. The genotyping success rate of our empirical dataset ($n = 7{,}210$ samples) was 95.1%, and 1,755 unique individuals were identified. Analysis of the empirical data indicated that reduced sampling intensity had a greater impact on density estimates in smaller ranges. The number of captures and spatial recaptures was strongly correlated with precision, but not absolute relative bias. The best sampling designs did not differ with estimated population density but differed between large and small ranges. We provide an efficient framework implemented in R to estimate the detection parameters required when designing SCR studies. The framework can be used when designing a monitoring program to minimize effort and cost while maximizing effectiveness, which is critical for informing wildlife management and conservation.

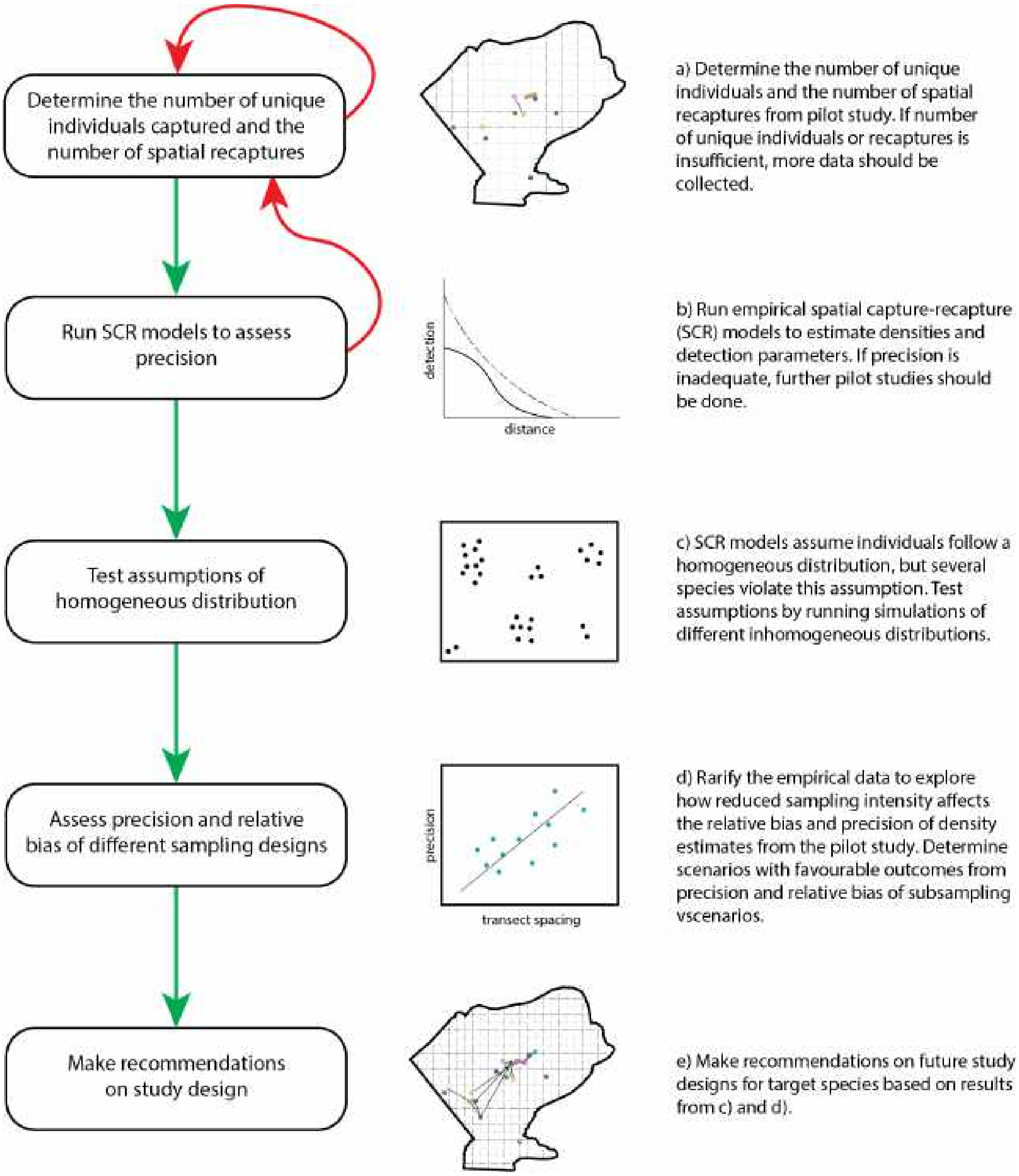
2.2 INTRODUCTION

Robust abundance estimates are fundamental parameters for managing wildlife populations, and central to understanding extinction risk (Campbell et al. 2002; Lande 1993; Shaffer 1981). Monitoring and understanding variation in abundance is critical for recovery efforts of threatened and endangered populations; however, producing accurate population estimates remains a challenge for many species. This is particularly true for species that occur at low density or in low abundance, that are cryptic, or that exhibit elusive behaviours which make capture difficult (Pollock et al. 2006; Kéry et al. 2011). Nonspatial capture–recapture (CR) analyses have been the standard method used to estimate abundance of many vertebrate species; however, spatially explicit capture–recapture (SCR) models are becoming the new standard because they are robust to small sample sizes, and can accommodate low capture probabilities (Borchers and Efford 2008; Efford et al. 2009; Royle et al. 2013; Ivan et al. 2013). By including spatial information of captured individuals directly into the analyses, SCR models resolve issues surrounding the effective trapping area and are robust to assumptions about geographic closure that are common issues in nonspatial CR studies (Royle et al. 2013; Efford and Fewster 2013). Recapturing individuals at different locations also provides information on individual activity centers, which are used to estimate animal density within the study area (Borchers and Efford 2008; Royle et al. 2013).

SCR models directly depend on adequate numbers of unique individuals and recaptures at multiple spatial locations (Sun et al. 2014; Efford and Boulanger 2019). Simulations are recommended to enable the assessment of sampling design on SCR parameter estimates, to inform optimal sampling design (Royle et al. 2013). Such studies have primarily focused on large carnivores, such as black bears (*Ursus americanus*; Clark 2019; Sollmann et al. 2012; Sun et al. 2014; Wilton et al. 2014), and a few additional taxa (Kristensen and Kovach 2018; Tobler and Powell 2013), while limited work has been done on organisms occurring at low densities over large areas and with more limited home ranges. Noninvasive genetic sampling approaches can be used to alleviate the challenges associated with surveying rare and elusive species, by constructing capture histories from DNA collected from feces, hair, or other noninvasively collected samples (Kristensen and Kovach 2018; Lampa et al. 2013; Waits and Paetkau 2005). Noninvasive methods often result in higher capture rates and lower expense than traditional capture–recapture methods (Lampa et al. 2013; Prugh et al. 2005; Waits and Paetkau 2005), and SCR is increasingly being used in combination with noninvasive methods (Kristensen and Kovach 2018; Lamb et al. 2018; Royle et al. 2013). Knowledge of the target species' home range size helps inform the spatial sampling design, providing reference values for the baseline detection probability (Sollmann et al. 2012; Sun et al. 2014). Efford and Boulanger 2019 presented formulae to determine the precision of new study designs by computing the expected number of detected individuals and expected number of recaptures that strongly correlate with precision. However, these formulae require reference values for density and detection parameters (Efford 2019b), which may not be available for less studied species.

Here, we developed a framework to assess results from empirical studies to inform sampling designs (Figure 2.1). The framework consists of (1) determining the number of unique individuals captured and spatially recaptured from empirical data; (2) fitting SCR models under the assumption of homogeneous distribution to estimate the detection parameters $g0$ (detection probability) and σ (spatial extent of an individual's use of the landscape) to assess the precision of the density estimates; (3) running simulations to assess the influence of the species' behaviour on density estimates and relative bias; (4) using empirical data to assess different sampling designs and assess precision and relative bias of the estimates; and (5) making recommendations on study design based on the resulting precision and relative bias of the estimates. The framework is implemented in R [@Team2018], using maximum likelihood methods.

To collect empirical data, we completed aerial surveys across the ranges of seven boreal caribou populations in Alberta, Canada. These ranges varied in size, exhibited differences in estimated caribou population density, and contained different levels of natural and anthropogenic disturbances (Figure 2.2; see Appendix 2.1 for details). For each caribou population, we used an aerial transect survey design to conduct noninvasive genetic sampling, through the collection of caribou fecal pellets. While we studied boreal



a) Determine the number of unique individuals and the number of spatial recaptures from pilot study. If number of unique individuals or recaptures is insufficient, more data should be collected.

b) Run empirical spatial capture-recapture (SCR) models to estimate densities and detection parameters. If precision is inadequate, further pilot studies should be done.

c) SCR models assume individuals follow a homogeneous distribution, but several species violate this assumption. Test assumptions by running simulations of different inhomogeneous distributions.

d) Rarify the empirical data to explore how reduced sampling intensity affects the relative bias and precision of density estimates from the pilot study. Determine scenarios with favourable outcomes from precision and relative bias of subsampling vscenarios.

e) Make recommendations on future study designs for target species based on results from c) and d).

FIGURE 2.1: Framework for assessing results from empirical SCR studies and informing sampling designs

caribou, our approach for assessing study design is applicable to other species and systems.

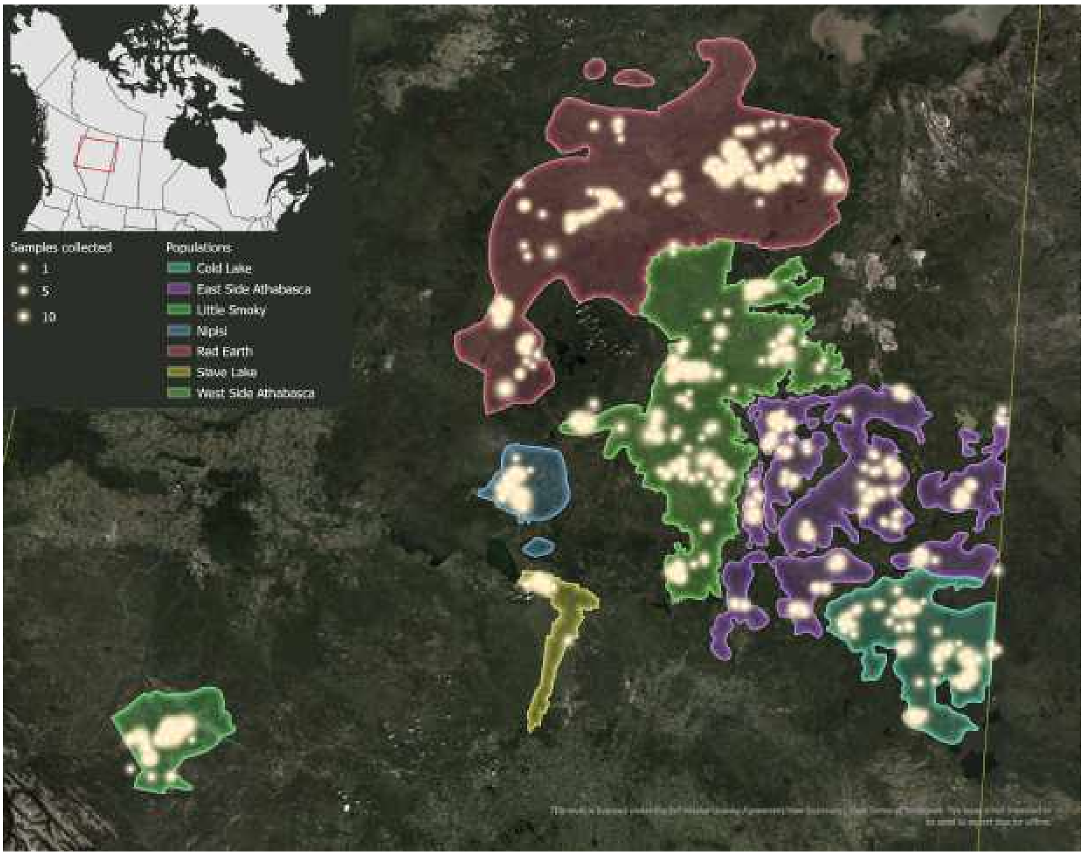


FIGURE 2.2: Seven boreal caribou population ranges in Alberta sampled for fecal DNA.

2.3 MATERIALS AND METHODS

2.3.1 *Fecal pellet collection and genetic analysis*

For each population, we flew 3 surveys to collect fecal pellets during winter (December to March), with sampling occasions spaced approximately one month apart. Following the aerial survey protocol outlined in Hettinga et al. 2012, aerial transects were systematically flown at 3-km intervals across each entire caribou population range using rotary- or fixed-wing aircraft, or a combination of both aircraft, to locate caribou feeding locations, for a total of 69,070 km flown across the seven ranges (Table 2.1). Once located, personnel landed at each feeding site and collected fecal samples; this included collecting samples from backtracking on caribou trails. At each feeding site, approximately 1.4 times more samples than the number of boreal caribou thought to have been present were collected to allow for a balance between capturing most individuals at a site and not recapturing the same individuals too many times. All pellet samples were kept frozen at −20°C until DNA extraction was performed. In the laboratory, fecal samples were thawed and the mucosal coat surrounding the pellets was removed for DNA analysis. The extraction protocol used to amplify the DNA is outlined in Ball et al. 2007. Following quantification of target caribou DNA, samples were diluted down to a working stock concentration of 2.5ng/ul. We amplified the DNA at 9 variable fluorescently labeled microsatellite loci (FCB193, RT7, RT1, NVHRT16, BM888, RT5, RT24, RT6, OHEQ; Bishop et al. 1994; Cronin et al. 2005; Wilson et al. 1997) to generate individual-specific genetic profiles, along with caribou-specific Zfx/Zfy primers for sex identification. The amplification protocol is outlined in Ball et al. 2007. Following amplification, each sample was genotyped on the ABI 3,730 DNA Analyzer (Applied Biosystems). Microsatellite alleles were scored with the program GeneMarker v1.91® (SoftGenetics, State College, PA) and followed a protocol documented in Flasko et al. 2017 and McFarlane et al. 2018. Unique individuals were identified using the program ALLELEMATCH (Galpern et al. 2012). We retained samples that amplified at ≥ 5 loci and re-amplified apparent unique genetic profiles represented by a single sample using two independent scorers to confirm unique individual identities (Hettinga et al. 2012). An error rate per locus was calculated using these re-amplification results.

	Survey Year	Area (km^2)	Distance Flown (km)	Number of Samples Collected	Number of Samples Successfully Scored	Number of Unique Genotypes	Genotyping Success (%)	Number of Spatial Recaptures
Little Smoky	2014-2015	3,027	3,048	855	835	108	97.7	36
Cold Lake	2014	7,108	7,098	844	781	261	92.5	148
ESAR	2013	12,803	13,113	1,382	1,254	401	90.7	188
WSAR	2015	15,322	16,198	1,687	1,613	490	95.6	314
Nipisi	2018	2,057	2,119	417	415	67	99.5	72
Slave Lake	2018	1,485	1,501	206	190	42	92.2	38
Red Earth	2017	24,051	16,880	1,819	1,777	386	97.7	530
Total	-	65,853	59,957	7,210	6,865	1,755	-	1,326

TABLE 2.1: Sampling data

2.3.2 *Framework*

Empirical SCR modeling

We used a maximum likelihood approach implemented in the R package *secr* (R Core Team 2019; Efford 2018) to estimate boreal caribou densities. SCR models are comprised of a submodel for the distribution of animals in the area of study (population density, D), and a submodel for the detection process, given the detection probability (the intercept of the detection function, $g0$) and given a parameter for scaling the detection function (the spatial extent of an individual's use of the landscape - σ; Borchers and Efford 2008). For our empirical data, we treated each survey as an occasion within a single session. We discretized the study area into a 1,500 m grid of proximity detectors (which record the presence of individuals at each detector without restricting movement; Efford et al. 2009), and each grid was sampled in each occasion with the same search intensity. The area of integration for SCR models needs to be large enough such that animals residing beyond the study area have a negligible chance of being detected (Borchers and Efford 2008; Efford 2004; Royle and Young 2008). We therefore defined our state-space with a 15-km^2 buffer around all study areas. We ran models for females, males, and both females and males together.

We estimated the parameters of the SCR detection function ($g0$ and σ) by maximizing the conditional likelihood, and derived density from the top AIC_C-ranked models (Anderson et al. 1994; Borchers and Efford 2008). We used the hazard exponential form of the detection function, as area search data models the cumulative hazard of detection (Efford 2011). Models assumed that individuals were identified correctly, populations were demographically closed during sampling, and detections were independent conditional on activity centre (Borchers and Efford 2008; Efford 2004). We assessed sources of variation on the detection parameters with time and behaviour effects on both *g0* and σ.

Testing assumptions of homogeneous distribution

Boreal caribou is a nonmigratory ecotype of caribou and have relatively small home ranges compared to wide-ranging carnivores such as brown bears (Graham and Stenhouse 2014; Lamb et al. 2018) and black bears (Whittington and Sawaya 2015). Boreal caribou exhibit a fission-fusion social structure and dynamics, with group size fluctuating throughout the year and frequent exchanges between groups; group size is lowest during spring and summer when cows become solitary for calving, increases before the rut, and may increase or decrease during the winter (Thomas and Gray 2002). To assess how the distribution of the animals (i.e., clustering) affected the precision and relative bias of our estimates, we simulated different population distributions at the individual level using three of our empirical datasets (Little Smoky, Cold Lake, and Slave Lake). Different distributions can be used for the simulations including a homogeneous Poisson distribution, inhomogeneous, or clustered Poisson distributions (Efford 2019a). The chosen population distribution should reflect the distribution of the study species. Our empirical data approximated a Neyman-Scott clustered Poisson distribution which was then used for the simulations (Efford 2019a). To simulate multiple detections in very close proximity, we set the spatial scale (σ) of the 2D kernel for locations within each cluster to be 1. To simulate varying levels of clustering, we varied the fixed number of individuals per cluster (see Figures S2.2.1-S2.2.3). We selected starting values for *D*, *g0*, and σ from the empirical model runs (Table 2.1). We carried out all simulations in the secr R package (Efford 2018; R Core Team 2019).

Population	D (95% CI)	CV(D)	g0 (95% CI)	σ (95% CI)	Home Range (km^2) (95% CI)	N (95% CI)
Cold Lake	61.9 (46.3-82.9)	0.15	0.015 (0.007-0.031)	3363.2 (2215.1-5240.1)	800 (347-1941)	353 (276-452)
ESAR	50.6 (42.9-59.6)	0.08	0.024 (0.015-0.039)	1778.8 (1451.8-2180.5)	224 (149-336)	647 (549-763)
Little Smoky	31.1 (22.8-42.5)	0.16	0.028 (0.006-0.124)	1603 (799.6-3213.9)	182 (45-730)	94 (69-129)
Nipisi	30.7 (22.8-41.4)	0.15	0.053 (0.027-0.104)	1941.6 (1419.6-2658.9)	267 (142-500)	63 (47-85)
Red Earth	16.1 (14.4-17.9)	0.05	0.022 (0.019-0.026)	3124.8 (2935.3-3326.5)	690 (609-782)	387 (347-430)
Slave Lake	25.9 (17.2-39.1)	0.21	0.247 (0.061-1.023)	1226 (772.4-1952.3)	106 (42-269)	38 (25-58)
WSAR	43 (38.5-48.1)	0.06	0.013 (0.011-0.016)	2868.9 (2701.5-3046.6)	582 (516-656)	659 (590-737)

TABLE 2.2: Spatially-explicit capture–recapture density estimates for boreal caribou in Alberta, Canada. Density estimates (D) are per 1,000 km^2, SE(D) is the standard error of the density estimate, CV(D) is the coefficient of variation (SE of density estimate/density estimate), g0 indicates the capture probability at the home range center, σ is the spatial scale parameter in meters, and N is the abundance over the study area

Assessing precision and relative bias of different sampling designs using empirical data

We repeated the empirical population analyses with subsamples of data to explore how reduced sampling intensity affected the relative bias and precision of the density estimates from our empirical study. We rarified the data by reducing the number of sampling occasions and reducing the number of aerial transects flown. For the reduced number of sampling occasions, all possible 2-occasion combinations were run (occasions 1 and 2; occasions 2 and 3; and occasions 1 and 3). Aerial transects were removed from the original spatial field data, keeping either every second or third transect line to emulate sampling strategies of 6 km or 9 km transects. Only the samples collected along the remaining transect lines were retained, and only those detectors along the remaining transect lines were used in the analysis. We used the coefficient of variation (CV) as the metric for precision, and calculated the absolute relative bias ($\mathrm{RB} = (\hat{D} - \mathrm{D})/\mathrm{D}$) as the metric for bias (as in Tobler and Powell 2013; Kristensen and Kovach 2018; Efford and Fewster 2013; Efford and Boulanger 2019). We compared estimates from the reduced datasets ($\hat{D}$) to those based on the empirical dataset (D). We considered models with CV < 20% (Pollock et al. 1990) and relative bias < 15% (Otis et al. 1978) as favourable outcomes. Models with CV < 30% and $|\mathrm{RB}| < 20\%$ can also be considered favourable (Kristensen and Kovach 2018), because high precision may be difficult to achieve for rare and low-density species.

We calculated the precision and relative bias of each subsampling scenario. To determine how the number of captures, number of recaptures, and number of spatial recaptures (recaptures at different locations) influence the precision and relative bias of the estimates, we correlated the precision and relative bias of the estimates with these parameters for each scenario, and then globally.

2.4 RESULTS

2.4.1 *Capture and spatial recapture rates*

A total of 7,210 samples were collected and 6,865 were successfully genotyped (average 95.1% genotyping success), resulting in the identification of 1,755 unique individuals from the seven populations detected a total of 1,326 times (unique site-occasion-animal detections (spatial recaptures); Table 2.1). Only four allelic dropout amplification errors occurred (error rate < 0.001%). The number of captures ($n = 85$–931) varied with range size, and proportion of captures that were recaptured (34%–58%), and spatially recaptured (31%–57%) was highest in Red Earth and lowest in ESAR (Table S2.3.1, Table 2.1). We had similar recapture and spatial recapture rates for females and males (Table S2.3.2, Table S2.3.4).

2.4.2 *Empirical model performance*

Density estimates for the seven populations ranged from 16.1 to 61.9 caribou/1,000 km^2 (Table 2.2). The coefficient of variation varied from 5% to 21% for both sexes combined, from 7% to 22% for females, and from 8% to 54% for males (Table 2.2, Table S2.3.3, Table S2.3.5). The average detection probability was low ($g0 < 0.06$; Table 2.2) for all populations except the first sampling occasion for Slave Lake ($g0_{t1} = 0.66$, $g0_{t2} = 0.036$, $g0_{t3} =$

0.44). σ differed among populations, ranging from 1,226 m in Slave Lake to 3,363 m in Cold Lake (Table 2.2).

2.4.3 *Assumptions of homogeneous distribution*

Results of simulations showed that clustering of caribou detections did not impact the precision or relative bias of the density estimates (Appendix 2.2). Median density estimates remained similar and slightly above the starting density for all levels of clustering density (μ) for the three simulated populations. The simulated Cold Lake population estimates retained the highest precision and were relatively unbiased, despite clustering, which corresponds with the precision found for the empirical model (Table 2.2). The simulated Little Smoky and Slave Lake population density estimates had lower precision than Cold Lake when caribou were clustered, but median density estimates were not affected by clustering, and density estimates from both populations remained unbiased (Appendix 2.2). Using a threshold value for precision of CV $<$ 20%, Little Smoky and Slave Lake had inadequate median levels of precision at all levels of μ. These populations had similar (Little Smoky $= \sigma$ 1,600 m) or smaller (Slave Lake $= \sigma$ 1,200 m) σ values compared to the chosen detector spacing of 1,500 m (Appendix 2.4). The detector spacing of 1,500 m for the empirical studies for these populations was too wide relative to σ, with very few spatial recaptures of individuals (36 in Little Smoky, 38 in Slave Lake over three occasions), as the detector spacing was larger than σ.

2.4.4 *Precision and relative bias of reduced sampling designs*

In total, 36 different subsampling scenarios were run for each population, for a total of 252 models. Precision and relative bias were positively correlated for all sexes (both sexes $r = 0.557$, $p < .0001$, female $r = 0.597$, $p < .0001$, male $r = 0.634$, $p < .0001$). Precision decreased (increased CV) and relative bias increased (divergence from the estimate from the full dataset) with increased transect spacing and reduced number of occasions (Figures 2.3-2.4). Several scenarios failed to converge for Little Smoky and Slave Lake at the reduced 6 km and 9 km transects due to low numbers of individuals and no recaptures, resulting in 227 completed models. The Little Smoky and Slave Lake ranges are two of the geographically smallest ranges (Table 2.1; Figure 2.2), and samples in these areas were clustered geographically (Figure 2.2). The detection function scaling parameter (σ) for the empirical data for Little Smoky and Cold Lake were smaller than the detector spacing of 1,500 m and reducing the number of transects increased the detector spacing even further, leading to the detector spacing being significantly larger than the σ estimates for these populations.

Precision of the subsampling scenarios was influenced by the number of unique individuals, number of recaptures, and number of spatial recaptures (Figure 2.5). Precision was negatively correlated with the number of individuals, with precision decreasing with fewer captured individuals (Table S2.3.6, Figure 2.5); all models that failed to run had no recaptures of individuals. The larger ranges of Cold Lake, ESAR, WSAR, and Red Earth had more unique individuals than the smaller ranges of Little Smoky, Nip-

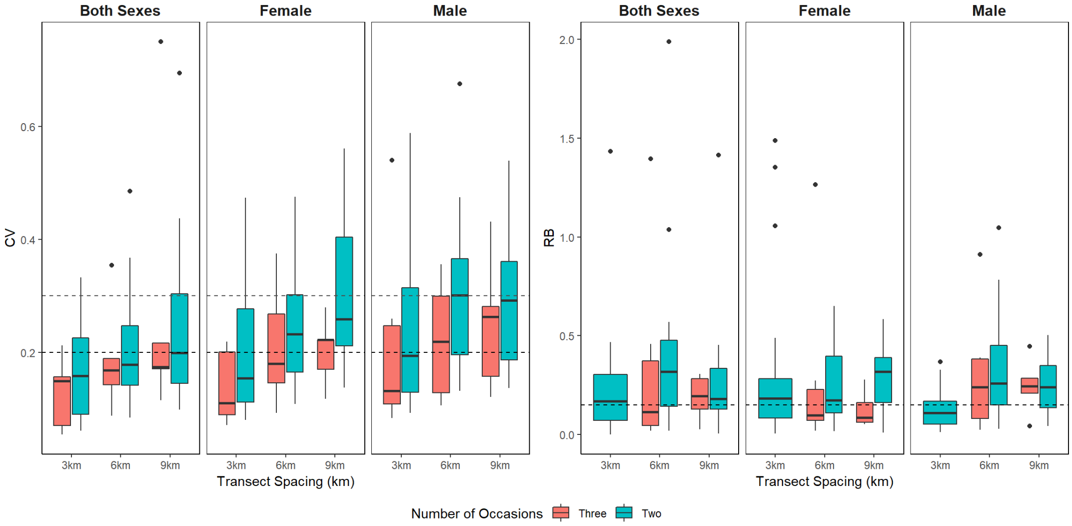


FIGURE 2.3: Measures of precision CV and bias (absolute relative bias, |RB|) for boreal caribou density estimates from subsampled empirical data (two or three sampling occasions, transect spacings of 3, 6, and 9 km) for both sexes, females and males. Dashed lines for CV represent 20% and 30% CV, and the dashed lines on RB represent 15% RB. Note: some outliers were dropped for data display

isi, and Slave Lake (Figure 2.5). When determining the influence of the number of individuals on model precision, all models with three occasions had adequate precision (<20% CV) for both sexes in the larger populations. The number of unique individuals had a greater influence in the smaller ranges, leading to inadequate precision in Little Smoky, Nipisi, and Slave Lake (Figure 2.5), with no significant correlation between precision and the number of unique individuals in Slave Lake (both sexes) and Little Smoky males (Table S2.3.6). CV was negatively correlated with the number of recaptures (Table S2.3.7) and spatial recaptures (Table S2.3.8), with lower precision in the smaller populations compared to the larger populations. All models with three occasions for the larger populations fell below the 20% CV threshold for all sex models (Figure 2.5). Even when decreasing the number of occasions to two, the larger ranges still performed well with adequate precision, as these subsets still provided an adequate number of recaptures of individuals for the models to run and precision was significantly correlated to the number of recaptures (Table S2.3.7, Figure 2.5). The smaller ranges did not perform as well when the data were reduced to two occasions; several models only retained one recapture of an individual, which resulted in a CV of nearly 100% (Figure 2.5), and the number of recaptures or spatial recaptures was not significantly correlated with precision (Slave Lake both sexes, Little Smoky males, Slave Lake males; Tables S2.3.7-S2.3.8).

While there was a strong relationship between precision and the number of individuals and recaptures, this was not the case for relative bias (Tables S2.3.6-S2.3.8; Figure 2.5). Except for Nipisi (all sexes) and Red Earth females, the number of captures, number of unique individuals, recaptures, or spatial recaptures was not significantly correlated with relative bias (Tables S2.3.6-S2.3.8). Removing the third session resulted in more bias compared to removing the first and second sessions (Figure 2.6).

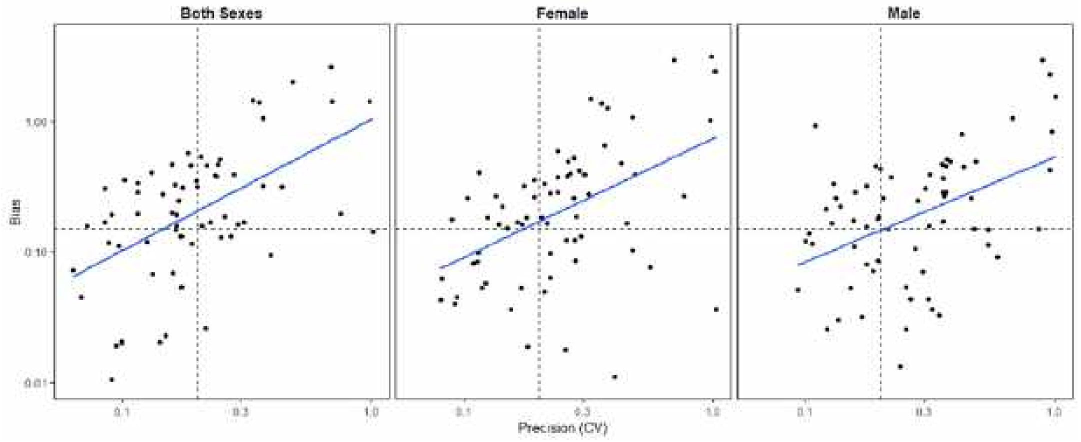


FIGURE 2.4: Relationship between absolute relative bias (|RB|) and precision (Coefficient of Variation) for boreal caribou density estimates from subsampled empirical data (two or three sampling occasions, transect spacings of 3, 6, and 9 km) for both sexes, females and males. Dashed line for CV represents 20% CV, and the dashes lined on RB represent 15% RB

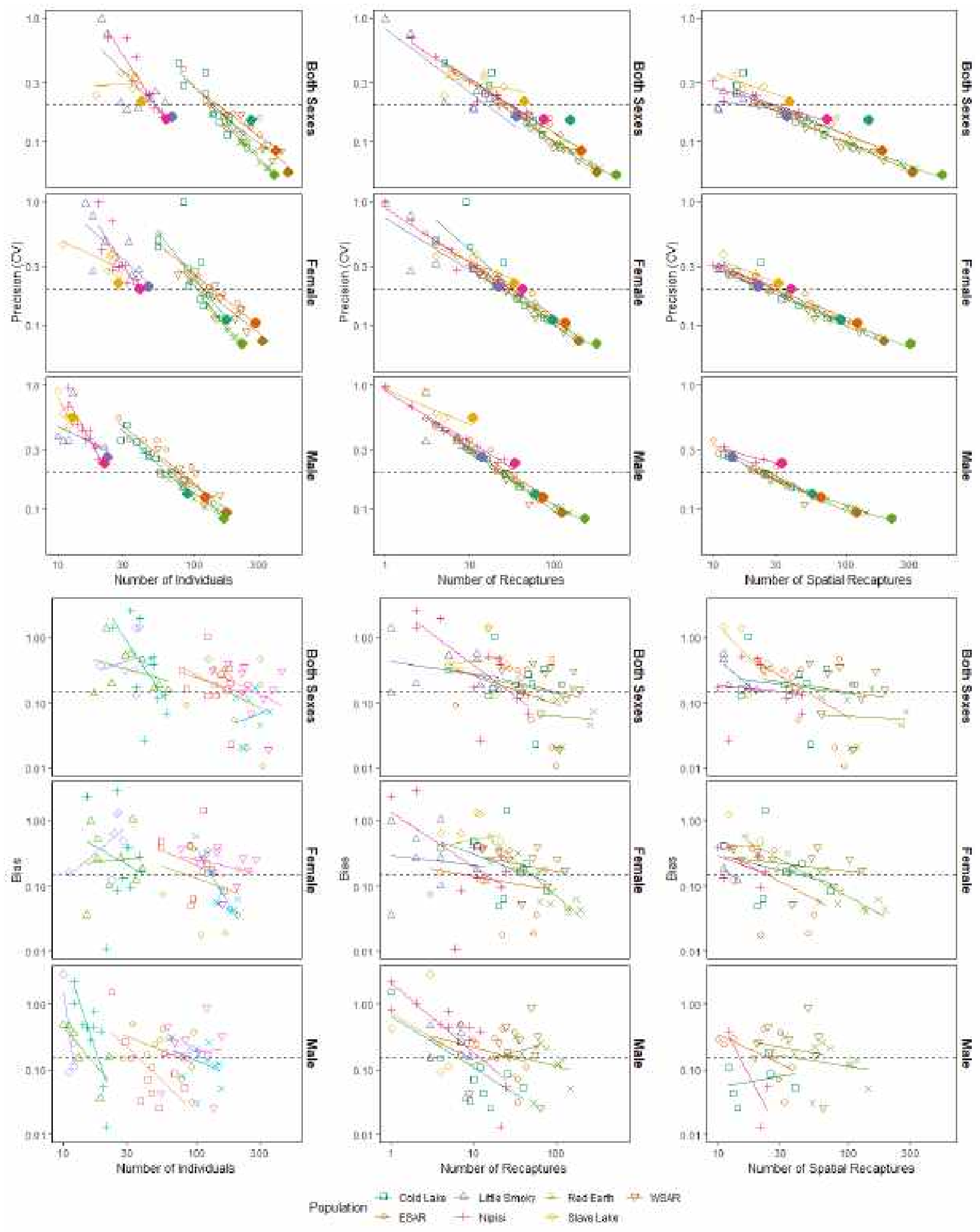


FIGURE 2.5: The relationship between the number of captures and recaptures and the precision (CV) and bias (absolute relative bias, |RB|) of density estimates for 7 populations of boreal caribou from subsampled empirical data (two or three sampling occasions, transect spacings of 3, 6, and 9 km) for both sexes, females and males. For each population, fewer unique individuals are sampled as the data are rarified to simulate decreasing sampling intensities, with filled circles indicating the full empirical datasets. Dashed line for CV represents 20% CV, and the dashed lines on bias represent 15% bias

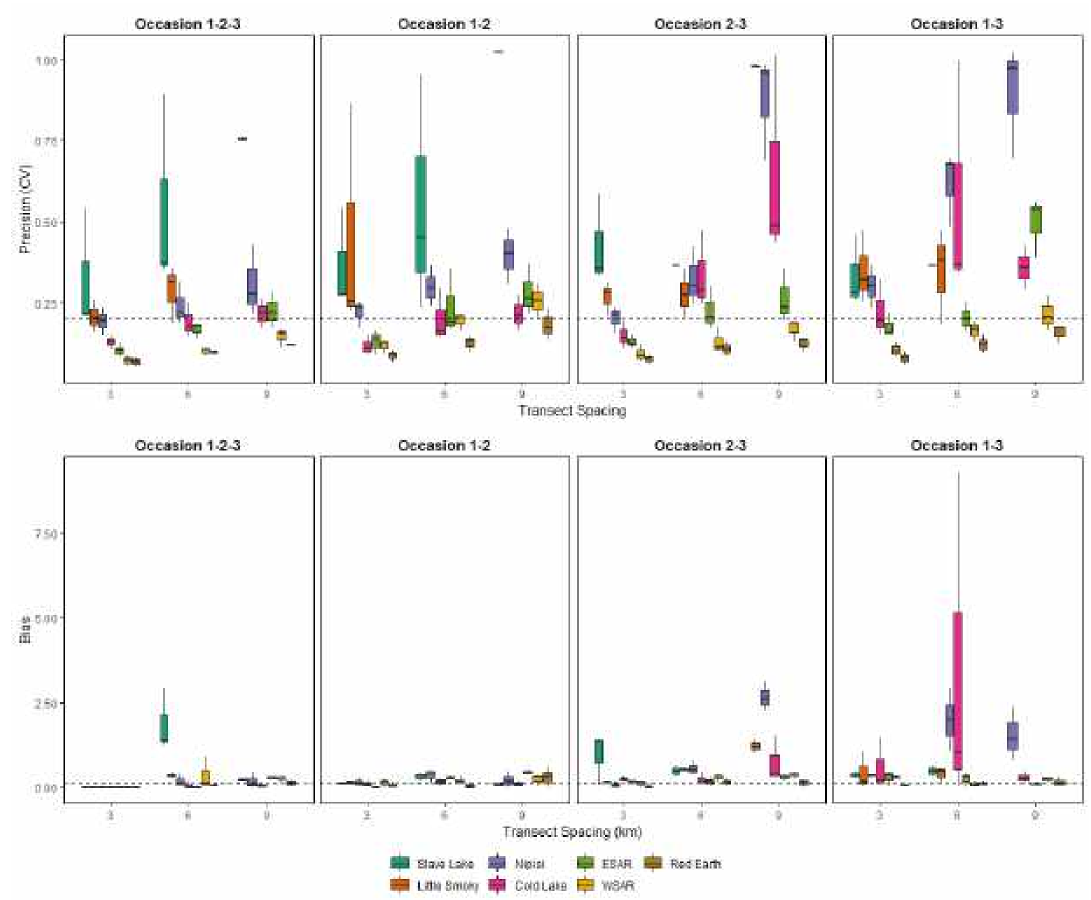


FIGURE 2.6: Measures of precision (CV) and bias (absolute relative bias, |RB|) boreal caribou density estimates from subsampled empirical data (two or three sampling occasions, transect spacings of 3, 6, and 9 km) for both sexes, females and males in each range. Note that some bias values were not displayed on the graph as they were extremely inflated. Dashed line for CV represents 20% CV, and the dashed lines on bias represent 15% bias

2.5 DISCUSSION

We provide an efficient framework for estimating detection parameters required for SCR studies and assessing empirical study designs for species where baseline detection data is not available. Our results using seven empirical datasets indicate that our genotyping protocol was highly successful, our capture and recapture rates were sufficient, and our study design was appropriate in producing precise and reliable density estimates. We followed the aerial survey protocol outlined in @Hettinga2012 to inform our sampling design and obtained similar recapture rates between sampling occasions. We found that the detection parameters *g0* (detection probability) and σ (the spatial extent of an individual's use of the landscape) varied among our study populations and between sexes (Table 2.2, Table S2.3.3, Table S2.3.5). Our results were robust to reduced sampling intensity (both in frequency and spatially), with the best study design dependent upon range size, and not dependent upon estimated population density or the spatial distribution of individuals.

For multiple species, the SCR model assumption that animals are independently and uniformly distributed over a study area is often violated, as is the case for boreal caribou (Després-Einspenner et al. 2017; López-Bao et al. 2018; Stevenson et al. 2015). The fission–fusion social structure and dynamics exhibited by boreal caribou during the winter months leads to frequent exchanges between small, dynamic groups (Thomas and Gray 2002). Our simulation results show that SCR models performed reliably; the grouping and movement patterns of boreal caribou during our sampling period had minimal impact on the precision or relative bias of the density estimates. Density estimates from the simulations were estimated slightly high (Appendix 2) across all clustering levels, but the source of bias was not related to the clustering simulations, as the precision and relative bias remained consistent when varying the level of clustering. Few studies have looked at the effect that nonindependence of individuals has on SCR methodologies. López-Bao et al. 2018 simulated scenarios of nonindependence and spatial aggregation of individual wolves (*Canis lupus*) with only a slight underestimation in population abundance estimates of aggregated individuals, while Després-Einspenner et al. 2017 were unsure to what extent the measures of uncertainty in their study of a community western chimpanzees (*Pan troglodytes verus*) were underestimated. Bischof et al. 2020 found that SCR models are robust to moderate levels of aggregation and cohesion, with low to moderate aggregation and cohesion not impacting the bias and precision of density and σ estimates. Inferences from SCR density estimates for species with small group sizes can be trusted even if grouping is ignored (Bischof et al. 2020). Although the fission–fusion social structure of caribou leads to frequent exchanges of individuals between groups, boreal caribou were rarely resampled together as a group or as a pair in our study (unpublished data).

Study designs can be inappropriate when poorly matched with the spatial behaviour of the target species (Williams et al. 2002). Detector arrays that are significantly smaller than one home range, or extreme detector spacing that leads to few or no spatial recaptures can result in biased SCR estimates

(Efford and Boulanger 2019; Efford 2011; Sollmann et al. 2012; Tobler and Powell 2013). Reducing the sampling intensity had a greater impact on populations with smaller range sizes regardless of density; reducing the number of transects flown led to extreme detector spacing with few or no spatial recaptures. Increasing the temporal period of sampling or decreasing the width between transects flown can be an effective way of increasing the number of detected captures and recaptures available for analysis, which increases precision; however, increasing the temporal sampling period can also violate the assumption of population closure and lead to biased estimates (Dupont et al. 2019). We found that the effects of reducing the number of sampling occasions on density estimates was influenced by the timing of the survey. If resources were only available to perform 2, rather than 3, sampling sessions, we recommend focusing on collecting samples early in the winter, rather than later in the winter, as we achieved relatively unbiased estimates ($|RB| < 20\%$) when retaining December, January, or February sampling occasions. Weather conditions during March surveys were not always favourable, with poor snow conditions and warm temperatures creating difficulties for finding animals and identifying fresh tracks and feeding areas.

Results from our empirical study provides a range of estimates that can be used for simulating surveys of boreal caribou in other locations. For poorly studied species, completing an initial empirical study is critical for obtaining accurate detection probability estimates. Due to the clustered, nonhomogeneous distribution of boreal caribou, extensive sampling of the entire population is recommended to ensure that clusters of caribou are not missed during sampling. Our subsampling scenarios showed how less extensive sampling in smaller ranges can miss a large portion of the population, increasing the relative bias and imprecision of the density estimates. Applying the same sampling design to all seven of our study populations proved to be suboptimal; detector spacing for the smaller populations relative to sigma led to imprecise estimates. Our subsampling scenarios were systematically done by reducing the sampling effort through reduced detectors, occasions, or a combination of both. Our study system was extensive, with large and spatially representative sample sizes, leading to 252 models used in assessing the precision and bias of our reduced sampling scenarios. We advocate that researchers with smaller study systems use multiple subsets and averages where meaningful.

Our analytical framework allowed us to examine the results of empirical surveys in depth, providing confidence in the density estimates. Through different simulations we were able to explore how relative bias and precision of estimates vary when assumptions are violated. We showed that the number of individuals and recaptures of individuals can be used to predict precision, but that they cannot be used to predict relative bias. Efford and Boulanger 2019 state that subsampling of data to emulate different configurations of detectors, or different temporal sampling can be prohibitively slow, due to model fitting being computer-intensive; however, we found that even for our largest population model (24,737 km^2, 386 unique individuals, and 545 recaptures), modeling with time and behaviour effects on both $g0$ and σ ran relatively quickly (∼7–10 days on a high-performance computer cluster) in a maximum likelihood framework, where the density model was fitted by maximizing the conditional likelihood.

We recommend the combination of noninvasive DNA sampling, together with SCR modeling and distribution simulations, to be an effective, accurate and precise approach to monitoring wildlife.

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APPENDIX 2.1: CARIBOU RANGES AND SAMPLING PROTOCOL

Woodland caribou (*Rangifer tarandus caribou*) are a wide-ranging deer species found throughout Canada's boreal forests, and face increasingly severe threats across their range from habitat loss, habitat fragmentation, and increased predation from landscape changes; populations have steadily decreased throughout most of their range, with the southern limit of boreal caribou distribution receding northward since the 1990's (COSEWIC 2002; Environment Canada 2011; Festa-Bianchet et al. 2011; Hervieux et al. 2013; Schaefer 2003). Boreal caribou require large areas of undisturbed, continuous habitat, preferring mature to old-growth coniferous forests abundant with lichens, or peat lands and muskegs along with upland and hilly areas (Courtois et al. 2003; Environment Canada 2012; Rettie and Messier 2000; Stuart-Smith et al. 1997). Both natural and anthropogenic disturbances affect the spatial distribution and habitat selection of boreal caribou. Maintaining low densities is a key behavioural pattern for boreal caribou to avoid predation and ensure adequate recruitment rate and adult survival, but altered habitats from human land uses are no longer optimal for boreal caribou (e.g. Smith et al. 2000).

Boreal caribou present a good opportunity for evaluating optimal sampling design for non-invasive SCR studies. Boreal caribou are a non-migratory ecotype of caribou and have relatively small home ranges compared to wide-ranging carnivores such as brown bears (Graham and Stenhouse 2014; Lamb et al. 2018) and black bears (Whittington and Sawaya 2015), for which most prior SCR sampling design studies have been performed (Sun et al. 2014; Wilton et al. 2014). Boreal caribou are habitat specialists, and maintain low population densities as an anti-predator strategy (Environment Canada 2012; Rettie and Messier 2001), adding further challenges to abundance estimation. We assessed seven populations of boreal caribou from Alberta, Canada: Cold Lake, Little Smoky, East Side Athabasca River (hereafter referred to as ESAR), West Side Athabasca River (hereafter referred to as WSAR), Red Earth, Slave Lake, and Nipisi.

The Cold Lake range (6,724 km^2) in north-eastern Alberta and adjacent areas in western Saskatchewan and shares a border with the ESAR range. 87% of the Cold Lake range is disturbed from natural and anthropogenic sources (primarily through extraction of natural resources such as oil, gas and timber), with wildfire accounting for 30% of the current disturbance within the range (Government of Alberta 2017). Seismic lines, pipelines and abandoned wells make up a large legacy footprint within the range, with active restoration of seismic lines occurring in portions of the range (Government of Alberta 2017). The Cold Lake Air Weapons Range is located within the Cold Lake caribou range boundary. The Little Smoky range (3,084 km^2) is the last remaining boreal population of caribou occurring in the eastern slopes of west-central Alberta (Government of Alberta 2017). 99% of the Little Smoky range is disturbed from natural and anthropogenic sources (primarily petroleum, natural gas and forestry), with wildfires accounting for less than 1% of the disturbance within the range (Government of Alberta 2017). The ESAR range (13,160 km^2) is located in north-eastern Alberta, comprised of seven disjuncted sub-range areas, and shares a border with the Cold Lake range. 88% of the ESAR range is disturbed from natural and anthropogenic sources (primarily forestry, oil sands, petroleum and natural gas), with wildfire accounting for 32% of the current disturbance within the range (Government of Alberta 2017). The ESAR range is highly fragmented, with nearly 20,000 km of seismic lines and numerous wells, roads and pipelines throughout the range (Government of Alberta 2017). The WSAR range (15,727 km^2) is located in northern Alberta, and shares a border with the Red Earth boreal caribou population. 84% of the WSAR range is disturbed from natural and anthropogenic sources (primarily human footprint from legacy seismic lines, pipelines, wells, roads, forest harvest and transmission lines), with wildfire accounting for only 6% of the disturbance within the range (Government of Alberta 2017). The Red Earth range (24,737 km^2) is located in northern Alberta, and shares a border with the WSAR boreal caribou population. 68% of the Red Earth range is disturbed from natural and anthropogenic sources (primarily from forestry, oil sands and natural gas), with wildfires accounting for 38% of the total disturbance (Government of Alberta 2017). The Slave Lake range (1,516 km^2) is located in central Alberta. 99% of the Slave Lake range is disturbed from natural and anthropogenic sources (primarily forestry, petroleum, mineral and aggregate resource extraction), with wildfires account for 37% of the current disturbance within the range (Government of Alberta 2017). The Nipisi range (2,104 km^2) is located in central Alberta. 94% of the Nipisi range is disturbed from natural and anthropogenic sources (primarily forestry, oil, and gas), with wildfires accounting for only 8% of the current disturbance within the range (Government of Alberta 2017).

Sample collection information

We collected 867 samples from the Little Smoky caribou range and excluded 12 non-caribou samples (putative deer) and 20 samples that were contaminated or extremely poor quality. The resulting dataset of 835 samples representing 108 unique genotypes (73 females and 35 males) amplified at ≥ 7 loci, including 5 profiles that occurred once within the dataset (hereafter, singletons). From the WSAR region, we collected 1,701 samples including 15 non-caribou samples (14 deer plus 1 putative moose) and 73 samples that were contaminated or extremely low quality. The resulting dataset from WSAR included 1,613 samples representing 489 unique genotypes (316 females and 173 males), 98% of which amplified at ≥ 7 loci, and 130 singletons. We collected 1,460 samples from the ESAR region, including 78 non-caribou samples (deer) and 122 samples that were contaminated or extremely low quality. The resulting dataset from ESAR included 1,254 samples representing 401 unique genotypes (281 females and 120 males), 92% of which amplified at ≥ 7 loci, and 122 singletons. From the Cold Lake region, we collected 931 samples, including 87 non-caribou samples (putative deer) and 62 samples that were contaminated or extremely low quality. The resulting dataset from Cold Lake included 781 samples representing 261 unique genotypes (172 females and 89 males), 93% of which amplified at ≥ 7 loci, and 87 singletons. Only four unique genotypes were seen in more than one range (3 genotypes in both ESAR and Cold Lake and 1 genotype in both ESAR and WSAR) (Hileman et al. 2018, unpublished data). Conditions during the March survey in Cold Lake were particularly difficult, with temperatures as high as +8°C during some afternoons, compounded by the fact that flying was only permitted in the Cold Lake Air Weapons Range during weekends; only 16 sites were visited during this survey, and ~1/3 of the number of samples were collected compared to during January and February surveys.

Additional SCR model information

Aerial transects were flown 3 km apart; discretizing our search data to 1500 meters represents half the width of the aerial transects, which is the distance observers can see out of each side of the helicopter. Initial exploratory analyses were completed from 750 metre to 2500 metre discretize spacing, at intervals of 250 meters (8 different discretizations in total) to determine the best spacing; discretization of 1500 meters was the best performing discretization (see Appendix 4). The area of integration for SCR models needs to be large enough that animals residing beyond the study area have a negligible chance of being detected (Efford 2004; Borchers and Efford 2008; Royle and Young 2008). We therefore defined our state-space with a 15 km^2 buffer around all study areas. Models were run with both males and females modelled together, and sexes were run separately to get sex-specific estimates. We estimated the parameters of the SCR detection function ($g0$ and σ) by maximizing the conditional likelihood. We used the hazard exponential form of the detection function, as area search data models the cumulative hazard of detection (Efford 2011); initially, the hazard halfnormal and hazard exponential detection functions were compared via the Akaike Information Criterion adjusted for small sample sizes (AIC_C; Burnham and Anderson 2002) to determine the best fitting detection function for the data. We estimated density as a derived parameter from the top AIC_C-ranked models. Models assumed that individuals were identified correctly, populations were demographically closed during sampling, and detections were independent conditional on activity center (Borchers and Efford 2008; Efford 2004). We evaluated support for the following sources of variation in $g0$ and σ by comparing AIC_C values among candidate models: (1) four possible behavioural responses – individual detection probability increases or decreases at a particular surveyed area depending on detection at previous occasion(s) (bk); individual detection probability increases or decreases at a particular surveyed area depending on detection at the immediate preceding occasion (Bk); detection probability of a particular surveyed area depends on whether an individual was detected there at previous occasion(s) (k); detection probability of a particular surveyed area depends on whether an individual was detected there at the immediately preceding occasion (K); and (2) two possible time effects, with detection varying with the sampling occasion (t) or whether there was a tendency for higher or lower individual detectability along the course of the study (T; Borchers and Efford 2008; Efford and Mowat 2014).

We assumed detections to be independent between individuals; violating this assumption can lead to overdispersion, which does not affect the point estimates of density or model parameters, but can lead to underestimated variance, and over-parameterized models to be selected by AIC_C (Anderson et al. 1994; Borchers and Efford 2008).

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APPENDIX 2.2: INHOMOGENEOUS POPULATION SIMULATIONS

Population	Range Size (km^2)	Density (ha)	$g0$	σ	Detector spacing	number of occasions	number of runs
Little Smoky	3,027	0.00030	0.030	1600	1,500	3	100
Cold Lake	7,108	0.00060	0.015	3400	1,500	3	100
Slave Lake	1,485	0.00025	0.250	1200	1,500	3	100

TABLE S2.2.1: Simulated population parameters used in clustering simulations

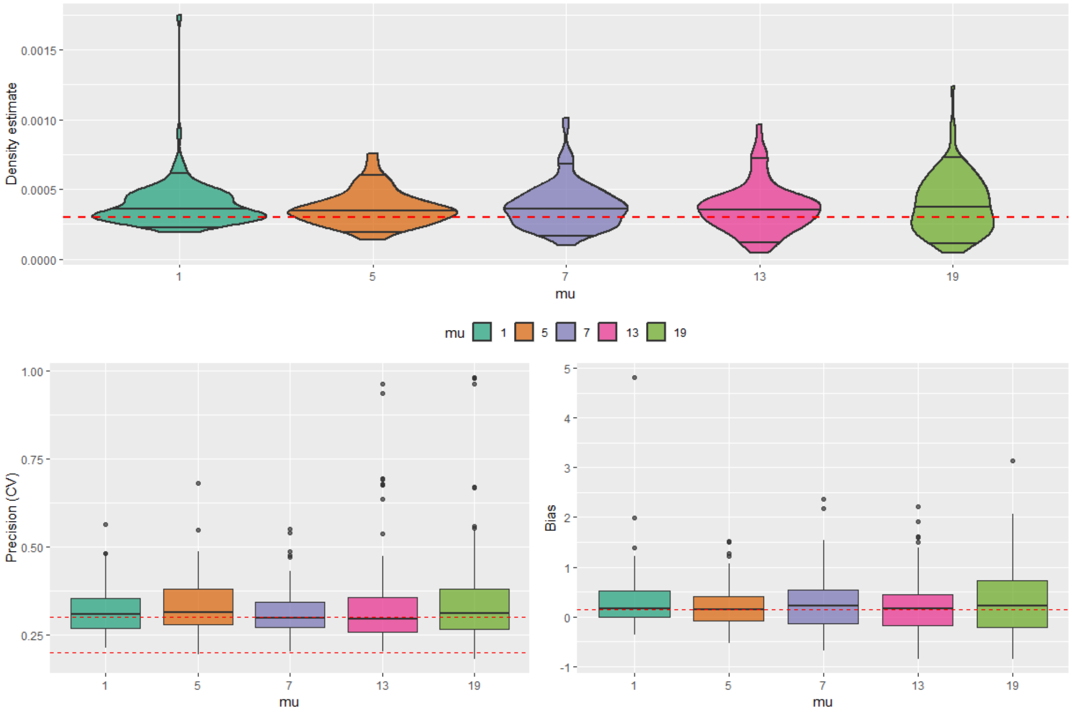

FIGURE S2.2.1: Little Smoky simulation results. Top shows the distribution of simulated density estimates for each level of clustering (mu), with horizontal dotted line representing the initial density. Bottom left shows distribution of precision (CV), with horizontal dotted lines representing 20% and 30% CV. Bottom right graph shows distribution of relative bias, with the horizontal dotted line representing 20% bias

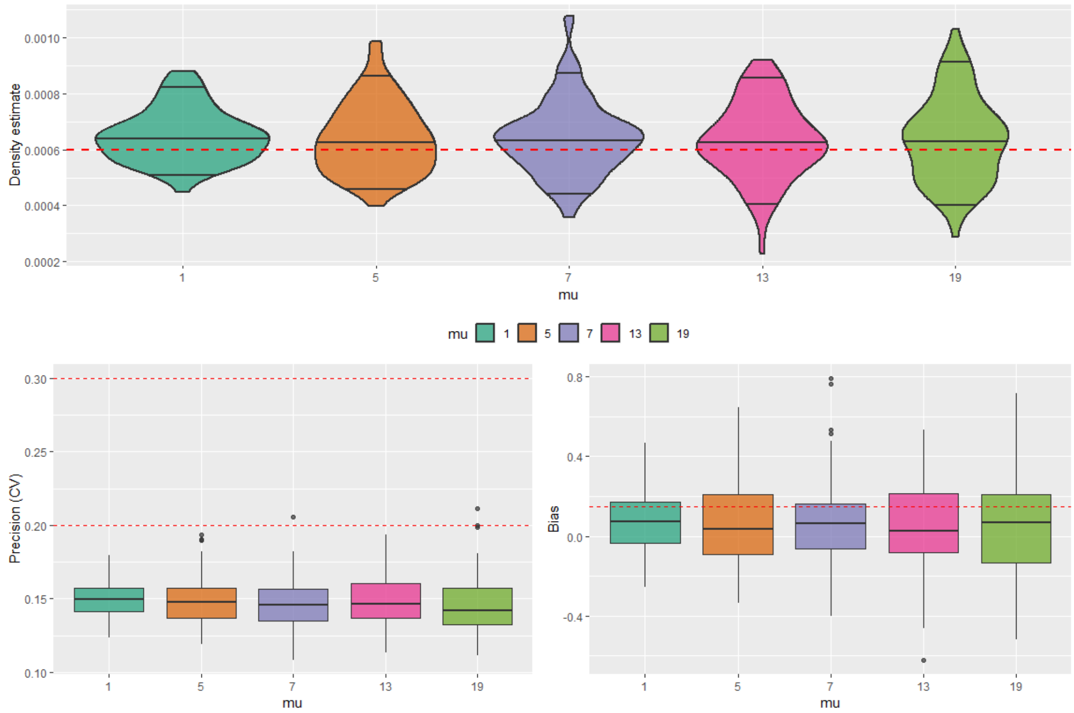

Figure S2.2.2: Cold Lake simulation results. Top shows the distribution of simulated density estimates for each level of clustering (mu), with horizontal dotted line representing the initial density. Bottom left shows distribution of precision (CV), with horizontal dotted lines representing 20% and 30% CV. Bottom right graph shows distribution of relative bias, with the horizontal dotted line representing 20% bias

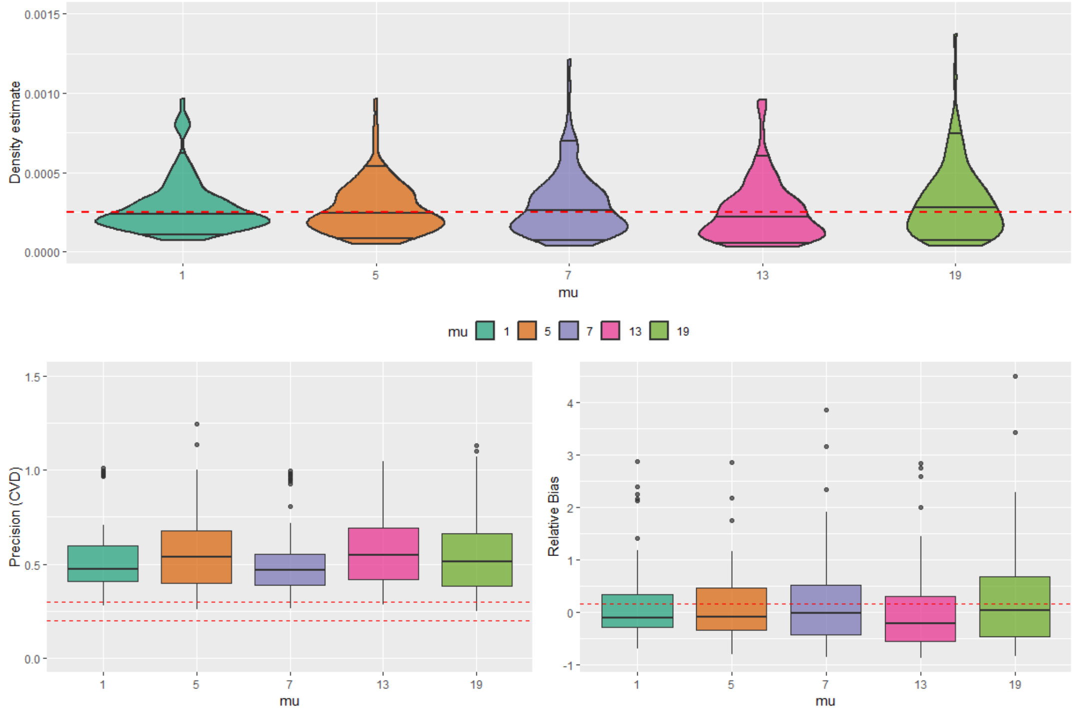

Figure S2.2.3: Slave Lake simulation results. Top shows the distribution of simulated density estimates for each level of clustering (mu), with horizontal dotted line representing the initial density. Bottom left shows distribution of precision (CV), with horizontal dotted lines representing 20% and 30% CV. Bottom right graph shows distribution of relative bias, with the horizontal dotted line representing 20% bias

APPENDIX 2.3: SCR MODEL RESULTS AND CORRELATION RESULTS

Both Sexes

Population	Number of Individuals	Number of Captures	Number of Recaptures	Number of Spatial Recaptures
Cold Lake	261	416	155	148
ESAR	400	606	206	188
Little Smoky	69	105	36	36
Nipisi	62	138	76	72
Red Earth	388	931	543	530
Slave Lake	41	85	44	38
WSAR	489	805	316	314
Total	1,710	3,086	1,376	1,326

TABLE S2.3.1: Both sexes capture data

Females

Population	Number of Individuals	Number of Captures	Number of Recaptures	Number of Spatial Recaptures
Cold Lake	172	267	95	92
ESAR	280	413	133	123
Little Smoky	46	68	22	22
Nipisi	40	82	42	39
Red Earth	223	539	316	307
Slave Lake	28	61	33	31
WSAR	316	511	195	193
Total	1,105	1,941	836	807

TABLE S2.3.2: Female capture data

Population	D (95% CI)	SE(D)	CV(D)	*g0* (95% CI)	σ (95% CI)	N (95% CI)
Cold Lake	36.7 (29.6-45.5)	4.03	0.11	0.023 (0.011-0.048)	2593 (1877-3649)	261 (210-323)
ESAR	37.6 (30.6-46.1)	3.93	0.10	0.022 (0.013-0.038)	1874 (1500-2342)	481 (392-590)
Little Smoky	21.7 (14.6-32.4)	4.46	0.20	0.008 (0.002-0.028)	3085 (1764-5396)	66 (44-98)
Nipisi	20.8 (14.2-30.4)	4.07	0.20	0.048 (0.02-0.115)	2091 (1393-3145)	43 (29-62)
Red Earth	9.2 (8-10.6)	0.66	0.07	0.028 (0.019-0.041)	2928 (2485-3449)	221 (193-255)
Slave Lake	14.8 (9.7-22.7)	3.25	0.22	0.422 (0.1-1.824)	1134 (703-1842)	22 (14-34)
WSAR	27.9 (24.1-32.3)	2.10	0.08	0.038 (0.026-0.056)	2679 (2155-3334)	428 (369-496)

TABLE S2.3.3: Spatially-explicit capture-recapture density estimates for female boreal caribou in Alberta, Canada. Density estimates (D) are per 1000 km^2, SE(D) is the standard error of the density estimate, CV(D) is the coefficient of variation (SE of density estimate/density estimate), *g0* indicates the capture probability at the home range center, σ is the spatial scale parameter in meters, and N is the abundance over the study area.

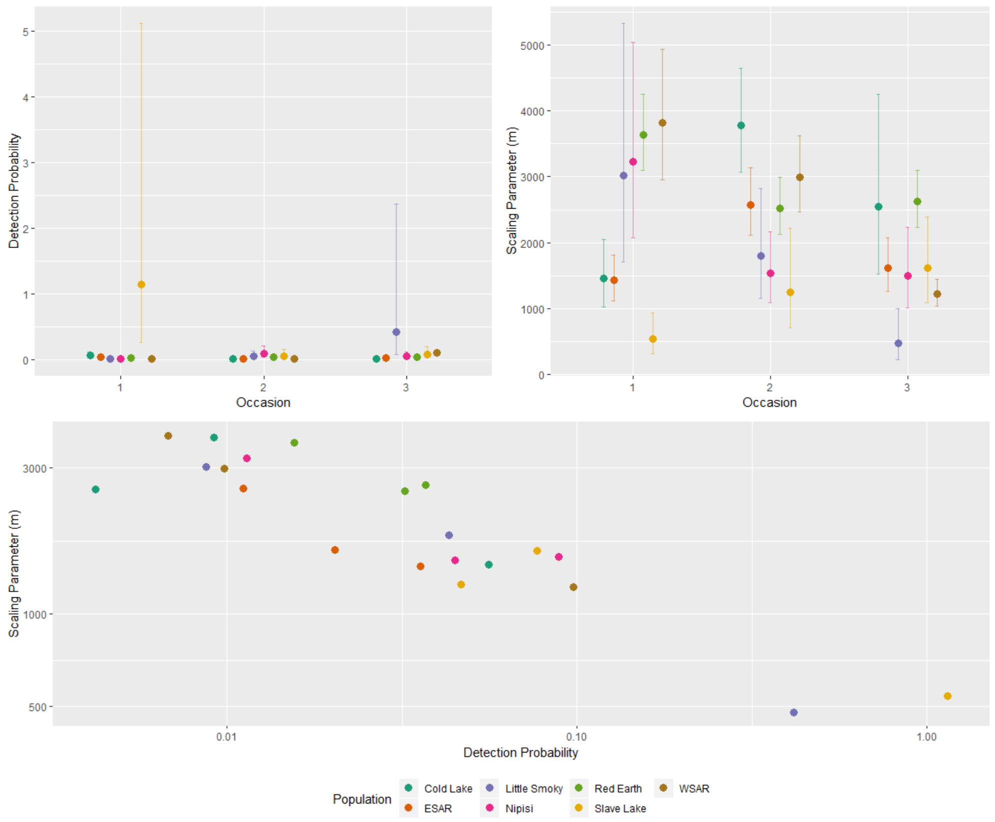

FIGURE S2.3.1: Female detection probability ($g0$) and scaling parameter (σ) by population designs

Males

Population	Number of Individuals	Number of Captures	Number of Recaptures	Number of Spatial Recaptures
Cold Lake	89	149	60	56
ESAR	120	193	73	65
Little Smoky	23	37	14	14
Nipisi	22	56	34	33
Red Earth	165	392	227	222
Slave Lake	13	24	11	7
WSAR	173	294	121	121
Total	605	1,145	540	518

TABLE S2.3.4: Male capture data

Population	D (95% CI)	SE(D)	CV(D)	*g0* (95% CI)	σ (95% CI)	N (95% CI)
Cold Lake	15.6 (12-20.1)	2.05	0.13	0.053 (0.024-0.12)	1788 (1310-2444)	111 (86-143)
ESAR	11.9 (9.3-15.1)	1.48	0.12	0.045 (0.031-0.065)	1506 (1298-1748)	152 (119-194)
Little Smoky	9.1 (5.5-15)	2.37	0.26	0.051 (0.021-0.122)	1002 (600-1673)	28 (17-46)
Nipisi	9.9 (6.3-15.6)	2.32	0.23	0.074 (0.036-0.156)	1607 (1266-2040)	20 (13-32)
Red Earth	6.8 (5.8-8)	0.57	0.08	0.031 (0.02-0.02)	2477 (2047-2998)	163 (138-192)
Slave Lake	15.6 (5.8-42.2)	8.44	0.54	0.023 (0.005-0.106)	1558 (925-2626)	23 (9-63)
WSAR	13.4 (11.1-16.1)	1.26	0.09	0.024 (0.013-0.045)	3347 (2592-4321)	205 (171-247)

TABLE S2.3.5: Spatially-explicit capture-recapture density estimates for male boreal caribou in Alberta, Canada. Density estimates (D) are per 1000 km^2, SE(D) is the standard error of the density estimate, CV(D) is the coefficient of variation (SE of density estimate/density estimate), *g0* indicates the capture probability at the home range center, σ is the spatial scale parameter in meters, and N is the abundance over the study area.

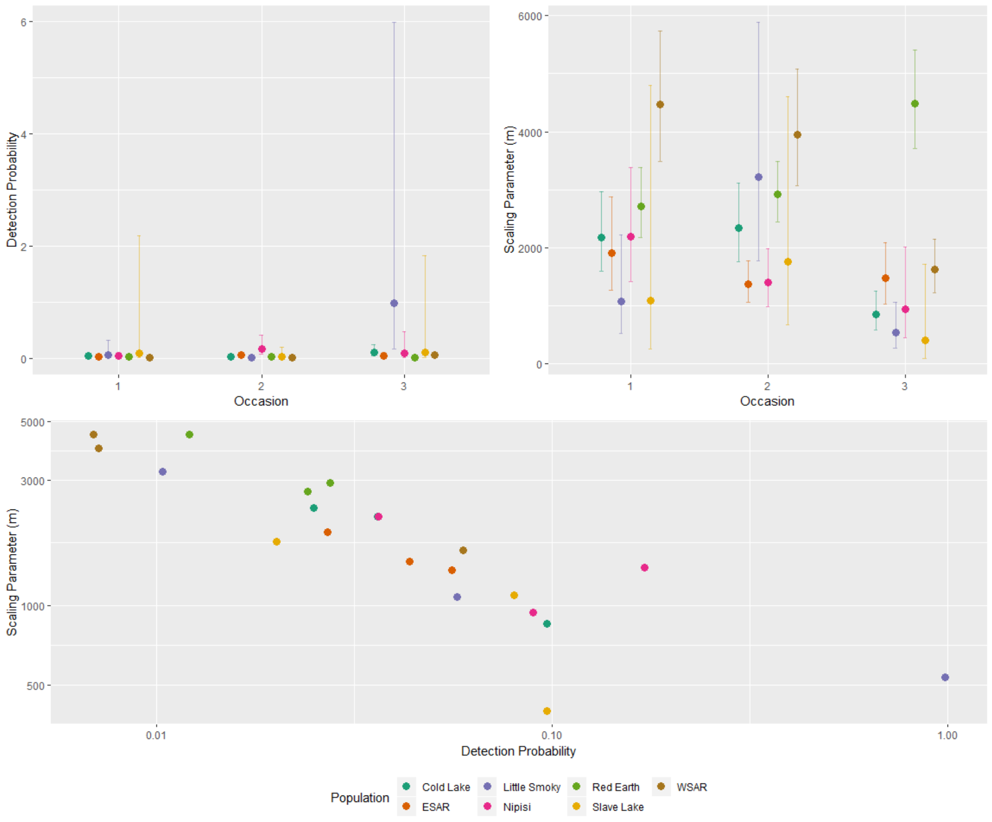

FIGURE S2.3.2: Male detection probability (*g0*) and scaling parameter (σ) by population

Correlation results

Population	Sex	CV(D)	RB
Cold Lake	Both Sexes	-0.758 (0.00428)	-0.21 (0.535)
ESAR	Both Sexes	-0.791 (0.00217)	-0.21 (0.535)
Little Smoky	Both Sexes	-0.729 (0.0167)	-0.429 (0.249)
Nipisi	Both Sexes	-0.856 (0.000383)	-0.646 (0.0318)
Red Earth	Both Sexes	-0.963 (8.13e-06)	0.0389 (0.921)
Slave Lake	Both Sexes	-0.00178 (0.997)	0.289 (0.53)
WSAR	Both Sexes	-0.866 (0.000271)	-0.351 (0.29)
Cold Lake	Female	-0.576 (0.05)	-0.187 (0.582)
ESAR	Female	-0.766 (0.00369)	-0.459 (0.156)
Little Smoky	Female	-0.736 (0.0152)	-0.0597 (0.879)
Nipisi	Female	-0.808 (0.00147)	-0.603 (0.0494)
Red Earth	Female	-0.903 (5.7e-05)	-0.754 (0.00736)
Slave Lake	Female	-0.745 (0.0338)	0.519 (0.232)
WSAR	Female	-0.854 (0.000402)	-0.322 (0.335)
Cold Lake	Male	-0.718 (0.0086)	-0.513 (0.107)
ESAR	Male	-0.857 (0.000366)	-0.368 (0.266)
Little Smoky	Male	-0.386 (0.393)	-0.794 (0.0592)
Nipisi	Male	-0.918 (2.59e-05)	-0.636 (0.0354)
Red Earth	Male	-0.921 (2.18e-05)	-0.45 (0.165)
Slave Lake	Male	-0.903 (0.0136)	-0.283 (0.644)
WSAR	Male	-0.821 (0.00106)	0.153 (0.653)

TABLE S2.3.6: Correlation results (r2) between the number of individuals and precision (CV(D)) and relative bias (RB) for each population and sex. Significance level (p-value) in brackets.

Population	Sex	CV(D)	RB
Cold Lake	Both Sexes	-0.654 (0.0211)	-0.234 (0.489)
ESAR	Both Sexes	-0.717 (0.00875)	-0.278 (0.407)
Little Smoky	Both Sexes	-0.671 (0.0338)	-0.428 (0.251)
Nipisi	Both Sexes	-0.693 (0.0125)	-0.667 (0.0249)
Red Earth	Both Sexes	-0.859 (0.00146)	-0.208 (0.591)
Slave Lake	Both Sexes	-0.62 (0.101)	0.158 (0.735)
WSAR	Both Sexes	-0.847 (0.000502)	-0.174 (0.609)
Cold Lake	Female	-0.6 (0.0393)	-0.322 (0.335)
ESAR	Female	-0.682 (0.0145)	-0.452 (0.162)
Little Smoky	Female	-0.647 (0.0432)	-0.349 (0.357)
Nipisi	Female	-0.687 (0.0137)	-0.686 (0.0198)
Red Earth	Female	-0.79 (0.00226)	-0.689 (0.0191)
Slave Lake	Female	-0.873 (0.0046)	0.0834 (0.859)
WSAR	Female	-0.827 (0.000906)	-0.299 (0.372)
Cold Lake	Male	-0.622 (0.0308)	-0.431 (0.186)
ESAR	Male	-0.823 (0.00101)	-0.391 (0.234)
Little Smoky	Male	-0.628 (0.131)	-0.302 (0.56)
Nipisi	Male	-0.722 (0.00795)	-0.682 (0.0207)
Red Earth	Male	-0.878 (0.000171)	-0.408 (0.213)
Slave Lake	Male	-0.594 (0.214)	-0.244 (0.692)
WSAR	Male	-0.803 (0.00166)	0.211 (0.534)

TABLE S2.3.7: Correlation results (r2) between the number of recaptures and precision (CV(D)) and relative bias (RB) for each population and sex. Significance level (p-value) in brackets.

Population	Sex	CV(D)	RB
Cold Lake	Both Sexes	-0.653 (0.0213)	-0.228 (0.5)
ESAR	Both Sexes	-0.72 (0.00832)	-0.235 (0.488)
Little Smoky	Both Sexes	-0.671 (0.0338)	-0.428 (0.251)
Nipisi	Both Sexes	-0.704 (0.0106)	-0.678 (0.0219)
Red Earth	Both Sexes	-0.861 (0.00139)	-0.208 (0.591)
Slave Lake	Both Sexes	-0.615 (0.105)	0.0571 (0.903)
WSAR	Both Sexes	-0.845 (0.000547)	-0.179 (0.599)
Cold Lake	Female	-0.595 (0.0411)	-0.314 (0.347)
ESAR	Female	-0.685 (0.014)	-0.442 (0.173)
Little Smoky	Female	-0.647 (0.0432)	-0.349 (0.357)
Nipisi	Female	-0.704 (0.0106)	-0.703 (0.0159)
Red Earth	Female	-0.789 (0.00226)	-0.684 (0.0203)
Slave Lake	Female	-0.882 (0.00377)	0.00505 (0.991)
WSAR	Female	-0.826 (0.000921)	-0.289 (0.389)
Cold Lake	Male	-0.623 (0.0306)	-0.422 (0.196)
ESAR	Male	-0.83 (0.000829)	-0.355 (0.285)
Little Smoky	Male	-0.628 (0.131)	-0.302 (0.56)
Nipisi	Male	-0.729 (0.00713)	-0.688 (0.0193)
Red Earth	Male	-0.879 (0.000163)	-0.409 (0.212)
Slave Lake	Male	-0.523 (0.287)	0.125 (0.841)
WSAR	Male	-0.799 (0.00184)	0.194 (0.568)

TABLE S2.3.8: Correlation results (r2) between the number of spatial recaptures and precision (CV(D)) and relative bias (RB) for each population and sex. Significance level (p-value) in brackets.

APPENDIX 2.4: COMPARING DIFFERENT DISCRETIZE SPACINGS

These tests were run on Little Smoky. Plotting the results of the top models from each spacing. As we increase the discretize spacing, we are increasing the 95% confidence intervals. Males performed similarly from 750 m to 2250 m but were inflated at 2500 m. Females performed similarly from 750 m to 1500 m, but greater than 1500 m the estimates were inflated.

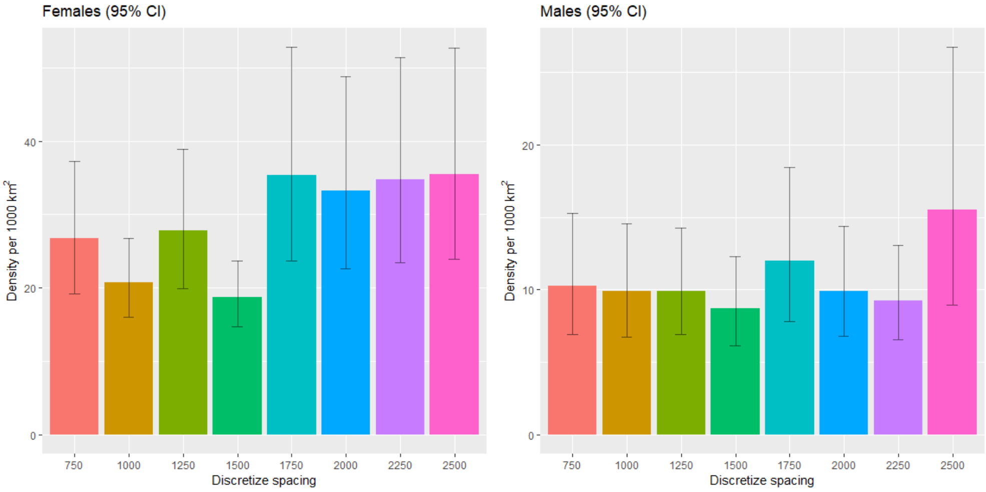

FIGURE S2.4.1: Resulting density estimates from various discretize spacing widths for females and males

All models were run at 1500 m discretize spacing. Originally 2500 m was used for the three populations (Little Smoky, A la Peche and Cold Lake), but 1500 m was selected as the best spacing. Transect lines were flown 3000 m apart; it is likely that choosing a spacing of 2500 m was incorrect as it did not reflect the flight transect spacings. Selecting a discretize spacing of 1500 m represents half the width of the flight transects.

3

Spatial familial networks to infer demographic structure of wild populations

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Contributions: SM implemented the analysis with contributions from MM. MM coordinated the samples collection, PW coordinated DNA extraction and analysis. SM wrote the first draft of the manuscript with help from MM. All authors contributed to subsequent drafts and gave final approval for publication.

3.1 ABSTRACT

In social species, reproductive success and rates of dispersal vary among individuals resulting in spatially structured populations. Network analyses of familial relationships may provide insights on how these parameters influence population-level demographic patterns. These methods, however, have rarely been applied to genetically derived pedigree data from wild populations.

Here, we use parent–offspring relationships to construct familial networks from polygamous boreal woodland caribou (*Rangifer tarandus caribou*) in Saskatchewan, Canada, to inform recovery efforts. We collected samples from 933 individuals at 15 variable microsatellite loci along with caribou-specific primers for sex identification. Using network measures, we assess the contribution of individual caribou to the population with several centrality measures and then determine which measures are best suited to inform on the population demographic structure. We investigate the centrality of individuals from eighteen different local areas, along with the entire population.

We found substantial differences in centrality of individuals in different local areas, that in turn contributed differently to the full network, highlighting the importance of analyzing networks at different scales. The full network revealed that boreal caribou in Saskatchewan form a complex, interconnected familial network, as the removal of edges with high betweenness did not result in distinct subgroups. Alpha, betweenness, and eccentricity centrality were the most informative measures to characterize the population demographic structure and for spatially identifying areas of highest fitness levels and family cohesion across the range. We found varied levels of dispersal, fitness, and cohesion in family groups.

Synthesis and applications: Our results demonstrate the value of different network measures in assessing genetically derived familial networks. The spatial application of the familial networks identified individuals presenting different fitness levels, short- and long-distance dispersing ability across the range in support of population monitoring and recovery efforts.

3.2 INTRODUCTION

Population genetic analyses are used to inform on the genetic composition of a population and the forces that explain the changes to that composition (Griffiths et al. 2000). A larger number of analytical approaches have been developed to delineate populations and assess the extent and patterns of gene flow and dispersal (e.g., Galpern et al. 2014; Jombart et al. 2008; Pritchard et al. 2000). More recently, graph-theoretic approach has been used to assess population genetic structure (Dyer and Nason 2004), investigate sex-specific dispersal processes and network structures in landscape genetics (Bertrand et al. 2017), and analyze spatial patterns of genetic variation across a species' range (Fortuna et al. 2009). In parallel, pedigree reconstructions have been done to inform on demographic parameters (Creel et al. 2003; Gobush et al. 2009; Lucena-Perez et al. 2018; McFarlane et al. 2018), yet network analyses and genetically derived pedigrees have been used as two separate methodological frameworks. Here, we suggest that the combination of these methods may highlight the interconnectedness between individuals (Escoda et al. 2019; Morrison 2016), differences in reproductive success (McFarlane et al. 2018), and ultimately inform on the demographic structure of a population.

Reconstructing a reasonably complete and accurate familial network from pedigree data is especially relevant for endangered species, providing information on mating patterns and reproductive success (Lucena-Perez et al. 2018; Manlik et al. 2016). However, collecting reliable parentage information for cryptic and elusive species is difficult or directly unfeasible; pedigree information obtained through direct field observations is often limited to females and may consistently overlook cryptic mating (Coltman et al. 1999; Gottelli et al. 2007). Molecular markers, such as microsatellites, have been used to infer parentage and familial relationships in wild populations (Pemberton 2008) and assess individual heterogeneity in survival and reproduction (Bolnick et al. 2011; Hamel et al. 2009; Kendall et al. 2011). Such heterogeneity can be the result of a number of common processes, such as persistent social rank (e.g., Holst et al. 2002; Stockley and Bro-Jørgensen 2011), unequal allocation during parental care (e.g., Johnstone 2004; Manser and Avey 2000), fine-scale spatial habitat heterogeneity (Bollinger and Gavin 2004; Franklin et al. 2000; Manolis et al. 2002), and genetics (Meyers and Bull 2002; Nussey 2005).

Graph theory (Harary 1969) is widely used in ecology to assess functional and structural connectivity (Fall et al. 2007; Urban and Keitt 2001; Wagner and Fortin 2005). Graphs are represented as a network of nodes and edges, where edges imply a level of connection between the nodes (Urban and Keitt 2001). Several network-based measures are commonly used to quantify indirect connections between nodes (e.g., individuals, habitat patches; Table 3.1). Each measure captures a distinct aspect of the network. Alpha centrality is a generalization of eigenvector centrality given to directed graphs; while eigenvector centrality is a measure of the influence of a node in a network, alpha centrality allows nodes to have external sources of influence that does not depend on that node's connection to other nodes (Bonacich and Lloyd 2001). Betweenness centrality indicates how central a node is in a network, based on the number of shortest paths between pairs of nodes that pass through that node (Freeman 1977). Closeness centrality measures how fast information can spread from a given node to all other reachable nodes in a network, and the Latora closeness centrality is used in networks with disconnected components (Latora and Marchiori 2001). Degree centrality represents the number of edges connected to a node; in directed graphs, in-degree counts the number of edges directed toward the node, and out-degree counts the number of edges that leaves the node toward other nodes (Harary 1969). Eccentricity centrality is the maximum distance from a node to any other node, representing the importance of a node within a network, determining the influence of a particular node within a network (Hage and Harary 1995). A priori selection of network measures is important to avoid including several spuriously correlated measures (Webber et al. 2020). Although some network-based centrality measures may overlap, each measure captures a distinct aspect of the network; nodes with high scores for one measure may not necessarily have a high score in other measures.

Metric	Type	Definition
Alpha centrality	Indirect	Alpha centrality of all vertices. A generalization of eigenvector centrality to directed graphs. Alpha centrality indicates the overall connectivity of a node both direct and indirect connections (Bonacich and Lloyd 2001)
Betweenness centrality	Indirect	Quantifies the number of times a node lies along the shortest path between two other nodes in the network (Freeman 1977)
Closeness centrality	Indirect	A centrality measure based on the shortest path length between a node and other nodes in the network. The Latora closeness centrality is used in networks with disconnected components (Latora and Marchiori 2001)
Degree centrality	Direct	The number of edges connected to a node (Harary 1969)
Eccentricity centrality	Indirect	The maximum non-infinite length of a shortest path between n and another node in the network (Hage and Harary 1995)

TABLE 3.1: Node-based measures of connectivity.

Here, we infer population demographic structure by assessing different node-based measures of centrality obtained from a familial pedigree network. First, we use microsatellite data to identify parent–offspring relationships and construct a spatial familial network from all relationships (familial pedigree) of boreal caribou in Saskatchewan, Canada. Then, we create a spatial familial network to identify local area networks with varying distributions of centrality measures, determining whether high centrality measures and edge-to-node ratios at the fine scale correspond to high centrality in the full network. Spatially analyzing familial networks is inherently difficult due to the presence of inferred individuals, whose spatial locations are unknown. By using the centrality measures from the aspatial network in the spatial network of individuals, the network connections to the inferred individuals can be brought into a spatial framework. We also assess the structure and cohesiveness within the full network using edge removal to identify boundaries that run between subgroups (Girvan and Newman 2002; Lusseau and Newman 2004; Newman and Girvan 2004), with a particular focus on parts of the range presenting different levels of anthropogenic disturbance. Our findings allow us to discuss how different measures of network centrality can be used to spatially identify areas of highest fitness levels, dispersal and reproductive skew across the landscape in support of population monitoring and recovery efforts.

3.3 MATERIALS AND METHODS

Boreal caribou are part of the Boreal Caribou designatable unit (COSEWIC 2011), listed as Threatened under the federal Species at Risk Act (Environment Canada 2012) and as Vulnerable in Saskatchewan (SKCDC 2020). In response to the listing, the Government of Saskatchewan initiated a comprehensive monitoring program along with range planning efforts with the goal of achieving a self-sustaining boreal caribou population (Johnson et al. 2020; Saskatchewan Ministry of Environment 2013). The southern range boundary of boreal caribou in Saskatchewan has moved northward over the last century, and habitat in the Boreal Plains has become increasingly fragmented and reduced in area (Arsenault 2003; Rock 1992). Further studies have shown reduced movement of female caribou and low adult survival in the Boreal Plains (Arsenault and Manseau 2011). Boreal caribou in Saskatchewan maintain a natural clinal pattern of genetic structure, with isolation by distance and isolation by resistance shaping spatial patterns of genetic variation (Galpern et al. 2012b; Galpern et al. 2014; Priadka et al. 2019). More information on Saskatchewan's boreal caribou habitat can be found in Appendix 1.

3.3.1 *Fecal pellet collection and genetic analysis*

We used samples from across the boreal caribou range in Saskatchewan, Canada, collected during winters of 2013—2019 (Figure S3.1.1; Table 3.2). This dataset was assembled primarily from systematic noninvasive fecal pellet surveys where aerial transects were systematically flown using a fixed—wing aircraft to locate caribou catering locations (sites where caribou paw to uncover terrestrial lichens). Additional samples (90) from the northern part of the Saskatchewan Boreal Shield were obtained from blood blots or vials collected from individual boreal caribou handled during radio-collaring (McLoughlin 2019; Priadka et al. 2019). All samples were kept frozen at —20°C until DNA extraction was performed.

Sampling Area	Survey Years	Sample Type	Number of Samples Collected	Number of Samples Successfully Scored	Number of Unique Genotypes	Genotyping Success (%)	Dropouts (%)	False Alleles (%)
Flin Flon	2014	Fecal	336	320	104	95.2	0.0077	0.032
La Ronge	2013 & 2015	Fecal	497	403	162	81.1	0.0032	0.0097
SK Boreal Plains West	2016	Fecal	242	233	122	96.3	0	0
Patterson Lake	2018	Fecal	21	19	9	90.5	0.0089	0.036
SK2Central	2017	Fecal	452	371	150	82.1	0	0
SK Shield	2014	Fecal	99	98	98	99	0	0
SK Shield	2019	Blood	551	526	288	95.5	0	0
Total	-	-	2,198	1,970	933	-	-	-

TABLE 3.2: Sampling data

In order to generate individual-specific genetic profiles and familial pedigree networks, DNA samples were amplified at 15 variable microsatellite loci (BM848, BM888, Map2C, Bishop et al. 1994; FCB193, Buchanan and Crawford 1993; NVHRT16, Røed and Midthjell 1998; OHEQ, Jones et al. 2000; RT1, RT5, RT6, RT7, RT9, RT13, RT24, RT27, RT30,Wilson et al. 1997) along with caribou-specific Zfx/Zfy primers for sex identification. DNA was extracted by removing the mucosal layer of cells coating the fecal pellets and followed the extraction protocol outlined in Ball et al. 2007. Microsatellite alleles were scored with the program GeneMarker® (SoftGenetics, State College, PA) and followed a protocol documented in Flasko et al. 2017. Unique individuals were identified using the program ALLELEMATCH (Galpern et al. 2012a). We retained samples that amplified at ≥ 5 loci and re-amplified apparent unique genetic profiles represented by a single sample using two independent scorers to confirm unique individual identities (Hettinga et al. 2012). The rate of allelic dropouts (amplifications of only one of the two alleles for heterozygous individuals, producing false homozygotes; Taberlet et al. 1996) and false alleles (false allele amplifications; Bonin et al. 2004) were calculated using these re-amplification results.

3.3.2 *Defining familial relationships between individuals*

We identified familial relationships of boreal caribou in the study area by reconstructing parent–offspring relationships using COLONY v2.0.6.5 (Jones and Wang 2010). We calculated population allele frequencies using GenAlEx v6.5 (Peakall and Smouse 2012). Input parameters were set to allow for female and male polygynous mating systems without inbreeding avoidance, and the probability of mothers or fathers being present in the sampled dataset was set to 50% in the absence of other prior information. All sampled females were set as possible mothers, and all sampled males were set as possible fathers. COLONY infers the parental genotypes for each individual; inferred parents are genotypes that are not included in the candidate parent samples, either through that individual's genotype not being captured during sampling, or that parent is no longer living, resulting in a family network with more individuals than were sampled. Finally, individual fitness was calculated with the number of offspring each individual produced.

3.3.3 *Modeling the demographic structure of the population*

Identifying parts of the network that are highly connected and those individuals that are less connected to the network can help define the local and global structure of the familial network. We used the r package *CINNA* (Ashtiani et al. 2018) to calculate individual node-based measures of network centrality. Nodes represent individuals, and edges represent parent–offspring relationships, with directionality from parent to offspring. We calculated five direct and indirect node-based measures of centrality for each individual to quantify distinct aspects of centrality: alpha, betweenness, closeness, degree, and eccentricity centrality (Table 3.1). We calculated correlation coefficients between measures to only select statistically independent aspects of centrality. We used principal component analysis (PCA) to collapse variance among any dependent centrality measures, as suggested by Brent 2015, and to identify the most the most important centrality types based on our network structure. We used the r package *FactoMineR* (Lê et al. 2008) to run the PCA, and package *factoextra* (Kassambara and Mundt 2020) to visualize PCA results.

Network analysis

As boreal caribou mating system is polygamous, with individuals having multiple mating partners, a dense and complicated network is created; visually analyzing the aspatial network along with the node-based measures of network centrality allows for easier identification of patterns and trends within the network. We used Cytoscape v3.7.2 (Shannon et al. 2003) for the nonspatial analyses of the local and full familial networks. We created the familial network from the reconstructed parent–offspring relationships identified by COLONY. As each individual has their parents identified by COLONY, as well their offspring, a network can be created from the multigenerational relationships among individuals.

To assess network cohesiveness within the full network, we used the Girvan–Newman algorithm to look for boundaries that run between family groups to find natural divisions within the network by removing edges with the highest betweenness scores (Girvan and Newman 2002; Lusseau and Newman 2004; Newman and Girvan 2004). We used an edge betweenness centrality measure (Freeman 1977) calculated in the NetworkAnalyzer (Assenov et al. 2007) plugin for Cytoscape. Edge betweenness quantifies how

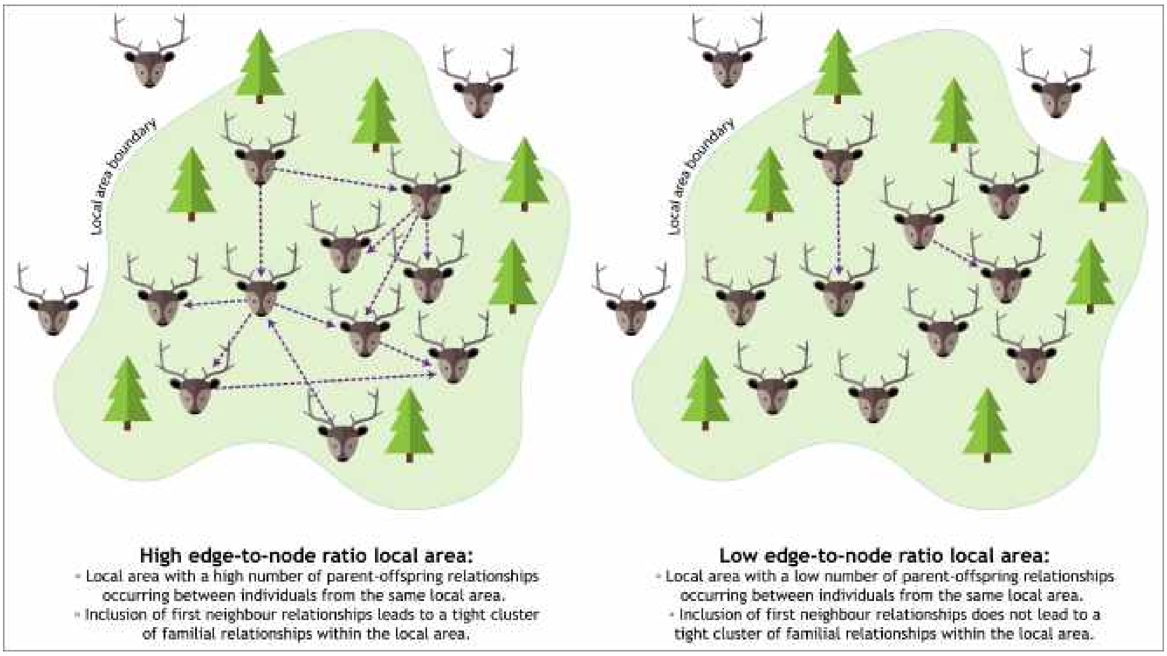

FIGURE 3.1: Edge-to-node ratio definition for local areas. Arrows indicate the direction of parent–offspring relationships. Edge-to-node ratio calculated by dividing number of edges within the local area by the number of individuals within the local area

often an edge is crossed when moving between any pair of individuals in the network; bottlenecks are identified in edges that have higher betweenness, as these edges are passed the most often when connecting individuals. Edges were systematically removed until groups can be identified.

Spatial application of network analysis

We examined how local areas presenting high and low edge-to-node ratios (Figure 3.1) contributed to the full network by comparing centrality measures across local areas within the network. The local areas were of management interest, had a comparable number of individuals and similar geographic sizes. We plotted the spatial locations of all sampled individuals and parent–offspring relationships in ArcGIS (ESRI Inc. 2018) to spatially identify local areas. Local areas were defined based on visual inspection of the sample locations, where areas with a large number of samples identified as local areas, and from these, we selected areas with the highest and lowest ratio of edges (parent-offspring relationships) to nodes (individuals) within the same local area to compare local area networks within the larger spatial familial network. Identifying local areas with a high number of edge-to-node ratios highlights areas within the full network presenting different degrees of familial cohesion, or where parent–offspring remain in the same geographical area. We examined the centrality measures for all sampled individuals within each local area network, as well as for their first neighbors (individuals one degree away from individuals in these areas—as inferred parents do not have spatial locations, this captures inferred individuals) and compared each local area network.

3.4 RESULTS

A total of 2,198 samples were collected (2,099 fecal and 99 blood blot). 1,970 were successfully scored (average success rate of 91.4%), and 933 unique individuals were identified (Table 3.2), representing roughly 20% of the estimated population abundance in Saskatchewan (S. McFarlane, unpublished data). Overall, the average dropout rate was 0.0028% and the average false allele rate was 0.011%. Pedigree reconstruction inferred an additional 310 females and 319 males, for a total familial network of 1,562 individuals. 355 males and 360 females were identified as parents. 1,487 (95.2%) individuals were linked in one network, with the remaining 75 individuals linked in five smaller clusters (Figure S3.2.1). We used the 1,487 individuals identified in the primary network for calculating node-based measures of centrality. The PCA identified alpha, betweenness, and eccentricity centrality as the centrality measures contributing the most to the components, and were all informative measures, capturing different aspects of individual centrality (Figure 3.2; Table 3.3).

	Degree Centrality	Eccentricity Centrality	Betweenness Centrality	Closeness Centrality
Alpha Centrality	-0.216	-0.124	0.152	0.208
Degree Centrality		-0.118	0.371	0.284
Eccentricity Centrality			-0.11	-0.544
Betweenness Centrality				0.234

TABLE 3.3: Correlation coefficients between node-based measures of network connectivity

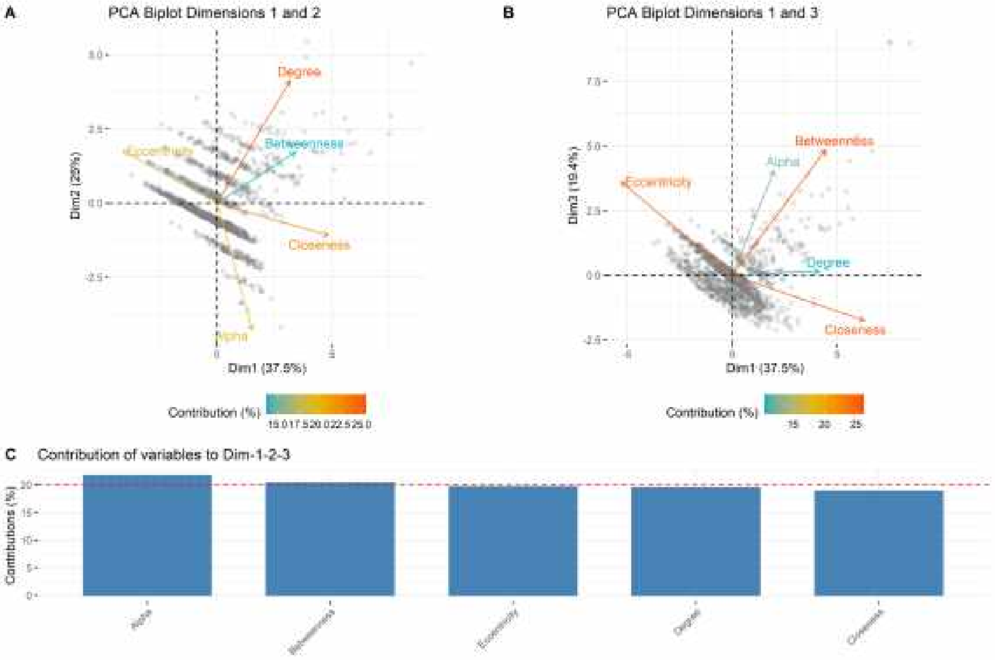

FIGURE 3.2: Principal component analysis (PCA) results for the node-based centrality measures. (a) PCA results for PC1 and PC2; (b) PCA results for PC1 and PC3; (c) contributions of node-based centrality measures in accounting for variability in PCs 1–3. The red dashed line represents the expected average contribution

3.4.1 *Spatial network analysis*

Local area networks

We identified 18 local area networks in order to determine the cohesiveness and centrality of individuals. The local areas with the lowest edge-to-node ratios were all located in the northern part of the Boreal Shield, with the high edge-to-node ratio areas found further south in the western part of the Boreal Plains and southern part of the Boreal Shield (Figure 3.3). We found differences between the distribution of centrality measures between high and low edge-to-node ratio local areas (Figure 3.4). The largest edge-to-node ratio was Canoe Lake in the western Boreal Plains (ratio of 15; Table S3.2.1, Figure S3.2.3). We identified three other local areas with similarly high edge-to-node ratios (Figure S3.2.4, Figure S3.2.5, Figure S3.2.6, Table S3.2.1). The smallest edge-to-node ratio (Central SK Shield) had zero parent–offspring relationships (Table S3.2.1; Figure S3.2.7). We identified two other local areas with similarly low edge-to-node ratios, with very few parent–offspring relationships occurring within these local areas (Figure S3.2.8-S3.2.9, Table S3.2.1), indicating that Boreal Shield individuals are not presenting the same proximity to related individuals as observed in the Boreal Plains. Overall, edge-to-node ratios correlated positively to closeness (Figure S3.2.2a), alpha (Figure S3.2.2c), betweenness (Figure S3.2.2d), and degree centrality (Figure S3.2.2e). However, edge-to-node ratios decreased with eccentricity centrality (Figure S3.2.2b), meaning areas with lower edge-to-node ratios were less central to the overall network.

When bringing in the first neighbors of all individuals within a local area, the high edge-to-node ratio areas formed a tighter cluster of individuals than in the low edge-to-node ratio areas. Including first neighbors in the area with the highest edge-to-node ratio (Canoe Lake) increased the ratio to 1.14 and connected 73.6% of individuals into one cluster (Figure S3.2.3). A large proportion of each high edge-to-node ratio local area became connected into one or two large clusters with the inclusion of first neighbors (Figure S3.2.4-S3.2.6). In comparison, including first neighbors in the lowest edge-to-node ratio local area (Central SK Shield) increased the ratio to 0.86, but did not connect many individuals into one cluster (only 12.8% of individuals; Figure S3.2.7), meaning areas with higher edge-to-node ratios represent tighter clusters of familial relationships.

Full network

Individuals from high edge-to-node ratio local areas were located more centrally within the full family network and clustered with other individuals from the same local area. Individuals from low edge-to-node ratio local areas were dispersed throughout the network and primarily found on the outer edges of the network (Figure 3.5). Although all local areas were of similar geographic size (Figure 3.3), individuals from low edge-to-node ratio local areas were not closely connected to each other in the network. Individuals from these local areas were not found within a few edges of other individuals from the same local area, indicating that individuals encountered in each low edge-to-node ratio local area are from different familial lines,

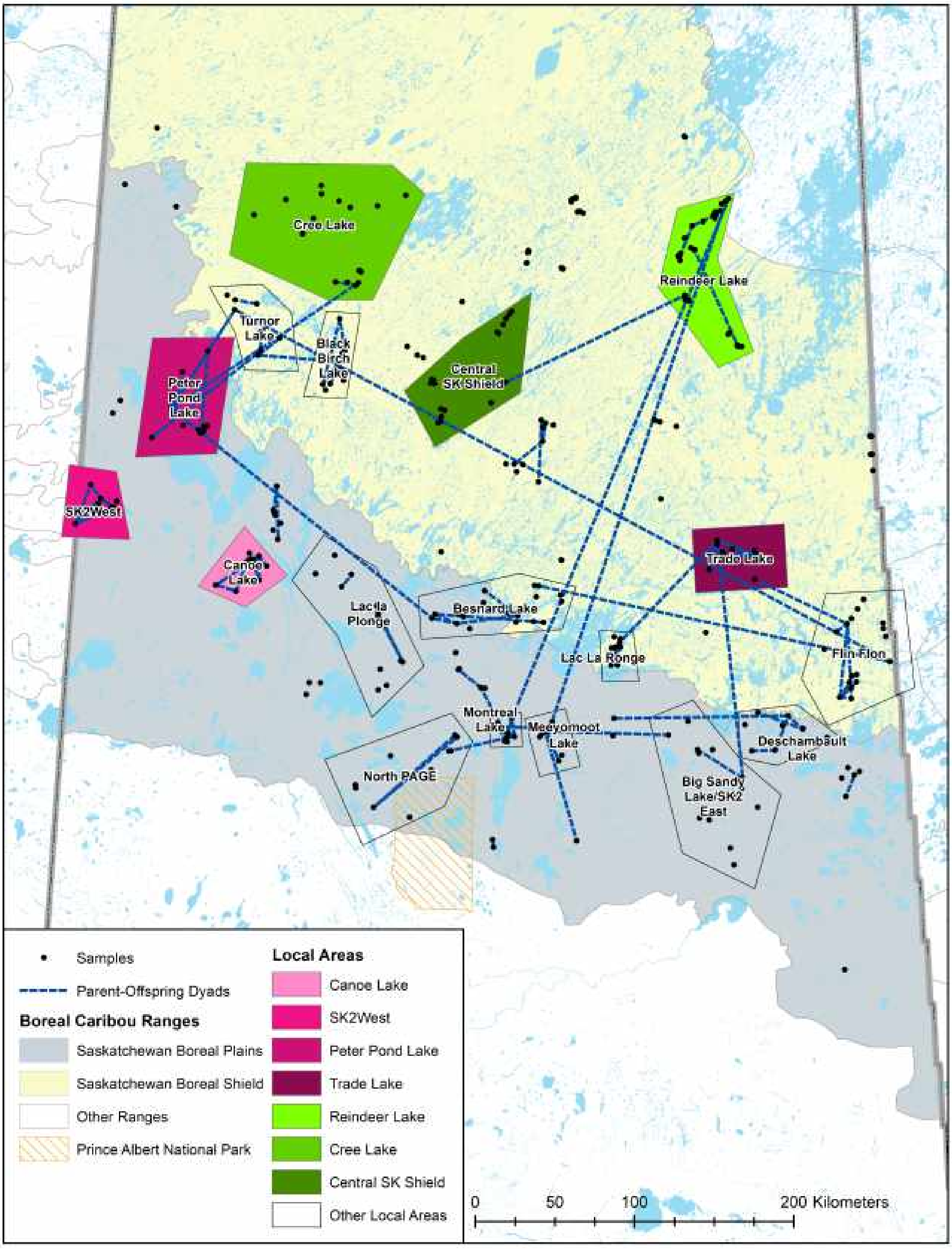

FIGURE 3.3: Locations of local areas. High edge-to-node ratio (pink) and low edge-to-node (green) local areas within the spatial familial network. Lines represent parent–offspring relationships

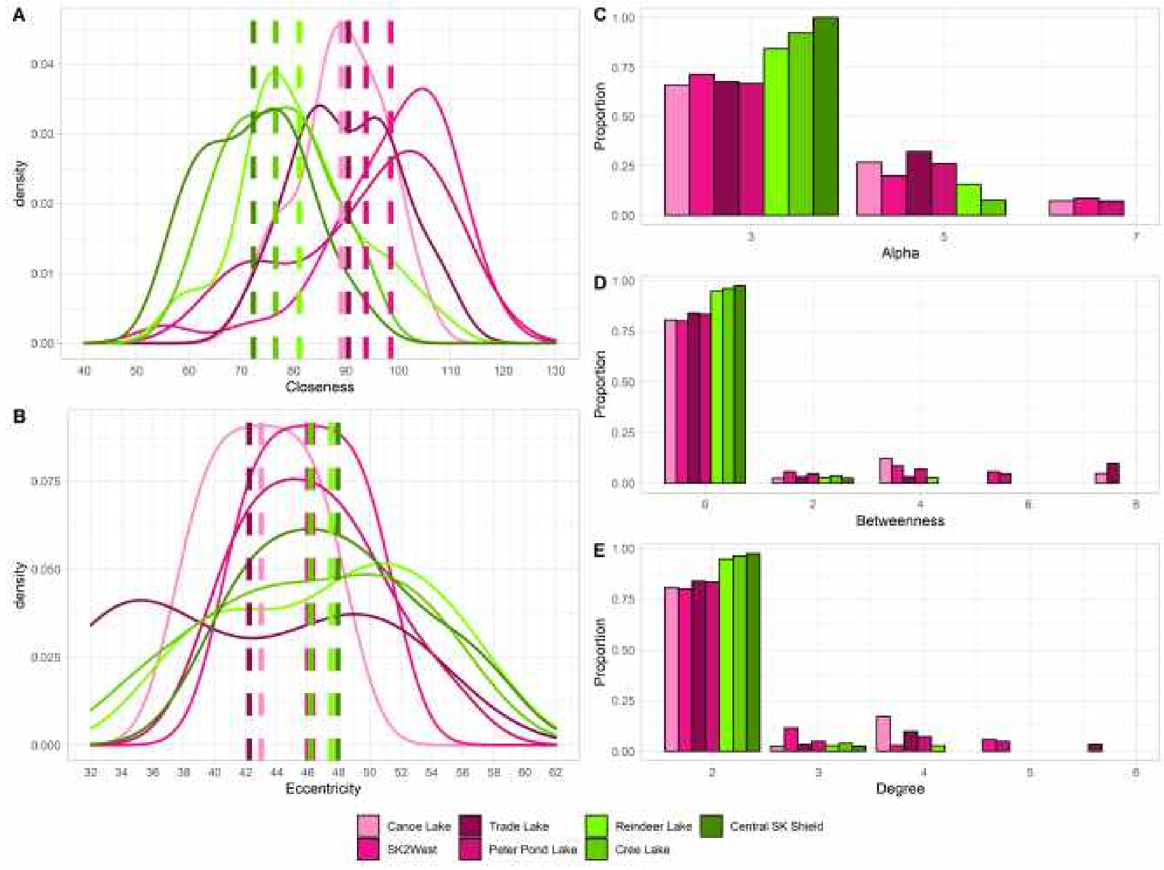

FIGURE 3.4: Distribution of node-based centrality measure values for boreal caribou in high edge-to-node (pink) and low edge-to-node (green) local areas in Saskatchewan: closeness centrality (a), eccentricity centrality (b), alpha centrality (c), betweenness centrality (d), and degree centrality (e). Dashes lines in (a) and (b) represent mean centrality values

or are dispersers that were sampled in that local area (Figure 3.5); as the edges in the familial network represent parent–offspring relationships, these individuals are not highly related to one another and do not form a cohesive group. In contrast, individuals from high edge-to-node local areas were highly connected to one another within the full network, indicating they are closely related, with a high density of familial ties (parent–offspring relationships).

Removal of edges with high betweenness did not alter the overall network structure (Figure S3.2.10). Most edges within the network had low betweenness centrality (score of 1 – 81.5% of edges; Table 3.4). Only 2.97% of edges were removed after sequentially removing edges with the highest edge betweenness score until only edges with an edge betweenness > 4 remained (Table 3.4). While edge removal did not lead to separated subnetworks, the high edge-to-node local areas from the Boreal Plains remained central and clustered within the edge removal network (Figure S3.2.10). Individuals from Trade Lake maintained a high level of clustering, but became separated from the main network, forming a separate subgroup (Figure S3.2.10). Removal of high betweenness edges did not result on individuals from low edge-to-node ratio areas becoming separate subgroups; individuals remained dispersed throughout the network (Figure S3.2.10).

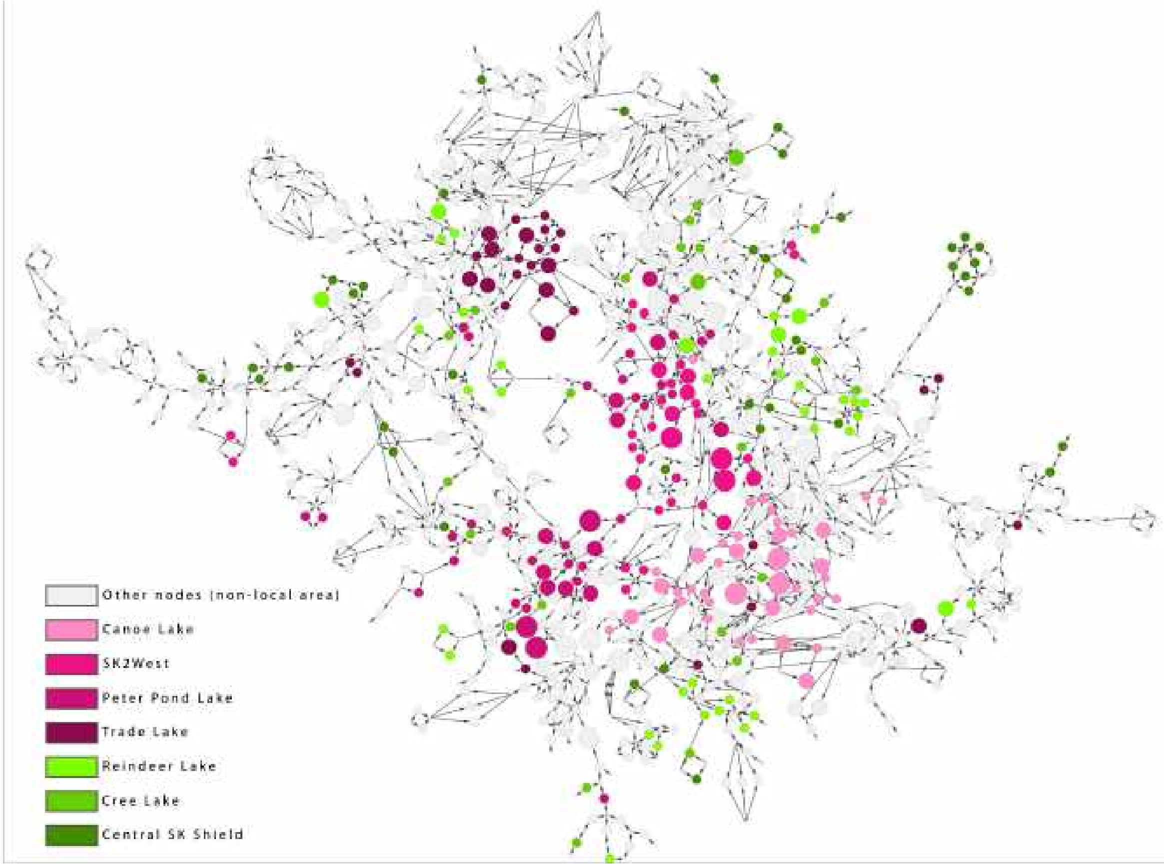

FIGURE 3.5: Boreal caribou familial network in Saskatchewan, Canada. Node size indicates alpha centrality score. Node colour represents both local area and edge-to-node ratios. All pink nodes represent individuals from local areas with high edge-to-node ratios, and green nodes represent individuals from local areas with low edge-to-node ratios

Edge betweenness	Count
20	1
18	1
12	5
9	2
7	5
6	9
5	30
4	26
3	201
2	50
1	1454

TABLE 3.4: Edge betweenness scores for each edge in the full familial network

3.5 DISCUSSION

Network analyses have been used in biological and ecological studies to quantify and explore the structure of populations across numerous taxa (Bertrand et al. 2017; Dyer and Nason 2004; Fortuna et al. 2009), but to our knowledge, this is the first to combine genetically derived pedigree data with network analysis to infer familial structure of wild populations. Network analyses are powerful and flexible methods for investigating the complex networks of interconnections between individuals within and between populations (Wasserman and Faust 1994). With a large interconnected network of 1,562 nodes (individuals) and 1,866 edges (parent–offspring relationships) between individuals, it can be difficult to identify significant differences within the network. By bringing the familial network into a spatial framework and incorporating aspatial node-based centrality measures, we were able to identify groups presenting different levels of cohesion within the network, with some local areas composed of clustered family groups and others presenting lower fitness or being more dispersed over the range. Comparing local area networks allowed us to identify areas of higher and lower fitness and connectivity in the overall boreal caribou familial network.

By identifying local areas within the network, we were able to gain a better understanding of which areas contributed most to the familial network. We found significant differences in centrality measures between local areas in the full familial network, and these variations in individual centrality would have remained hidden if only the full familial network was examined. We used five centrality measures in our network analysis of familial networks (Figure 3.4) and found that alpha, betweenness, and eccentricity centrality were the most informative measures of individual centrality (Figure 3.2). Degree centrality in familial networks represents the parents of an individual (in-degree) and the offspring of an individual (out-degree), giving a direct measure of an individual's reproductive output and fitness levels. It is important to note, however, that inferred individuals in the pedigree will always have an in-degree of 0, as it is not possible to infer the parents of inferred individuals, and in-degree will always be 2 for sampled individuals; in-degree values of 1 are possible when analyzing the subgroups alone. Alpha centrality is an important metric for familial networks, as it indicates those individuals who are connected to individuals who themselves are highly connected, giving an indication of individual fitness, even if that individual does not have a lot of direct connections (offspring). Reproductive output can be highly asymmetrical, with the number of offspring varying between individuals (McFarlane et al. 2018), and alpha centrality can indicate if that individual is part of a large extended family if they are connected to highly connected individuals. McFarlane et al. 2018 found significant differencet between fitness level in mountain caribou and showed that there could be genetic predisposition to higher fitness levels, with evidence of inbreeding avoidance. Maternal social rank influenced reproductive success in reindeer (R. tarandus), with higher fitness females having higher fecundity and earlier offspring date of birth than lower fitness females (Holand et al. 2004). We found that local areas with high edge-to-node ratios had a wider distribution of alpha and degree centrality, indicating that more higher fitness individuals are found in these local areas than in low edge-to-node local areas (Figure 3.3c), and are better connected to other well-connected individuals. Three of the four high edge-to-node ratio local areas we identified are located in the western part of Saskatchewan's Boreal Plains, which has the highest levels of both anthropogenic and fire disturbance in the Boreal Plains (**Figure S1.2**), and the tight family groups we observed in these areas may be a result of decreased dispersal propensity due to high levels of fragmentation between local areas.

Betweenness centrality is another important metric for network analysis, as it captures the interconnectedness of subgroups; individuals with high betweenness interact with individuals who do not interact with one another, therefore making betweenness important for maintaining group cohesion and connecting disparate parts of the network (Brent 2015). Our familial network was not comprised of subgroups, as most individuals (94.2%) had a betweenness centrality of 0, and 95.2% of all sampled individuals formed one large familial network. Even after the removal of edges with the highest edge betweenness, the overall network structure did not change, with most individuals still connected in one main network, with no clear subgroups (Figure S3.2.10). Our study species displays a polygamous mating system, with individuals potentially having multiple partners, producing a complex network of parent–offspring relationships and full- and half-siblings, with high interconnectedness among individuals across the network (Figure S3.2.1). Our highly interconnected network with no evidence of subgroups and low average betweenness centrality is the result of the polygamous mating system and high dispersal ability.

The high eccentricity centrality and low closeness centrality inform on the presence of small numbers of closely related individuals, and generally longer distance dispersing in the Boreal Shield when compared to the Boreal Plains. The Boreal Shield is less fragmented than the Boreal Plains, with significantly less anthropogenic disturbance (Table S3.3.1, Figure S3.3.1). Very few parent–offspring relationships occurred within or between the northern Boreal Shield local areas (Figure 3.3). This suggests that individuals in the Boreal Shield are not central to the familial network and have lower individual fitness, not reproducing many offspring that survive until fall (low degree centrality). Individuals in low edge-to-node local areas are not from the same familial lines and are not highly related to any other individuals in the network. The removal of high betweenness edges led to some individuals becoming disconnected from the full network, but these disconnected individuals were not from one local area, instead located throughout both ecozones, again highlighting the interconnectedness of the familial network.

In most animal network studies, nodes represent observed individuals, with relationships between pairs of individuals (dyads) defined by an association index (the time the pair of individuals spent together), with edges representing observed relationships, forming an interaction network (Morrison 2016; Whitehead and Dufault 1999). For many species, it is not possible or feasible to directly observe rare and elusive species, and therefore, association information cannot be obtained. Pedigree reconstruction can give direct information about dyads between closely related individuals (parent–offspring and full siblings), with these relationships forming the basis of the familial network. In comparison with association networks, in familial networks, only the sampled individuals are known or observed, and the edges between individuals and the unsampled individuals (parents) are inferred by the data analysis (Morrison 2016). Reconstructing a familial network from genetically derived pedigree data gives valuable information about the number of mating partners, the number of offspring, and the structure of the reproductive network of a population (McFarlane et al. 2018; Pemberton 2008). Pedigrees represent historical and evolutionary connections between generations; these relationships have long been recognized as reticulating but are instead commonly presented as simplified trees instead of networks, where reticulations caused by inbreeding are absent (Morrison 2016). Pedigrees represent a network of relationships, and therefore, reconstructed pedigrees inherently contain information that can be used to construct a network. With a wide spectrum of mating systems present in wildlife species (Clutton-Brock 1989), almost all species present pedigree networks, with multiple partners and/or offspring attributed to each individual, therefore creating a complex network of familial relationships (Morrison 2016). Although caribou present varying levels of individual fitness (McFarlane et al. 2018) and their distribution is spatially clustered across the range, our network does not appear to be vulnerable to sudden population crashes resulting from changes in population structure, isolation, and inbreeding. Our network was highly connected as a result of the polygamous mating system of caribou and ability for long range dispersal. Although family groups can be identified within the network, presenting varied levels of dispersal, fitness, and cohesion, the removal of edges with high betweenness did not change the overall network structure or lead to disconnected groups. Our individual-based familial network provides more precise information on the composition of different parts of the caribou range in Saskatchewan and their contribution to the overall population. The local areas were in some cases composed of isolated individuals presenting low fitness levels, individuals in smaller or larger groups presenting high fitness levels.

Network analyses are powerful methods to assist in wildlife conservation (Bertrand et al. 2017; Dyer and Nason 2004; Fortuna et al. 2009), but most wild populations cannot be directly observed, and demographic networks cannot be constructed. By constructing a familial network based on genetically derived parent–offspring relationships, we calculated informative measures to draw a much finer picture of their individual fitness levels, pattern of demographic structure, and relative contribution of local areas to the larger population. The spatial application of the familial network allowed us to identify areas with individuals of higher fitness levels, short- and long-distance dispersal ability across the range in support of population monitoring and recovery efforts.

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APPENDIX 3.1: CORRELATION AND PRINCIPAL COMPONENT ANALYSIS

Degree and betweenness were moderately positively correlated ($r = 0.371$, Table 3.4), and closeness and eccentricity were moderately negatively correlated ($r = -0.544$, Table 3.4). As no metrics were strongly correlated to one another, we retained all metrics for PCA analysis. Principal components 1-3 explained 82% of the variation and had eigenvalues ≥ 1 (Figure S1.2), with the variance explained dropping significantly after principal component 3 (Figure S1.2). Alpha, betweenness and eccentricity centrality were the most important metrics, explaining the most variation (21.7%, 20.4%, and 19.6%, respectively; S3.1.1). There was low variance between individuals, with weak differences in betweenness (94.2% of nodes had a betweenness centrality of 0).

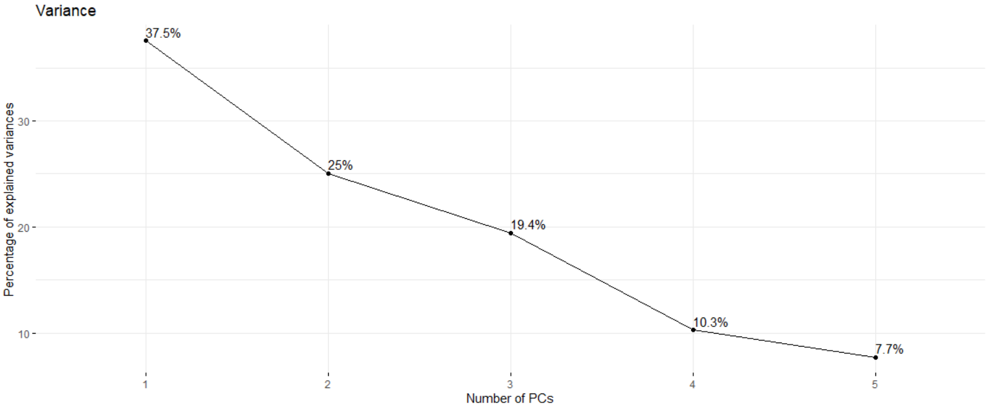

Figure S3.1.1: Scree plot showing the amount of variation retained by each principal component. X-axis represents the number of principal components (PCs) in the principal component analysis, and Y-axis is the amount of variation explained by each principal component (PC)

APPENDIX 3.2: SUBNETWORKS

Area	Ecozone	Nodes	Edges	Average Alpha	Average Betweenness	Average Closeness	Average Eccentricity	Average Degree
Canoe Lake	Plains	41	15	3.83	0.93	88.07	43.88	2.37
SK2West	Plains	35	12	3.74	0.80	96.30	45.91	2.34
Trade Lake	Shield	31	9	3.65	0.97	89.30	39.77	2.35
Peter Pond Lake	Plains	42	12	3.81	0.67	92.56	45.55	2.33
Montreal Lake	Plains	50	13	3.72	0.96	83.56	43.20	2.32
Meeyomoot Lake	Plains	44	10	3.59	0.86	91.13	48.45	2.30
Besnard Lake	Plains/Shield	55	12	3.73	0.69	81.99	46.56	2.24
Deschambault Lake	Plains	35	6	3.40	0.51	79.05	44.83	2.20
Lac La Ronge	Plains	35	6	3.46	0.34	83.43	47.97	2.17
North PAGE	Plains	25	4	3.40	0.32	78.81	43.92	2.16
Flin Flon	Shield	65	10	3.34	0.89	78.57	49.95	2.20
Turnor Lake	Shield	39	6	3.46	0.62	88.45	45.77	2.23
Lac la Plonge	Plains	45	5	3.22	0.22	77.28	46.60	2.11
Big Sandy Lake/SK2 East	Plains	41	4	3.39	0.20	85.78	43.59	2.10
Black Birch Lake	Shield	50	4	3.24	0.24	82.20	44.78	2.08
Reindeer Lake	Shield	38	3	3.32	0.16	80.36	48.71	2.08
Cree Lake	Shield	26	1	3.15	0.08	76.51	47.15	2.04
Central SK Shield	Shield	40	0	3.00	0.05	71.58	48.40	2.02

Table S3.2.1: Ratio of edges (parent-offspring relationships) and nodes (individuals) within areas of the spatial pedigree network in Saskatchewan

Metric	p-value
Alpha centrality	1.12e-07
Betweenness centrality	2.34e-05
Closeness centrality	1.88e-21
Degree centrality	3.70e-05
Eccentricity centrality	3.27e-09

Table S3.2.2: Significance values from two-sided t-tests for centrality metrics between high and low edge-to-node ratio subnetworks

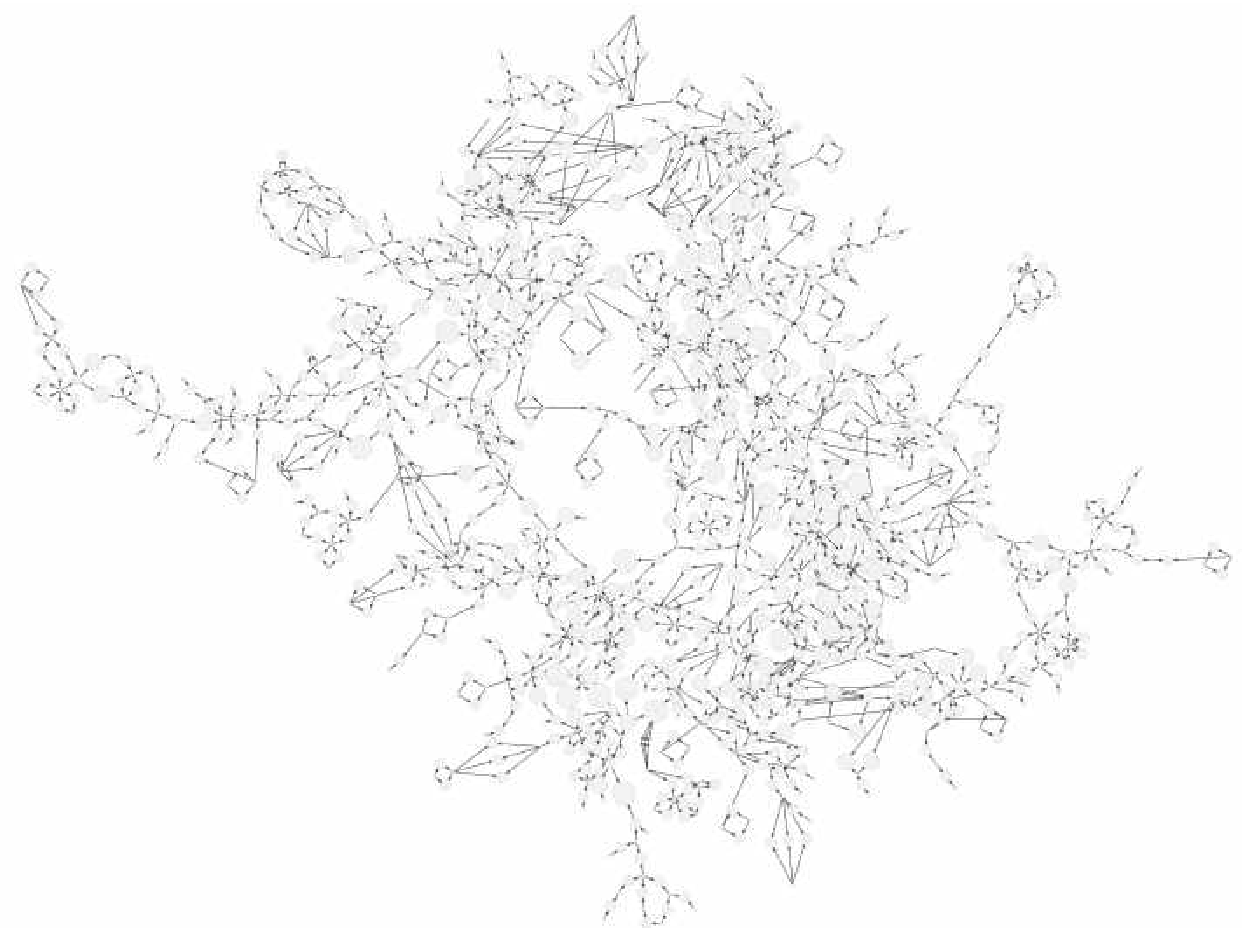

FIGURE S3.2.1: Boreal caribou full familial network in Saskatchewan, Canada. Node size indicates alpha centrality score. Edges represent parent-offspring relationships

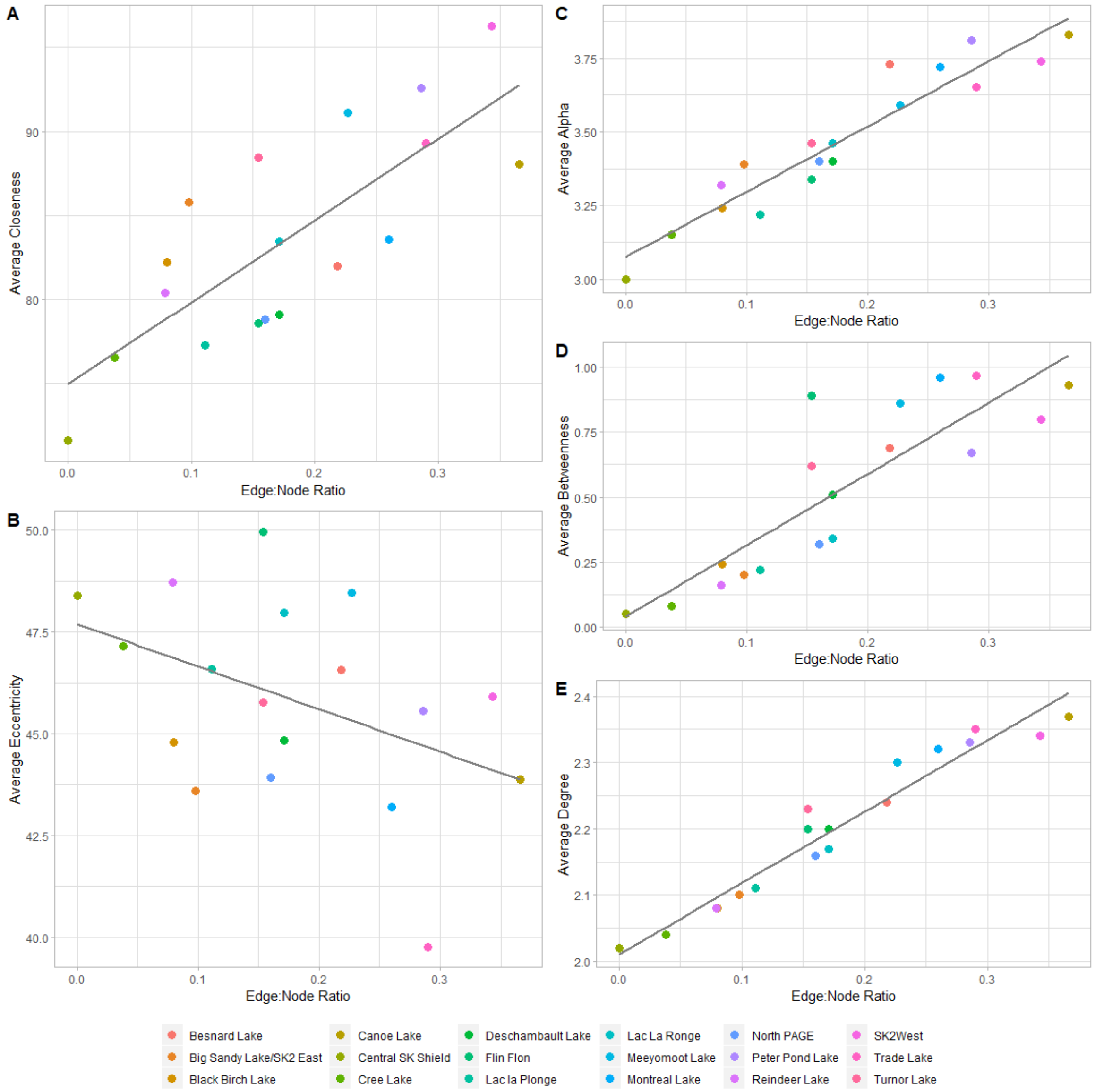

FIGURE S3.2.2: Average centrality measures with different edge:node ratios of subnetworks for the five centrality measures - closeness centrality (A), eccentricity centrality (B), alpha centrality (C), betweenness centrality (D), and degree centrality (E). Colours represent different local areas

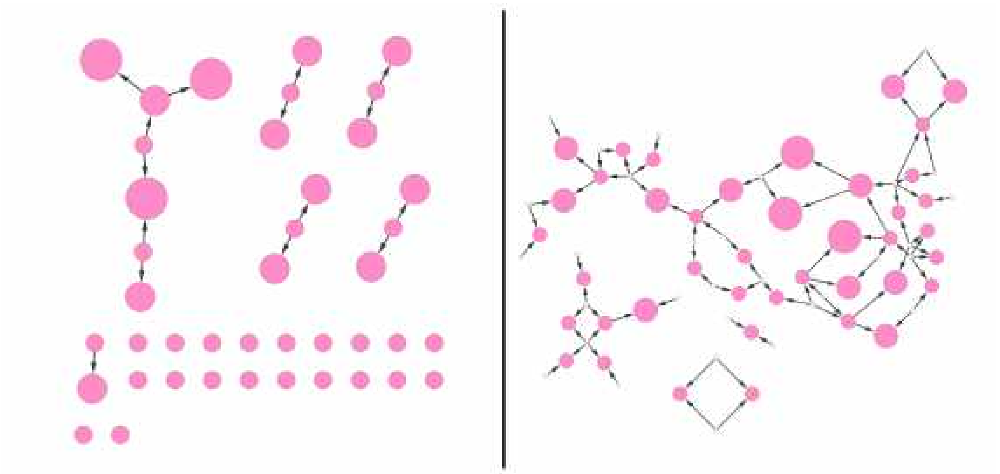

FIGURE S3.2.3: Canoe Lake high edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Pink nodes represent Canoe Lake individuals

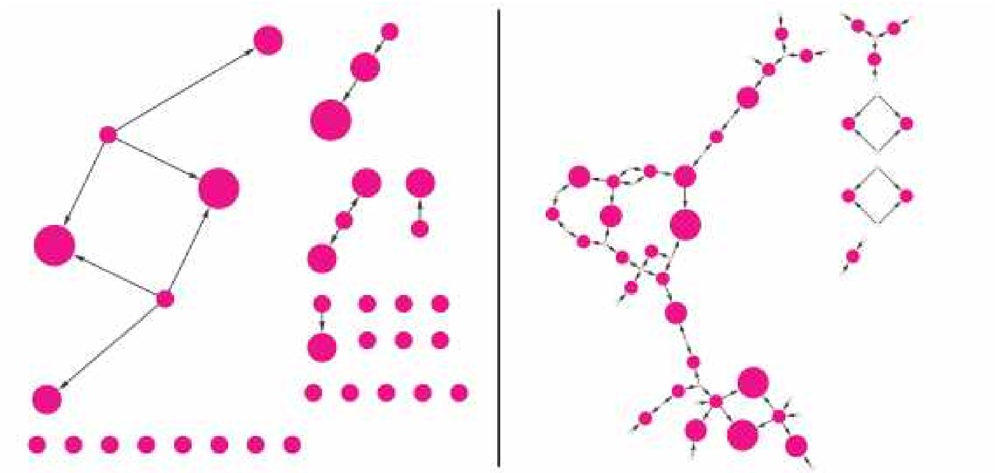

FIGURE S3.2.4: SK2West high edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Pink nodes represent SK2West individuals

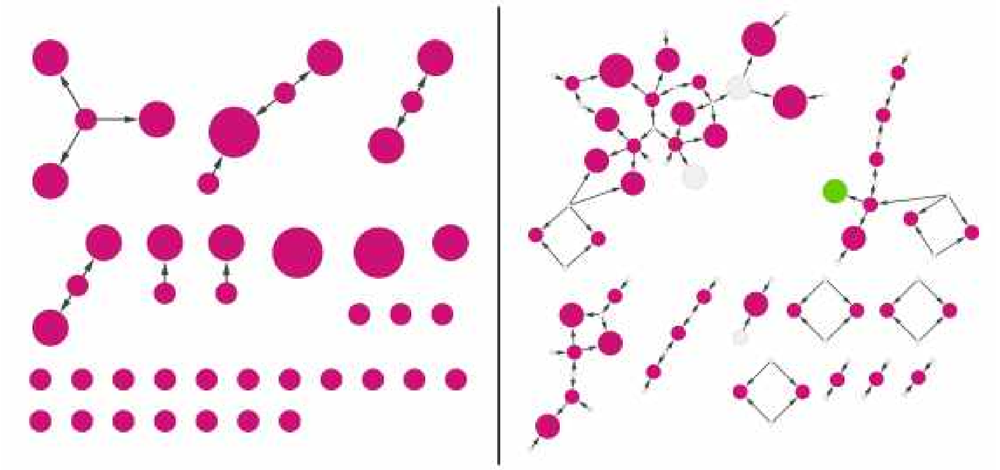

FIGURE S3.2.5: Peter Pond Lake high edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Pink nodes represent Peter Pond Lake individuals, green node represents Cree Lake first neighbour

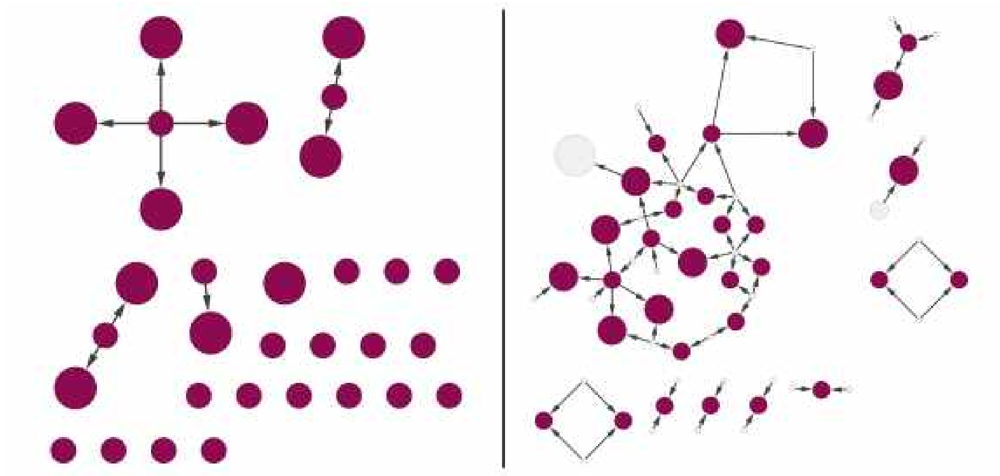

FIGURE S3.2.6: Trade Lake high edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Pink nodes represent Canoe Lake individuals

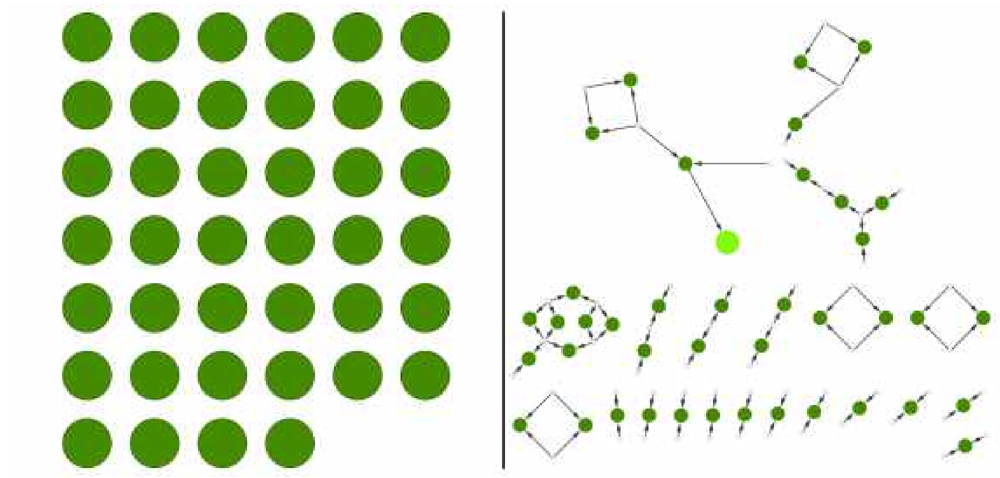

FIGURE S3.2.7: Central SK Shield low edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Dark green nodes represent central SK Shield individuals, light green node represents Reindeer Lake first neighbour

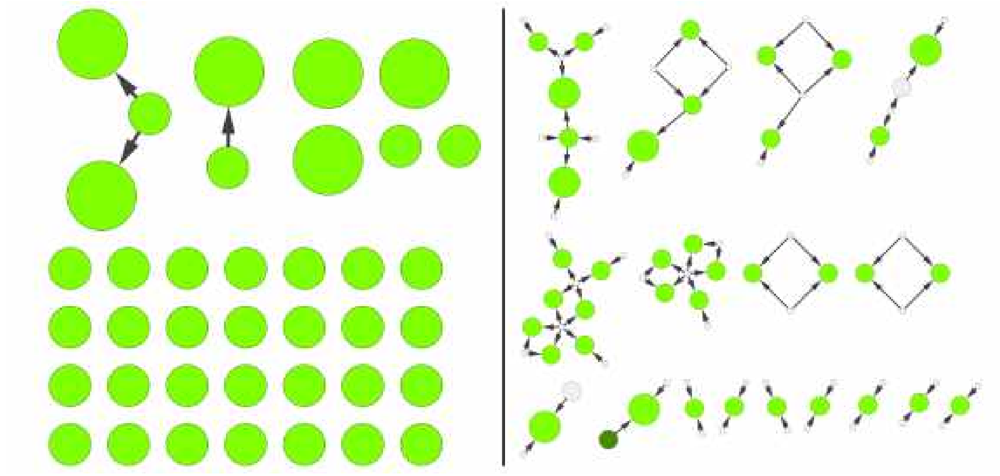

FIGURE S3.2.8: Reindeer Lake low edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Light green nodes represent Reindeer Lake individuals, dark green node represents Central SK Shield first neighbour

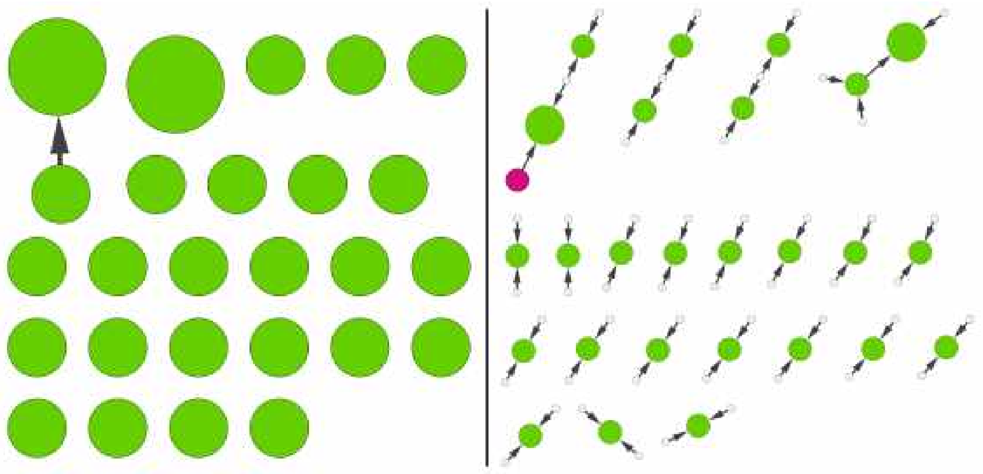

FIGURE S3.2.9: Cree Lake low edge-to-node ratio local area network of sampled individuals (left) and with first neighbours (right). Green nodes represent Canoe Lake individuals, white nodes represent inferred individuals, pink coloured node represents Peter Pond Lake first neighbour

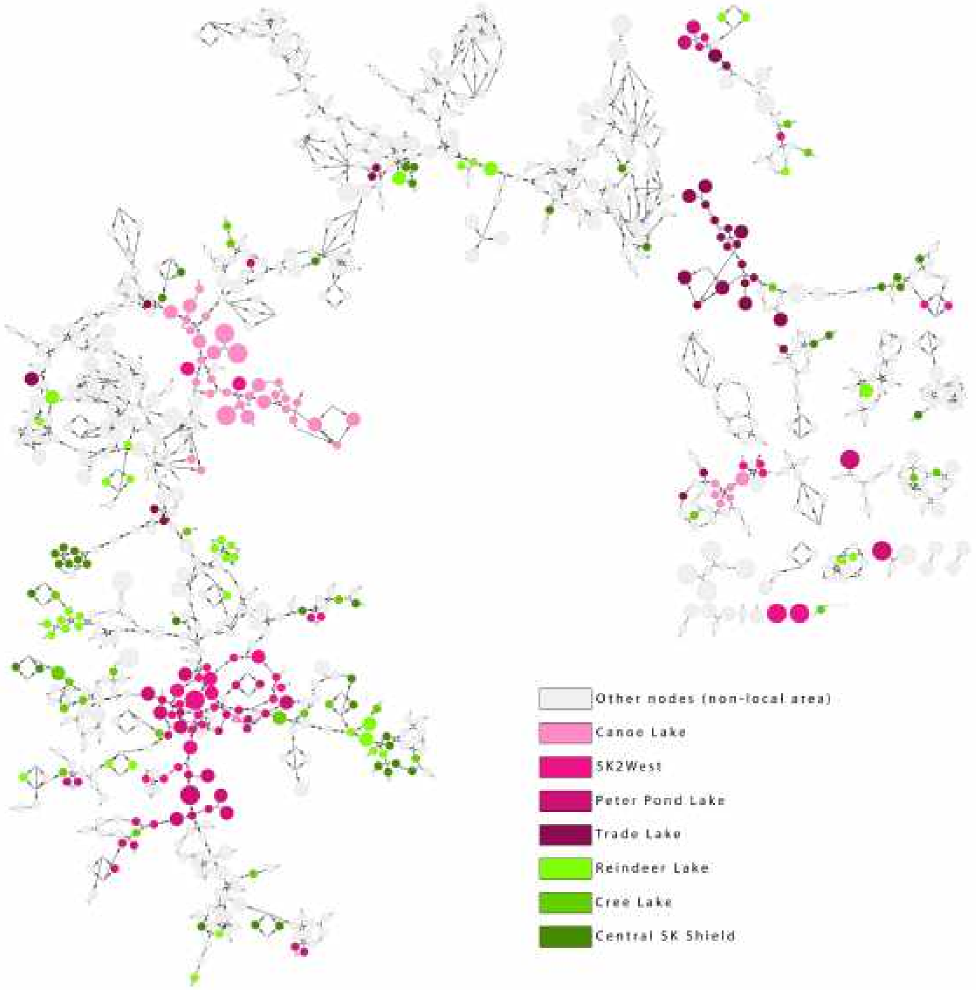

FIGURE S3.2.10: Boreal caribou familial network in Saskatchewan, Canada after removal of edges with edge betweenness > 4. Edge size indicates edge betweenness score, and node size indicates alpha centrality score. Node colour represents both local area and edge-to-node ratios. All pink nodes represent individuals from local areas with high edge-to-node ratios (Canoe Lake, SK2West, Peter Pond Lake, Trade Lake), and green nodes represent individuals from local areas with low edge-to-node ratios (Reindeer Lake, Cree Lake, Central SK Shield)

APPENDIX 3.3: ECOZONE INFORMATION

Saskatchewan's Boreal Plains ecozone is characterized by low rolling forested hills and plains, interspersed with fens, bogs, marshes, and lakes (Saskatchewan Ministry of Environment 2019b). The central Boreal Plains is an important area for boreal caribou as it provides a large proportion of high-value upland (pine-lichen forest) and lowland (peat land) caribou habitat (Saskatchewan Ministry of Environment 2019b). In this area, there is a history of industrial forest management activities, which results in a network of permanent and non-permanent roads and trails (Saskatchewan Ministry of Environment 2019b). Saskatchewan's Boreal Shield ecozone is characterized by conifer peat land complexes, muskegs and bogs, and upland moderate to dense mature conifer forests with abundance lichens (Environment Canada 2012). Saskatchewan's Boreal Shield represents a unique situation with very low anthropogenic disturbance and a high fire cycle, representing a relatively intact ecosystem little modified by humans, where natural ecological processes dominate (Environment Canada 2012). Boreal caribou have disappeared from the southern edge of the Boreal Plains due to agricultural development and habitat loss linked to anthropogenic activities and are at a higher risk of loss than boreal caribou in the Boreal Shield (Saskatchewan Ministry of Environment 2013). The proportion of area covered by anthropogenic disturbances is higher in the Boreal Plains than in the Boreal Shield (20.4% vs. 3.2%, respectively; Table tab:tableS3.3.1), which may represent a higher source of impact on Boreal Plains' caribou population. However, a highly active fire cycle has affected 56.5% of the Boreal Shield in the last 40 years (Table S3.3.1), putting Boreal Shield caribou at low to medium risk in this part of their range (Saskatchewan Ministry of Environment 2013).

		Fire		Anthropogenic		Total Disturbed	
	Area (km^2)	km^2	%	km^2	%	km^2	%
Boreal Plains	103,696	30,411	29.3%	21,122	20.4%	47,903	46.2%
Boreal Shield	175,511	99,187	56.5%	5,603	3.2%	107,710	61.4%

TABLE S3.3.1: Disturbance levels in the Saskatchewan Boreal Plains and Boreal Shield

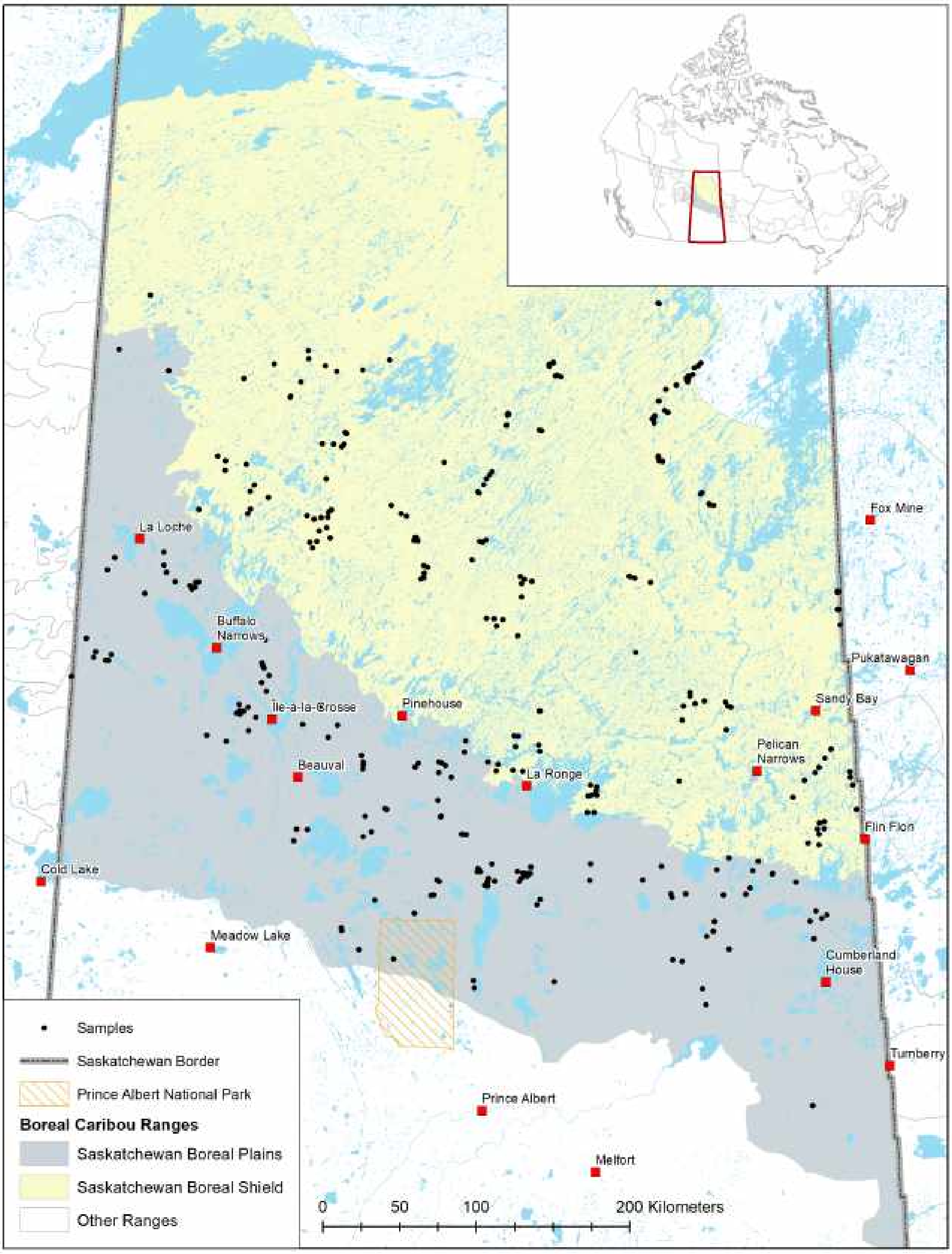

FIGURE S3.3.1: Study area and sampling surveys of boreal caribou in Saskatchewan, Canada

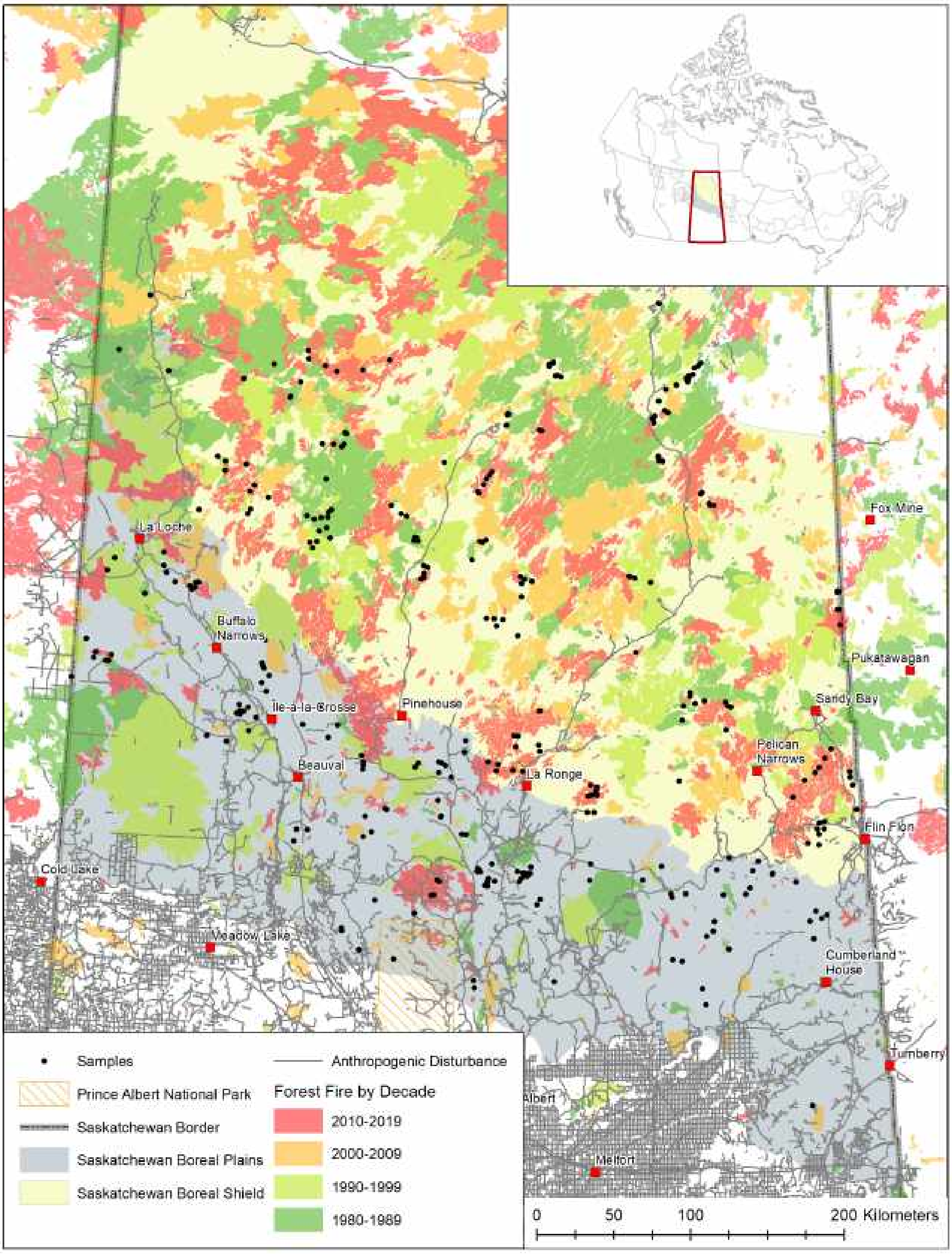

FIGURE S3.3.2: Anthropogenic and fire disturbance in Saskatchewan, Canada

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4

Sex-specific differences in familial networks, dispersal and reproductive success are driven by heterogeneity in density

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MM and GP conceived and designed the study. SM implemented the analysis and wrote the manuscript with help from MM and TJ. PW coordinated DNA extraction and analysis. DP coordinated and analyzed the spatial density covariate data. GM coordinated hormone extraction and analysis. All authors contributed to subsequent drafts and gave final approval for publication.

4.1 ABSTRACT

Density is an important demographic parameter that is commonly overlooked in studies of wild populations. Variation in habitat quality from disturbance can strongly influence a species' distribution, affecting population density by altering resource abundance and habitat structure, and influencing connectivity and spatial population dynamics. Here, we examined a range of spatially explicit demographic parameters in a wild population of a cryptic, large ungulate, boreal woodland caribou (*Rangifer tarandus caribou*). We determined the spatial density of caribou across the Boreal Plains of Saskatchewan, Canada, and then assessed how familial networks, dispersal distances, and reproductive success were affected by density. Using non-invasive genetic sampling, we used a spatial capture-recapture analytical framework with covariates to estimate spatial density of boreal woodland caribou across a 108,806 km^2 study area. We then reconstructed parent-offspring relationships to create a familial network and determined whether spatial density influenced sex-specific network centrality, dispersal distance, individual reproductive success, and the pregnancy status of females. We showed that caribou density greatly varied across the Boreal Plains and was primarily affected by landscape composition and fragmentation. Dispersal distances varied with density, with offspring moving shorter distances when parents were found in higher density areas. Density also had a significant effect on both male and female reproductive success with males showing positive density-dependence, and females showing negative density dependence. No differences were found in pregnancy rates of females occurring in high- and low-density areas. Females also presented lower closeness centrality and degree centrality in familial networks at higher densities meaning offspring are not dispersing as far away from their parents at high densities. The reconstruction of familial networks using genetic data showed that demographic parameters of both males and females were density dependent but, although high density areas do reflect good quality caribou habitat, we observed decreased dispersal rates and lower female recruitment rates. This highlights the importance of considering population parameters below the population level to inform on recovery actions needed for the species conservation.

4.2 INTRODUCTION

Density can affect many demographic parameters of wild populations, including dispersal (Travis et al. 1999; Matthysen 2005), kinship (De Bona et al. 2019), and reproductive success (e.g. McLoughlin et al. 2006; Hamel et al. 2009). In most species, density is heterogeneous across the landscape, with density patterns resulting from an individual's selective use of habitat resources to maximize fitness (Morris 2003), and from habitat disturbance (Tischendorf et al. 2005). Variation in habitat quality from disturbance can strongly influence a species' distribution, affecting population density by altering resource abundance and habitat structure, and influencing connectivity and spatial population dynamics (Łomnicki 1980; Smith et al. 2016). Habitat fragmentation can have negative or positive effects on population density in remnant habitat patches, shifting the balance between emigration and immigration (Tischendorf et al. 2005; Bowers and Matter 1997).

Density-dependence occurs when a population parameter (most often population dynamics such as population growth rate, vital rates, and reproduction) varies as a result of density (Hixon and Johnson 2009). Density-dependent demographic parameters have been observed in numerous large mammal species, with reproduction and growth rate decreasing with increased density (Fowler 1987). In cases where density influences mean vital rates, absolute and relative reproductive success of individuals in the population can change with population size or density, with absolute reproductive success and population growth rate decreasing with increasing population size (Sæther and Engen 2015). For example, McLoughlin et al. 2006 found that lifetime reproductive success of female red deer (*Cervus elaphus*) was inversely associated with local density, and reproductive benefits from selecting good-quality habitat decreased as density increased.

Here, we suggest applying well-studied concepts of resource selection (Manly et al. 2002; Boyce and McDonald 1999) as they relate to density-dependent demographic responses within spatially structured populations to further understand the impact of landscape fragmentation on population dynamics. Whereas a large number of studies have documented strong animal responses to landscape attributes and anthropogenic disturbances (e.g. Lendrum et al. 2012; Wasser et al. 2011; Nelson et al. 2012), fewer studies have examined the demographic response within remaining habitat patches (Merrick and Koprowski 2017; Sinnott et al. 2021) and the potential for these responses to mitigate or accelerate the impact of landscape change at the population level.

Dispersal, the movement of individuals through space away from their natal source, plays a critical role in the dynamics of spatially structured populations (Nathan et al. 2012; Ronce 2007). There is growing evidence that dispersal is a highly heterogeneous process (Bowler and Benton 2005; Fronhofer et al. 2018; Ducros et al. 2020), dependent on multiple factors such as resource availability (Aguillon and Duckworth 2015), predation risk (Bestion et al. 2014), or density (Matthysen 2005; Bitume et al. 2013). Density-dependent dispersal is common across many taxa and can be positive or negative depending on the mechanism driving dispersal (Matthysen 2005). Positive density-dependent dispersal can be a result of local competition increasing the likelihood of individuals dispersing to gain better fitness prospects by leaving high-density areas (Matthysen 2005; Travis et al. 1999), while negative density-dependent dispersal can result from high densities reducing dispersal probability due to increased likelihood of aggressive encounters (Matthysen 2005). Most studies of density-dependent dispersal predict that high patch density should result in increased dispersal (positive density-dependence; Travis et al. 1999; Poethke and Hovestadt 2002; Leturque and Rousset 2003), with few studies predicting that high patch density will result in decreased dispersal rates (negative density-dependence).

Dispersal distance is a fundamental characteristic of the dispersal process and is extensively used to understand how dispersal shapes post-dispersal population dynamics (Lepais et al. 2010; Serrano and Tella 2011; Nathan et al. 2012; Norman et al. 2019). Dispersal distance may be constrained by the costs of dispersal, including increased predation risk, decreased home range familiarity, and reduced opportunity for kin cooperation (Pusey 1987), while natural and anthropogenic landscape barriers can affect dispersal ability and success (Cousseau et al. 2020). In polygynous mammals, males are typically the dispersing sex, while females tend to be philopatric (Greenwood 1980; Loe et al. 2009; Fattebert et al. 2015). Females invest more in individual offspring than males in the absence of male parental care, and benefit from knowledge of local resources, leading to females breeding within or next to their natal range, gaining from inclusive fitness and forming familial clusters (Lambin et al. 2001). In contrast, male-biased dispersal can result from mate competition (inferior males disperse to avoid competition for mates with conspecific males; Dobson 1982), resource competition (individuals disperse to avoid competition for limiting resources such as food and space; Swenson et al. 1998) or inbreeding avoidance (males disperse to avoid breeding with related females; Gandon and Michalakis 2001).

Population density in patchy landscapes can be affected by several mechanisms, including boundary-crossing probabilities, dispersal, and mortality (Tischendorf et al. 2005). Increased fragmentation may reduce population density by reducing the availability of suitable habitat, increasing the time an individual spends in unsuitable habitat and may be subject to higher mortality, resulting in reduced population density (Tischendorf et al. 2005). Increased habitat fragmentation may also lead to increases in local population density through remnant habitat patches providing refuge from disturbance (Lancaster 2000; Keppel et al. 2011). Knowledge of the heterogeneity in population density and the drivers affecting density patterns of a species is critical for understanding how density influences population demography (Matthysen 2005; Rodrigues and Johnstone 2014). Estimating spatially-explicit density by incorporating landscape variables directly into density modeling can identify habitat patches that can support higher densities. Here, we used spatial capture-recapture (SCR) to estimate density of boreal woodland caribou (*Rangifer tarandus caribou*, hereafter referred to as boreal caribou) based on several landscape variables, such as availability of good-quality habitat, poor-quality habitat, and distance to anthropogenic disturbances. We hypothesized that caribou exhibit density dependence, with the spatial variation in caribou density leading to significant heterogeneity in demographic responses, negatively affecting reproductive success and positively impacting dispersal.

Boreal caribou in Saskatchewan provide an ideal system for testing demographic density response hypotheses, as they exhibit relatively small-scale movements, and occur throughout the province with no discrete populations (Galpern et al. 2012; Priadka et al. 2019; Ball et al. 2010; McFarlane et al. 2021). They select large tracks of mature to old-growth coniferous forests that provide abundance lichens, or wetlands mixed with upland areas, and avoid early-stage, successional deciduous forests (Stuart-Smith et al. 1997; Environment Canada 2012). Habitat alteration through anthropogenic disturbance generates indirect habitat loss for boreal caribou, through the conversion of old-growth coniferous forests to early-stage deciduous forests (Polfus et al. 2011; Rudolph et al. 2017). Roads and linear features facilitate predator movement, also impacting calf and adult survival (Dussault et al.

2012; Leblond et al. 2013). Dispersal is thought to be a gradual process, where the natal area is not totally abandoned as individuals disperse (Albon et al. 1992; Thomas and Gray 2002).

We used non-invasive genetic sampling and SCR modelling to generate a density layer. We fitted a suite of SCR models and compared homogeneous density models to models with habitat covariates of key features of anthropogenic disturbance such as roads, trails, power lines, seismic lines, and railways (Figure 4.1). We used the habitat-density relationship from the top-ranked SCR model to create a density surface for the Saskatchewan's Boreal Plains to test the demographic predictions. We constructed parent-offspring spatial familial networks (McFarlane et al. 2021) to gather demographic parameters on individual caribou including reproductive success and dispersal. Understanding and accounting for individual heterogeneity in reproductive success is critical for inferences about ecological patterns and processes; not considering the inherent reproductive differences between individuals can lead to incorrect interpretations (Weladji et al. 2008; Badger et al. 2020). Genetic parentage data can provide detailed information on individual-based reproductive success and dispersal of wild populations, allowing for a wider look at reproductive measures, and can include measures of reproductive success and dispersal for individuals who are not directly sampled (McFarlane et al. 2018). We also measured pregnancy rate from each sampled female to assess whether the lower reproductive success predicted in higher density areas corresponds to lower pregnancy rates, suggesting constraints on mating opportunities instead of lower birth or high mortality rates.

We also derived additional metrics from the familial networks to quantify variation in the contribution of individual caribou to the population. We have previously shown spatial variation in individual measures of centrality across Saskatchewan, with animals in the southern part of the province presenting higher edge-to-node ratio, suggesting higher number of parent-offspring relationships in those areas, along with connections to other highly connected individuals (McFarlane et al. 2021). We extend these analyses to examine the relationship between familial network metrics and density. We looked at degree centrality, alpha centrality, and closeness centrality (McFarlane et al. 2021). Degree centrality represents the number of edges connected to a node. Since the familial networks represent parent-offspring relationships, the network is directed and the metric reflects the out-degree counts or the number of edges that leaves the node toward other nodes (Harary 1969). We expect this measure to be negatively correlated with density for males due to high expected reproductive skew in males. Alpha centrality is a generalization of eigenvector centrality given to directed graphs; while eigenvector centrality is a measure of the influence of a node in a network, alpha centrality indicates that overall connectivity of a node, including both direct and indirect connections (Bonacich and Lloyd 2001). This metric reflects the reproductive success of both an individual and its descendants. Based on previous results (McFarlane et al. 2018), we expect this measure to also be correlated with an individual's reproductive success and to be negatively correlated with density for both sexes. Finally, we looked at closeness centrality which reflects the sum of the shortest path between a given node and all other nodes; individuals with higher closeness centrality being from larger families, capturing differences in dispersal and breeding with other familial groups (McFarlane et al. 2021). In association with a predicted positive relationship between dispersal and density, we expect higher closeness centrality values with higher densities with offspring dispersing further away from their parents at high densities. These predictions have seldom been tested in wild populations of long-lived mammal species, but the increasing availability of genetic data and advanced analytical methods are providing a unique opportunity to uncover fine scale population demographic responses to landscape conditions.

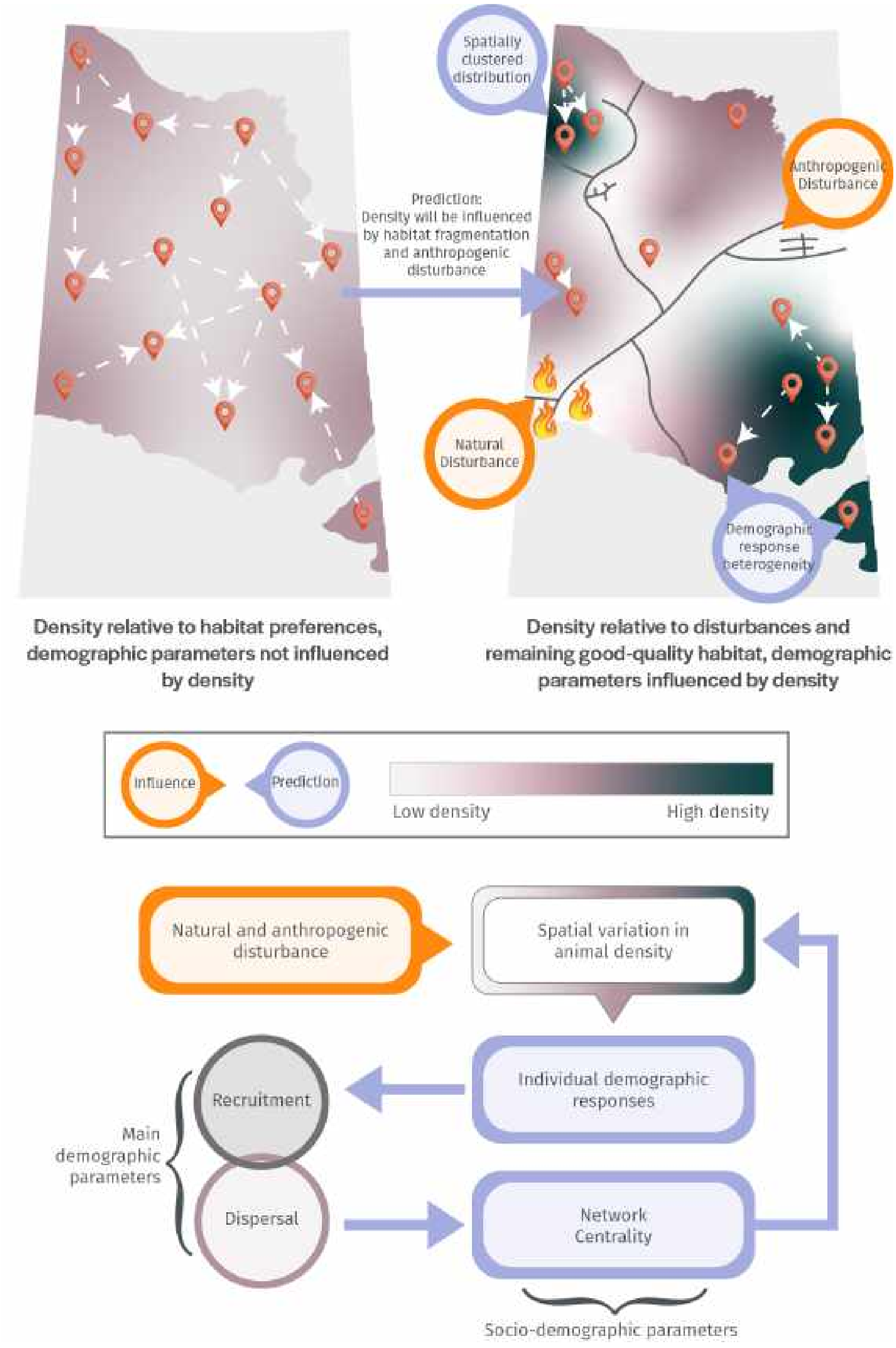

FIGURE 4.1: The effects of variable spatial density on demographic parameters

4.3 MATERIALS AND METHODS

4.3.1 *Study Area*

Data were collected from boreal caribou across the boreal plains ecozone in Saskatchewan, Canada (Figure S4.1.1). The boreal plains are characterized by mixed-wood forests, lakes, and large areas of low-lying peatlands (Saskatchewan Ministry of Environment 2019). Boreal caribou are part of the Boreal Caribou designatable unit (DU6) (COSEWIC 2011) and are listed as Threatened under the federal *Species at Risk Act* (SARA) (Canada 2012) and Vulnerable in Saskatchewan (SKCDC 2020). Due to relatively high levels of anthropogenic disturbance, boreal caribou populations in Saskatchewan's boreal plains are at a higher risk of decline and potential extirpation due to range retraction at the southern margin of the boreal caribou range (Arsenault 2003). See Appendix 1 for more details on the study area.

4.3.2 *Data collection and analysis*

Two surveys per year were conducted to collect fecal pellets for spatial capture-recapture analysis, with sampling occasions spaced approximately one month apart. Following the aerial survey protocol outlined in Hettinga et al. 2012, aerial transects were systematically flown at 3-km intervals across each survey area using rotary- or fixed-wing aircraft, or a combination of both, to locate caribou feeding locations. Saskatchewan's boreal plains ecozone is divided into three regions: SK2 East, SK2 Central, and SK2 East; SK2 Central was surveyed twice per year in 2017, 2018 and 2019, while SK2 East and SK2 West were each surveyed twice in 2020. Additional samples were collected across the boreal plains for population genetic surveys between 2013 and 2016 (Priadka et al. 2019). All samples were kept frozen at -20°C until DNA extraction was performed. We followed the DNA extraction protocol outlined in Ball et al. 2007 to generate individual-specific genetic profiles. To generate familial pedigree networks, we amplified DNA samples at 15 variable microsatellite loci (McFarlane et al. 2021).

4.3.3 *Demographic data*

Density

We used spatial capture-recapture (SCR) models to estimate the spatial density of boreal caribou in the Saskatchewan Boreal Plains. We created a multi-session spatial model with one session for each survey area (SK2 West, SK2 Central, and SK2 East) to obtain consistent density estimates across survey areas. We used a maximum likelihood approach implemented in the R package *secr* (Efford 2018; R Core Team 2019). The density model allows for the input of spatial covariates to create a heterogeneous density surface across the study area. We used three groups of spatial covariates to investigate the factors that affect population density and to obtain a spatially-explicit density surface: habitat (good-quality and poor-quality habitat), distance to anthropogenic disturbance (roads or linear features), and habitat potential (Appendix 1). Habitat data was extracted from the

2015 Land Cover of Canada dataset at 30-m resolution (Natural Resources Canada 2020). We predicted needleleaf forests and wetlands would have higher densities of caribou and selected these habitats to represent good-quality habitat. We predicted deciduous and mixed-wood forests (hereafter referred to as deciduous) would have lower densities of caribou and selected these habitats to represent poor-quality habitat.

We used the relationships between density and covariates from the top-ranked density model to create a density surface for each of the survey areas and extrapolated these density-covariate relationships across the Boreal Plains where density modelling did not occur. We constrained our extrapolation within the Boreal Plains and to include those samples that were collected just outside the Boreal Plains as an ecozone is an ecological unit with distinct biotic and abiotic features (Marshall et al. 1999). We calculated the median population density (per hectare) within a 12 km radius of each caribou location, based on the larger of the estimated home range radii for females (∼12 km) and males (∼6 km) calculated from the SK2Central population density estimation without any covariates (S. McFarlane, unpublished data). We chose to use the median density within the home range as boreal caribou move throughout their home range in search of lichen and to avoid areas of high predation risk (Canada 2012).

Reconstruction of familial relationships

We identified familial relationships of boreal caribou by reconstructing parent-offspring relationships using COLONY v2.0.6.5 (Jones and Wang 2010). COLONY uses a full-likelihood method for sibship inference and parentage assignment, assigning all sampled offspring to hypothetical maternal and paternal families (Wang 2004). Input parameters were set to allow for female and male polygynous mating systems without inbreeding avoidance, and the probability of mothers or fathers being present in the sampled data set was set to 50% in the absence of other prior information. COLONY infers the parental genotypes for missing parents; inferred parents are genotypes that are not included in the candidate parent samples, either by that individual not being captured during sampling, or that parent is no longer living, resulting in a family network with more individuals than were sampled. We used Cytoscape v3.7.2 (Shannon et al. 2003) to create a familial network from the reconstructed parent-offspring relationships identified by COLONY. Each individual has their parents identified by COLONY, as well their offspring, and a network can be created from the multigenerational relationships among individuals. As boreal caribou mating systems are polygynous, with individuals having multiple mating partners, a dense and complicated network is created; node-based measures of network centrality allow for easier identification of patterns and trends within the network. We confirmed the direction of all parent-offspring dyads by comparing the parent-offspring dyads against the full sibling and parent pair outputs provided by COLONY.

Network centrality

We used the protocol outlined by McFarlane et al. 2021 to identify individuals who are more central to the network. We used the r package *CINNA* (Ashtiani et al. 2018) to calculate individual node-based measures of network centrality. Nodes represent individuals and edges represent parent-offspring relationships, with directionality from parent to offspring. We quantified distinct aspects of network centrality using three node-based centrality measures: alpha, closeness, and degree centrality. Alpha centrality indicates those individuals who are connected to individuals who themselves are highly connected, giving an indication of individual reproductive success, even if that individual does not have a lot of direct connections (McFarlane et al. 2021). Reproductive output can be highly asymmetrical, with the number of offspring varying between individuals (McFarlane et al. 2018) and alpha centrality can indicate that an individual is part of a large extended family if they are connected to highly connected individuals. Degree centrality represents the number of edges connected to a node; in familial networks, the in-degree represents the parents of the individual, and the out-degree represents the number of offspring associated with that individual (Harary 1969; McFarlane et al. 2021). Closeness centrality has commonly been used to measure how fast information can spread from a given node to all other reachable nodes in a network (Latora and Marchiori 2001). In familial networks, individuals with higher closeness centrality come from more connected families, or larger families that have more generations represented in the sampling.

4.3.4 *Analyses*

Familial network and density

We ran sex-specific generalized linear models (GLMs) to determine the influence of density on the three individual network centrality measures using a Gaussian error structure. Each centrality measure was standardized between 0 and 1. To validate the familial network centrality measures used in these models (due to the lack of independence of data points present in network data), 10,000 random familial networks with a burn-in of 1,000 networks were generated using permutations. Each network was created by swapping mothers or fathers, and swapping offspring. As with the real data, each individual's network metrics were recalculated using these permuted networks. All global models were recalculated for each of the 10,000 permuted networks. The sizes of the coefficients were then compared to the size of the global models based on the original data. A p-value was calculated as the proportion of times the observed value was more extreme than the permutated values (Farine 2013). A network centrality measure effect was considered significant if this p-value was < 0.05 and the coefficients' confidence interval did not cross zero.

Dispersal and density

To test for density-dependent dispersal, we ran sex-specific GLMs with a Gaussian error distribution to determine the influence of density at the parental site on offspring dispersal. Dispersal events can be inferred when parents and offspring relationships reconstructed through sibship assignment are found in different locations (e.g. Fountain et al. 2017; Norman and Spong 2015). Although the actual dispersal route cannot be determined, recent gene flow and movement among locations can be inferred, and applying this method to many pairs of relationships, the population's dispersal patterns can be estimated (Escoda et al. 2017). We defined dispersal as the movement of offspring away from their natal source (Norman and Spong 2015), defining the natal source as the location of the parent. We calculated Euclidean dispersal distances in the R package *geosphere* (Hijmans 2019) for all parent-offspring dyads and used the maximum dispersal distance between the parent-offspring dyads to represent offspring dispersal.

Recruitment, pregnancy and density

We ran sex-specific binomial GLMs to determine the influence of density on the probability of female and male boreal caribou having offspring or not using a binary classification of individual reproductive success (did or did not have offspring) calculated from the reconstructed parent-offspring relationships. Following the protocol outlined by Flasko et al. 2017, fecal pregnane concentrations were measured to determine yearly female pregnancy status, using a threshold of 700 ng/g. Hormone levels are presented as nanogram per gram dry mass (ng/g). We ran binomial GLMs to determine the influence of density on pregnancy status of females.

4.4 RESULTS

A total of 2,616 samples were collected and 2,331 were successfully scored (average success rate of 92.1%), resulting in the identification of 762 unique individuals. 455 females, 298 males, and 9 individuals of unknown sex were identified. Overall, the average allele dropout rate was 0.0027% and the average false allele rate was 0.01%.

4.4.1 *Density estimation*

Our results suggest that densities of boreal caribou are low overall and animals are spatially clustered, with error below the 20% relative standard error threshold in all study areas (RSE = 11.5 - 13.9%), suggesting reasonably precise estimates. The top density model included good-quality habitat, a negative effect of poor-quality habitat, and a positive effect with increased distance to roads (Table **??**, Figure 4.2). Although density was low overall (maximum density of 270 caribou per 1000 km^2), there was substantial variation in the distribution of lower- and higher-density areas. Distance from roads was a large contributor to the high variation in spatial density; large undisturbed areas far away from roads had the highest densities (Figure 4.2, Figure 4.3). Poor-quality habitat was also a large driver of boreal caribou density, with density dropping to 0 in areas with >20% poor-quality (deciduous) cover.

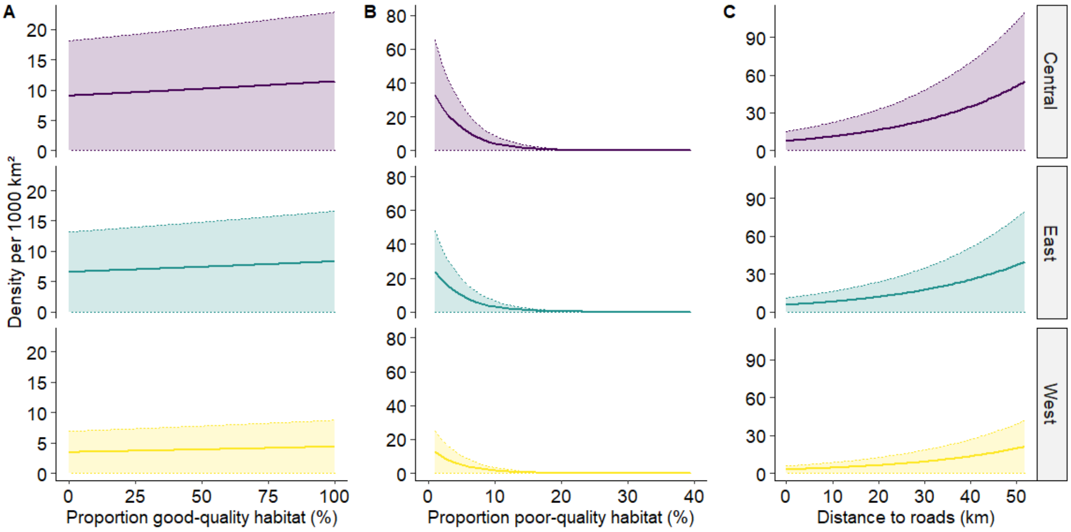

FIGURE 4.2: Predicted responses of the top density model showing the relationships between (A) good-quality habitat (needleleaf) and caribou density (with median values of poor-quality habitat and distance to linear features), (B) poor-quality habitat (deciduous) and caribou density (with median values of good-quality habitat and distance to linear features) and (C) distance to linear features and caribou density (with median values of good-quality and poor-quality habitat).

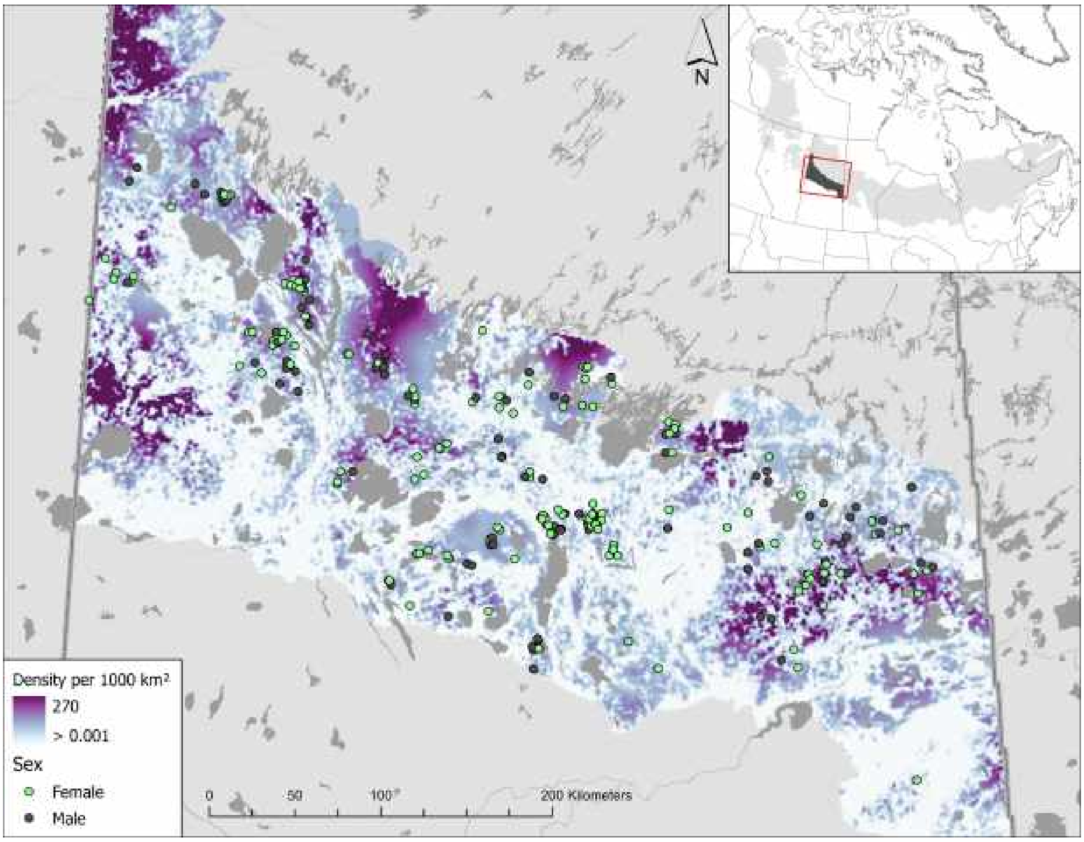

FIGURE 4.3: Spatially-explicit boreal caribou density across the Saskatchewan Boreal Plains caribou range. Boreal caribou density was associated with good-quality habitat, poor-quality habitat, and linear disturbances, with densities of boreal caribou low overall and spatially clustered, found primarily away from linear features and poor-quality habitat

4.4.2 *Familial network analysis*

Pedigree reconstruction inferred an additional 227 females and 231 males, for a total familial network of 1,220 individuals (Figure 4.4). 305 females and 270 males were identified as parents (47% of all individuals). Comparison of the observed network to the 10,000 permuted networks indicated that females with a lower density have a higher closeness centrality and higher degree centrality than expected given random familial relationships (Figure 4.5, Table 4.1).

Parameter	Females	estimate	p-value	Males	estimate	p-value
Alpha centrality	none	-0.0003	0.2	none	0.0003	0.44
Closeness centrality	negative	-0.0018	0.0008***	negative trend	-0.00093	0.1
Degree centrality	negative	-0.00044	0.0033***	none	0.00036	0.83
Dispersal (parent sex)	negative trend	-2.1e+02	0.068	none	-2.2e+02	0.23
Dispersal (offspring sex)	none	-1.1e+02	0.47	negative	-3.1e+02	0.0088***
Recruitment	negative	-0.012	0.043***	positive	0.019	0.038***
Pregnancy	none	-0.0024	0.69	-	-	-
Pregnane	positive	67	4.4e-23***	-	-	-

TABLE 4.1: Generalized linear model results for effect of density on several demographic parameters. P-values for centrality measures are obtained from permutations. *** indicates significant model results

4.4.3 *Dispersal and density*

In cases where an offspring was assigned a sampled mother or father, it was possible to infer effective offspring dispersal distance. Boreal caribou offspring disperse primarily within short distances of their parents; 86% of offspring dispersal events were < 40 km (Figure 4.6A). The largest dispersal distances were between fathers and their offspring (Figure 4.6). The maximum dispersal distance between fathers and their offspring was 232 km with a mean of 22 km (± 32 SD), while the maximum dispersal distance between mothers and their offspring was 152 km with a mean of 20 km (± 25 SD). There were 35 parent-offspring pairs where both the parent and offspring were only located together, with 49% of these being mother-daughter pairs.

Density at the parent location had no significant effect when accounting for parental sex, however, a negative trend was identified for mothers and her offspring ($p = 0.068$, Table 4.1). When accounting for the sex of the dispersing offspring, dispersal distance of male offspring was significantly related to density at the parent location, with longer dispersal distances when parent density was lower (Table S4.3.1, Figure 4.6B), while dispersal of female offspring from her parents was not significant (Table S4.3.1). Further investigation into sex differences in dispersal indicated that dispersal distance between mothers and her male offspring was also significant (Table S4.3.2), aligning with the significant results for male offspring and the trend identified for mothers.

4.4.4 *Recruitment, pregnancy and density*

We identified large reproductive skew in both sexes, with 87% of sampled males and 83% of sampled females not successfully producing calves who survived until fall. Pregnancy rates were substantially higher than the proportion of individuals who successfully reproduced; yearly female pregnancy rate ranged from 73.3% to 89.0%, with an overall pregnancy rate of 81.0%.

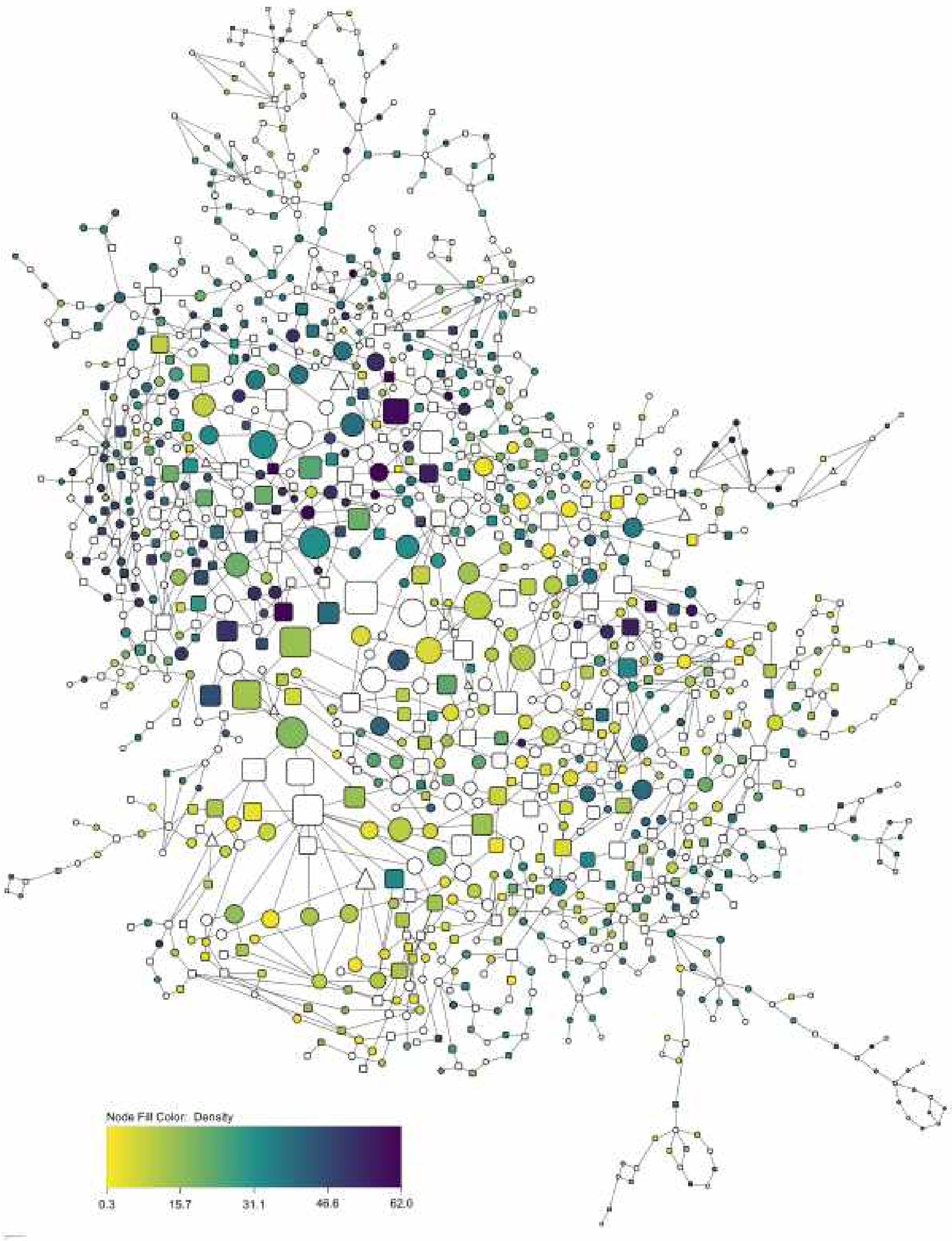

FIGURE 4.4: Boreal caribou familial network in Saskatchewan, Canada. Node size indicates closeness centrality score. Node colour represents median density where that individual was located. White nodes indicate inferred individuals where density could not be estimated. Rectangular nodes represent males, round nodes represent females, and triangular nodes represent individuals of unknown sex.

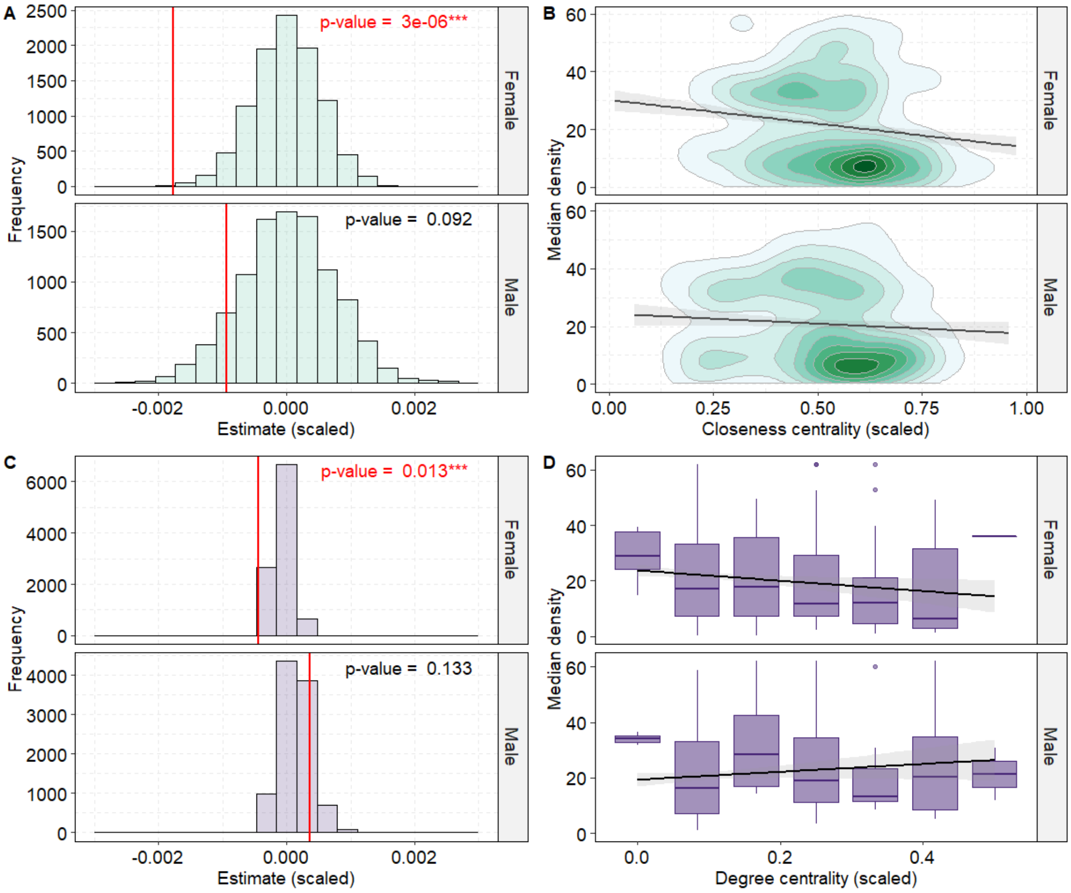

FIGURE 4.5: Sex-specific results of the effect of density on individual closeness centrality (A-B) and degree centrality (C-D). Histograms comparing closeness centrality (A) and degree centrality (C) of the real network to randomized networks, showing the observed model estimate of the actual network (vertical line) compared to 10,000 randomized networks. Significant p-values shown in red. Distributions of closeness centrality (B) and degree centrality (D) versus median density per individual. The 2D density plot represents the combined distribution of the two variables

Density significantly affected the reproductive success of both females and males (female $p = 0.043$, male $p = 0.038$; Table 4.1), but affected the sexes differently (Figure 4.7). For females, the predicted probability of successfully having offspring was highest at lower densities, while for males it was highest at high densities (Figure 4.7). Density did not significantly affect the pregnancy status of females (Table 4.1).

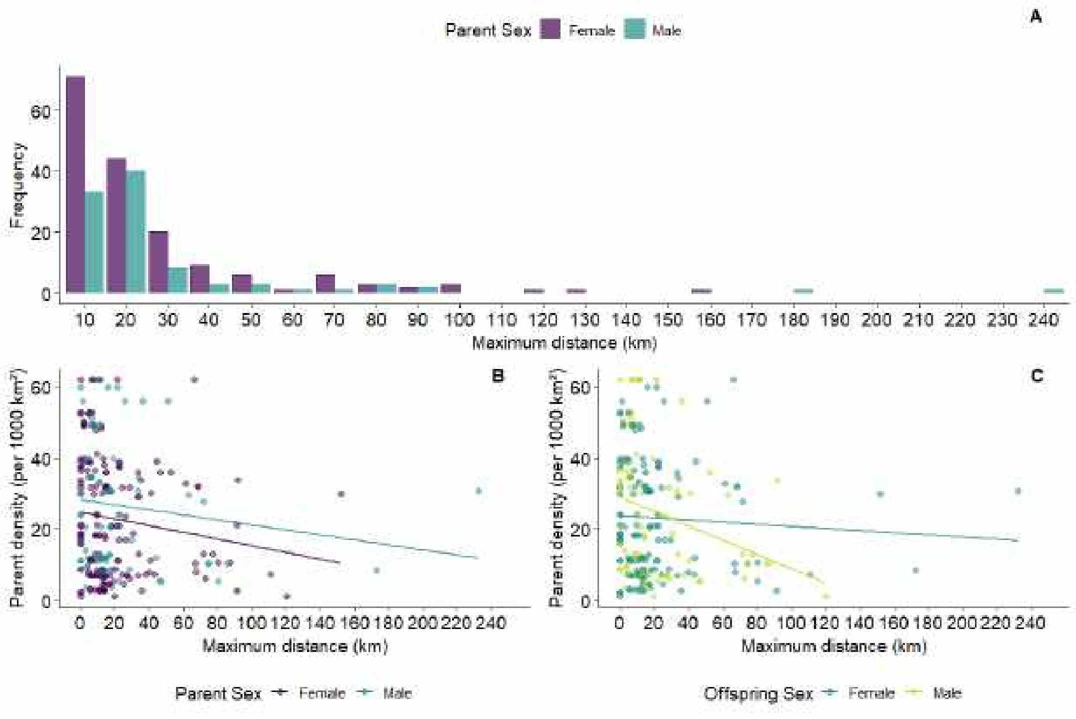

FIGURE 4.6: Frequency of maximum dispersal distances between parents and offspring by parent sex (A). Distribution of maximum dispersal distances versus density at the parent location by (B) parent sex and (C) offspring sex

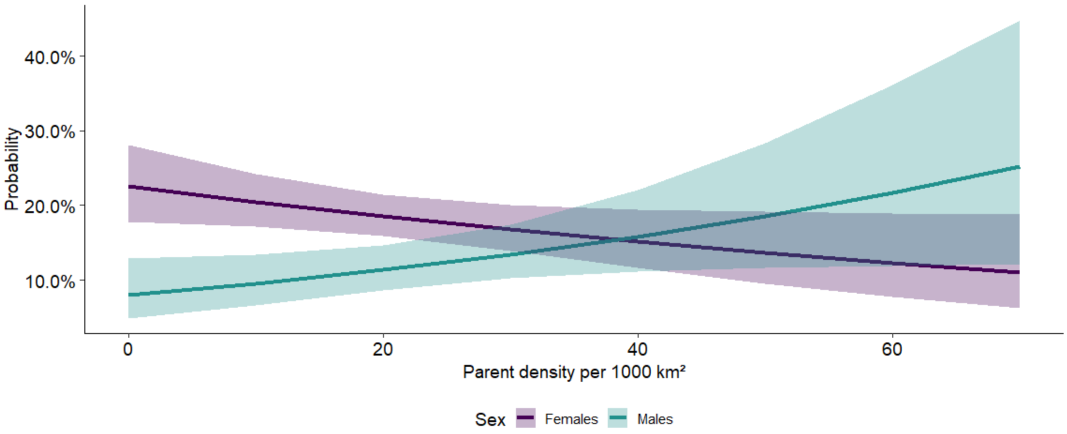

FIGURE 4.7: Marginal effects of the effect of density on the probability of having an offspring for females and males

4.5 DISCUSSION

Our study showed that there is significant variation in caribou density across the Boreal Plains in response landscape composition and anthropogenic disturbances. As predicted, we detected density-dependent demographic responses, with different responses in female and male caribou. Females in higher-density areas had significantly lower closeness centrality and degree centrality than expected (Table 4.1, Figure 4.5) in familial networks, and male offspring stayed closer to their parents when their parents were in higher-density areas (Table 4.1, Figure 4.6). When accounting for the sexes of parents and offspring, we identified significant density-dependent results for mother-son dispersal distances, with male offspring staying closer to their mothers when their mother was in higher-density areas (Table S4.3.2, Figure 4.6). Density also had a significant effect on both male and female reproductive success (Table 4.1). Males had a higher probability of successfully reproducing at higher densities, while females had a higher probability of reproducing at lower densities (Table 4.1, Figure 4.7), although no difference in pregnancy rate was found between females at high or low density. Adopting an individual-based approach allowed us to explain variation in demographic parameters at a finer scale, taking into account the animal's state. Our results demonstrate that the influence of density is not fixed but is dependent on both the sex of the individual and their associations, i.e. centrality, within the entire population (Table 4.1).

Our results showed that caribou density is dependent on landscape composition and fragmentation. Densities were highest in areas with high proportions of coniferous forests, low proportions of deciduous forests, and further away from roads. Roads are known to reduce density in many large mammalian species (Forman and Alexander 1998), including caribou (Beauchesne et al. 2014; Dyer et al. 2001; Leblond et al. 2011). Roads lead to habitat fragmentation, increasing access to caribou habitat for humans, predators such as wolves (*Canis lupus*), and alternative prey species such as moose (*Alces alces*) (Hebblewhite 2008; Whittington et al. 2011; Dickie et al. 2017). These disturbances can lead to behavioural shifts of individual caribou, leading to population level consequences by decreasing reproductive output, population growth, and survival (Johnson and St-Laurent 2011). As well as the direct loss of habitat and resources from road construction, road-avoidance behavioural shifts can lead to indirect habitat loss for caribou, as caribou avoid roads by several kilometres, leading to more high-quality habitat being lost (Polfus et al. 2011). Our results also highlight caribou avoidance of deciduous-dominated forests. Caribou density dropped to zero when the proportion of poor-quality habitat was greater than 20% (Figure 4.2). Deciduous forests are foraging areas for moose, an alternative prey species for wolves, and caribou avoidance of deciduous forests has been shown previously (Losier et al. 2015; Courtois et al. 2002), but our results show a steep decline in density in deciduous-dominated landscapes, indicating a significant avoidance of these habitats. Together, caribou density was lowest in areas of high proportions of deciduous forests and near roads, highlighting that caribou depend on old-growth forests with little disturbance.

Our pregnancy results indicated that the overall pregnancy rate was 81%, yet our familial network analysis found that only 17% of sampled females and 13% of sampled males successfully reproduced a calf that survived until fall. The difference between the high pregnancy rate and low successful reproduction rate (81% vs. 17%) suggests that calf mortality is high. Our reproduction rates are likely underestimates, as it is possible that not all living offspring were sampled. Calf survival in caribou is low, with calf loss to predation highest during the first month of life (Pinard et al. 2012; Stuart-Smith et al. 1997); predation by black bears (*Ursus americanus*) and wolves can account for more than half of calf mortalities (Pinard et al. 2012). The large proportion of animals found with no offspring can represent a significant component of the variation in the overall lifetime reproductive success of populations, but this research has focused primarily on male non-breeders (e.g. Janicke and Morrow 2018; McElligott and Hayden 2000; Richardson et al. 2020).

Our results clearly suggest sex-specific differences in reproductive success in areas of varying population densities. Caribou exhibit a polygynous mating system, with mating occurring in loose harems (Thomas et al. 1989), and males exhibit mate defense strategy, defending access to mates, with reproductive success of males dominated by larger and older males (Hirotani 1994). It may be beneficial for subordinate males to remain within these higher-density areas, remaining with a female group and wait for the decline of the sexual activity of dominant males, for the possibility of gaining the dominant position and the associated reproductive benefits (Hirotani 1994; Røed et al. 2002; Skogland 1989). At low densities, males may be more efficient at defending harems due to less competition from other males. The low reproductive probability observed for the female segment of the population is surprising and difficult to explain. There can be marked differences in individual quality among females; long-lived female reindeer had higher lifetime reproductive success (Weladji et al. 2006), and successful breeders had higher subsequent reproductive success than non-breeders and unsuccessful breeders (Weladji et al. 2008). Density can influence individual reproductive success; there was greater variance of female reproductive success in an alpine ibex (*Capra ibex*) population experiencing density-dependence than a population experiencing no density-dependence (Toïgo et al. 2002), while lifetime reproductive success of female red deer was inversely associated with density (McLoughlin et al. 2006). These results are similar to ours, with female caribou having higher reproductive probability at low densities (Figure 4.7).

With such a large proportion of the population not successfully reproducing, accounting for the contribution of all individuals is critical for correctly understanding demographic responses to variable spatial density. By building a familial network from parent-offspring relationships, we were able to account for the contribution of inferred individuals in the overall structure of the population. Density significantly influenced the degree and closeness centrality of females, with lower centrality in higher-density areas (Table 4.1). Degree centrality directly represents the reproductive output of an individual, and the negative effect of density on degree centrality of females corresponds with the negative effect of density on female reproductive success (Table 4.1). In familial networks, closeness quantifies how connected an individual is in terms of its direct and indirect connections with every other individual within a network - individuals with higher closeness centrality come from larger families and their relatives are also highly connected (Chapter 3). The decay in closeness centrality at higher densities is linked to the negative trend in dispersal distances (Table 4.1), with offspring not dispersing as far away from their parents at high densities and are therefore not breeding outside of their family group.

Obtaining dispersal data for caribou and other ungulates can be difficult due to long dispersal distances, and sex-biased dispersal may lead to differences in detection probability of dispersers and non-dispersers (Moore et al. 2014). No studies have assessed dispersal in caribou; here we successfully used parent-offspring relationships to inform on sex-specific dispersal in caribou. Density negatively affected dispersal distance, with offspring dispersing further when their parents were in lower density areas. Our parent density was used to reflect natal density, as natal density is what drives the decision to disperse, but does not control what level of density the dispersing individual will be able to land in. In most polygynous mammal species, males are the dispersing sex while females are philopatric (Greenwood 1980; Wolff 1997). For non-territorial species, such as ungulates, there should be no deterrence to juvenile dispersal from residents in other social units at all densities (e.g. Gosling 1985; Festa-Bianchet 1991; Sinclair 1992). Variation in natal dispersal has been linked to population density and group characteristics in several species, including feral horses (*Equus ferus caballus*; Marjamäki et al. 2013), African lions (VanderWaal et al. 2009), and degus (*Octodon degus*; Quirici et al. 2010). Anthropogenic disturbance can disrupt natal dispersal patterns, which can turn source populations into sinks (Fattebert et al. 2015). As caribou are dispersing shorter distances at higher density, and caribou density is driven by habitat availability and distance to roads, caribou may become trapped within remnant patches of suitable habitat that can support higher densities. These results further emphasize the impact of landscape fragmentation on population demography and the importance of ensuring that landscape conditions allow for the animals to maintain low population densities and spatial connectivity throughout the range.

We found that caribou density is greatly influenced by landscape composition and fragmentation, resulting in patches of higher-density areas that in turn resulted in individual heterogeneity in demographic responses. Caribou distribution is clustered to a few higher-density areas of suitable habitat, which may be influencing the demographic responses of individuals, as both the reproductive success of females and the dispersal distances of offspring were lower. To our knowledge, this is the first study looking at the effects of variable density across the range of a wild ungulate population on individual-level measures of reproductive success; on sex-specific reproductive and dispersal rates. This highlights the importance of considering the reproductive success value of different areas across the landscape in conservation.

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APPENDIX 4.1: STUDY AREA, LAND COVER AND DISTURBANCE DATA

Due to the large size of Boreal Plains and the large variation in habitat types, ecological conditions, anthropogenic disturbance and fire regime, the Government of Saskatchewan has developed three caribou administration zones representing important ecological differences (SK2 West, SK2 Central, and SK2 East; Saskatchewan Ministry of Environment 2019a), which do not represent discrete population boundaries, as caribou distribution is continuous across the range (Priadka et al. 2019). SK2 West and SK2 Central are characterized by low rolling forested hills and plains interspersed by bogs, fens, marshes, and lakes, with a relatively large proportion of high value upland (pine-lichen forests) and lowland (peatlands) caribou habitat (Saskatchewan Ministry of Environment 2019a). SK2 West has the highest combined levels of anthropogenic disturbance and wildfire, while SK2 Central has the highest level of anthropogenic disturbance with an intermediate fire cycle slightly less than SK2 West (Saskatchewan Ministry of Environment 2019b; Saskatchewan Ministry of Environment 2019a).

SK2 West has an extensive network of permanent and non-permanent roads from forestry activities, along with oil and gas activities including seismic exploration and oil and gas extraction in the south, and historic oil sands exploration in the northwest (Saskatchewan Ministry of Environment 2019b). Slightly increasing levels of forestry are expected in the future; current active natural gas extraction will continue, but new natural gas development is not expected in SK2 West (Saskatchewan Ministry of Environment 2019b). Forestry is the primary source of anthropogenic disturbance in SK2 Central, with an extensive network of permanent and non-permanent roads, with slightly increasing levels of forestry expected in the future (Saskatchewan Ministry of Environment 2019a).

We used land cover types from the 30m 2015 Land Cover of Canada (Natural Resources Canada 2020) that we determined to be the best land cover classes for determining boreal caribou density. We predicted wetland and needleleaf forests to have higher densities of caribou, while deciduous and grass and shrub would have lower densities of caribou. The LCC data was rescaled to 1km^2 spatial resolution, and the value in each 1km^2 grid cell represents the fraction of that class present per cell.

Linear anthropogenic disturbances also leads to habitat fragmentation that impedes movement and access to available resources, as well as providing predators easier access into formerly inaccessible habitats (Saskatchewan Ministry of Environment 2019a). Boreal caribou require large range areas comprised of undisturbed habitat, and polygonal disturbance may reduce the size of suitable habitat patches, and reduce connectivity between habitats (Saskatchewan Ministry of Environment 2019a; Environment Canada 2012).

Wetland is comprised of the LCC Wetland cover type: areas dominated by perennial herbaceous and woody wetland vegetation which is influenced by the water table at or near surface over extensive periods of time. This includes marshes, swamps, bogs, mangroves, etc. We predicted that these classes would have medium to high densities of caribou. Wetland was included in the analysis but was not significant in any of the models. This

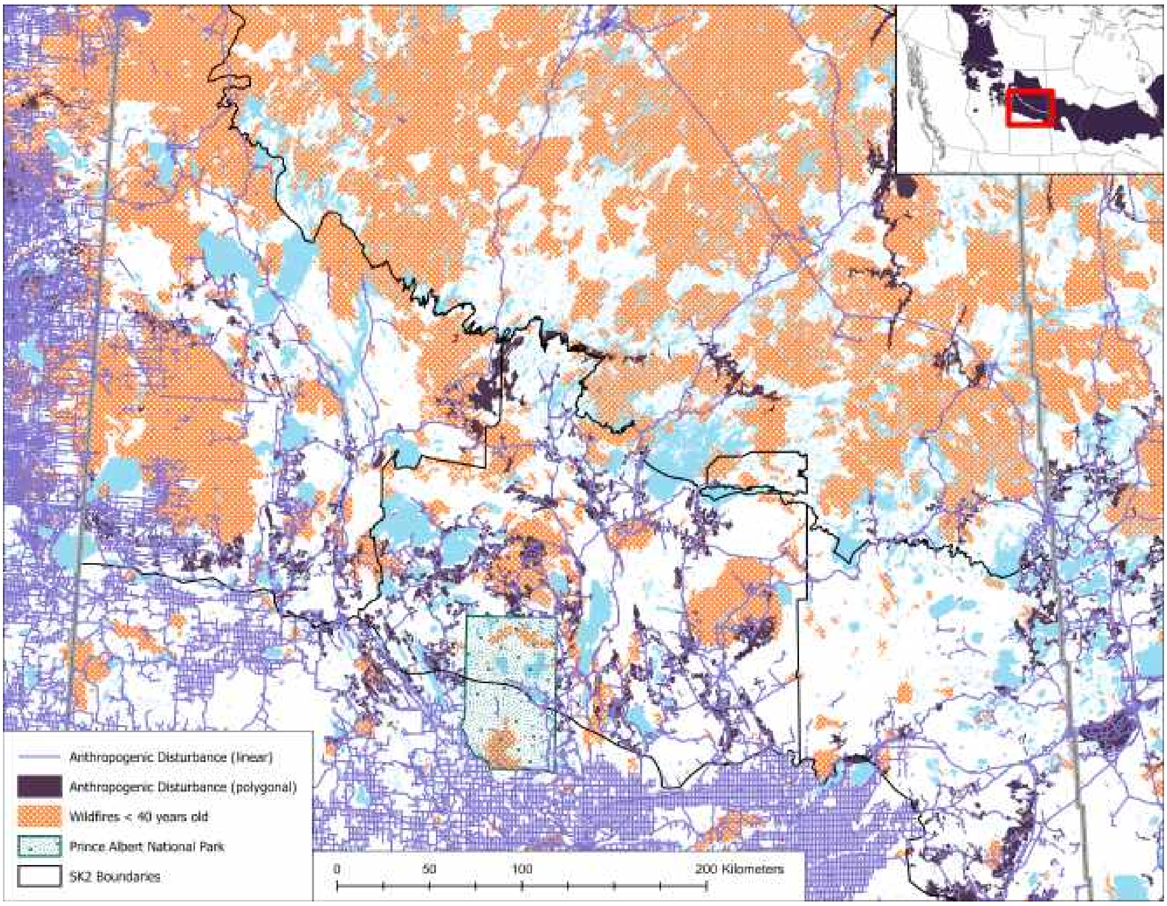

Figure S4.1.1: Anthropogenic and fire disturbance in the Saskatchewan Boreal Plains caribou range. Linear disturbance includes roads, railways, powerlines, pipelines, and seismic exploration lines. Polygonal disturbances include forestry cut-blocks, mines, reservoirs, built-up areas, well sites, and other features. Inset map shows location of Saskatchewan Boreal Plains caribou range within the distribution of boreal caribou in Canada. Base map is land cover classification (Environment Climate Change Canada 2015).

was in part likely due to the reduced class accuracy of wetlands in the land cover product relative to other classes (Latifovic et al. 2017).

Needleleaf is comprised of two LCC cover types: Temperate or sub-polar needleleaf forest (forests with the tree crown cover containing at least 75% of needleleaf species), and sub-polar taiga needleleaf forest (forests with shrubs and lichens present in the understory, and crown cover containing at least 75% needleleaf species). We predicted that these classes would have high densities of caribou.

Deciduous/mixed forest is comprised of two LCC cover types: Temperate or sub-polar broadleaf deciduous forest (forests with greater than 75% of tree crown cover represented by deciduous species) and Mixed Forest (forests where neither needleleaf nor broadleaf tree species occupy more than 75% of total tree cover, but are co-dominant). We predicted that these classes would have lower densities of caribou.

Grass and shrub is comprised of two LCC cover types: grassland (areas dominated by graminoid or herbaceous vegetation, generally accounting for greater than 80% of total vegetation cover) and shrubland (areas dominated by woody perennial plants with persistent woody stems less than 3 meters tall and typically greater than 20% of total vegetation). We predicted that these classes would have lower densities of caribou.

The quality of boreal caribou habitat was evaluated by ranking ecosites and mapping habitat potential within the provincial forest of central Saskatchewan (Saskatchewan Ministry of Environment 2019a). Forest ecosite habitat potential ranks were assigned by evaluating ecosite's potential to provide forage, refuge and calving habitat by a panel of biologists with expertise on boreal caribou habitat use in Saskatchewan (Saskatchewan Ministry of Environment 2019a). Forest ecosite habitat potential values were mapped at a 10m x 10m spatial resolution. Dispersal in highly mobile terrestrial mammals such as boreal caribou occurs over large spatial extents, and these species may be more influenced by patterns evident at broader spatial extents than by fine-grained landscape variation (Galpern et al. 2012); therefore the habitat potential data was rescaled to 1km^2 spatial resolution, and the value in each 1km^2 grid cell represents the mean habitat potential value.

We used the National Road Network (NRN) and CanVec land, man-made, resource management and transport linear features to create the distance to roads and distance to linear features layers. The linear feature layer includes roads, railways, trails, seismic lines, protection structures (dike, levees, etc.), pipelines, and power lines. Caribou are known to avoid habitats within several kilometres of human development (Dyer 1999; Environment Canada 2011; Hebblewhite et al. 2010; Mahoney and Schaefer 2002; Weir et al. 2007). We tested the effects of linear features by creating a distance to roads variable and a distance to all linear features variable.

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APPENDIX 4.2: DENSITY MODELING

SCR models consist of a submodel for the distribution of animals in the area of study (population density, D), and a submodel for the detection process, given the detection probability (the intercept of the detection function, $g0$) and give a parameter for scaling the detection function (the spatial extent of an individual's use of the landscape - σ; Borchers and Efford 2008; Efford et al. 2009).

Habitat and habitat potential covariates were resampled to 1 km^2 spatial resolution, with the value in each 1 km^2 grid cell representing the fraction of the 30 m cells for the selected class or classes. Disturbance data was extracted from the National Road Network (NRN) and CanVec land, man-made, resource management and transport linear features (Natural Resources Canada 2020; Statistics Canada 2015). Distance to disturbances was calculated in ArcGIS (ESRI Inc. 2018) and a spatial surface of distance to roads and distance to linear features (including roads) was calculated for the entire Boreal Plains.

We estimated the parameters of the SCR detection function ($g0$ and σ) by maximizing the conditional likelihood, and derived density from the top AIC$_C$-ranked models (Akaike 1974; Anderson et al. 1994; Borchers and Efford 2008). We used the hazard exponential form of the detection function, as area search data models the cumulative hazard of detection (Efford 2011). Models assumed that individuals were identified correctly, populations were demographically closed during sampling, and detections were independent, conditional on activity centres (Borchers and Efford 2008; Efford 2004). We first fit a series of detection models to the data using a homogeneous density surface ($D \sim 1$) with time (t), site-specific (k, site learned response), and behavioural (bk, animal x site-learned response) responses influencing $g0$ and σ (unpublished data). We used the top detection model ($t + bk$) in our subsequent density model runs.

Model[a]	AIC	ΔAIC	logLik	weight
D~session + needleleaf + deciduous.mixed + road_distance	5144.350	0.000	-2559.595	0.9901
D~session + needleleaf + deciduous.mixed + grass.shrub	5153.557	9.207	-2564.199	0.0099
D~session + deciduous.mixed	5161.660	17.310	-2570.424	0.0000
D~session + needleleaf + deciduous.mixed	5163.491	19.141	-2570.256	0.0000
D~session + needleleaf + road_distance	5254.073	109.723	-2615.548	0.0000
D~session + road_distance	5255.572	111.222	-2617.380	0.0000
D~session + needleleaf	5280.402	136.052	-2629.795	0.0000
D~session	5281.745	137.395	-2631.542	0.0000
D~session + grass.shrub	5283.496	139.146	-2631.342	0.0000

TABLE S4.2.1: Model selection table for spatially explicit capture-recapture models to predict the density of boreal caribou in the Saskatchewan Boreal Plains. Detection model for all models is $\lambda \sim t + bk$, $\sigma \sim t + bk$

[a] session = survey year; needleleaf = good-quality habitat (needleleaf forest); deciduous.mixed = poor-quality habitat (deciduous forest and mixed forest); road-distance = distance to roads (in metres).

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APPENDIX 4.3: GLM RESULTS

Model	Estimate	SE	p-value
Maximum dispersal distance (all)	-209.197	98.247	0.034***
Maximum dispersal distance (mothers and all offspring)	-211.28	114.856	0.068
Maximum dispersal distance (fathers and all offspring)	-221.242	182.138	0.228
Maximum dispersal distance (female offspring)	-112.105	154.74	0.47
Maximum dispersal distance (male offspring)	-307.623	115.199	0.009***

TABLE S4.3.1: Generalized linear model results for effect of density at parental location on dispersal distances of offspring. Results are for the entire population, as well as accounting for either the sex of the parent, or the sex of the offspring. *** indicates significant model results

Model	Estimate	SE	p-value
Maximum dispersal distance (mother-daughter)	-87.999	165.801	0.597
Maximum dispersal distance (mother-son)	-378.371	159.452	0.021***
Maximum dispersal distance (father-daughter)	-198.589	316.47	0.533
Maximum dispersal distance (father-son)	-200.671	162.019	0.224
Maximum dispersal distance (male offspring)	-307.623	115.199	0.009***

TABLE S4.3.2: Generalized linear model results for effect of density at parental location on dispersal distances of offspring when accounting for the sex of both the parent and the offspring. *** indicates significant model results

Model	Estimate	SE	p-value
Individual fitness	-0.003	0.005	0.548
Individual fitness (females)	-0.012	0.006	0.043***
Individual fitness (males)	0.019	0.009	0.038***

TABLE S4.3.3: Generalized linear model results for effect of density at parental location on individual fitness. *** indicates significant model results

Model	Estimate	SE	Comparison to permutations
Alpha centrality	-9.30e-05	1.19e-04	0.436
Closeness centrality	-1.47e-03	3.11e-04	0***
Degree centrality	-1.60e-04	1.42e-04	0.167
Female alpha centrality	-3.04e-04	1.52e-04	0.196
Male alpha centrality	3.04e-04	1.91e-04	0.441
Female closeness centrality	-1.77e-03	3.73e-04	0.001***
Male closeness centrality	-9.34e-04	5.53e-04	0.101
Female degree centrality	-4.36e-04	1.75e-04	0.003***
Male degree centrality	3.61e-04	2.40e-04	0.83

TABLE S4.3.4: Generalized linear model results for effect of density on network centrality of individuals. *** indicates significant model results

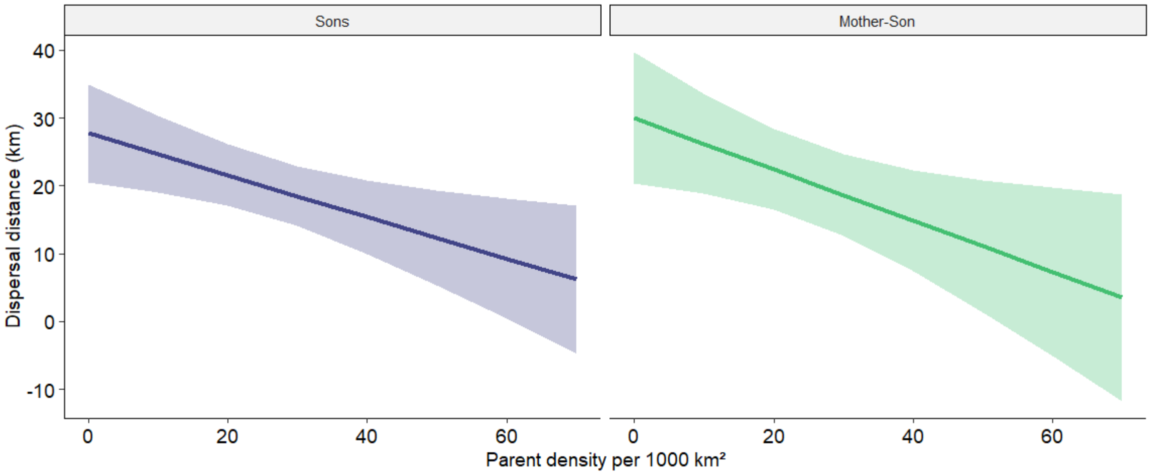

FIGURE S4.3.1: Marginal effects of the effect of parental density on the dispersal distance of offspring for sons and mother-son pairs

APPENDIX 4.4: NETWORK CENTRALITY RESULTS

Overall, alpha centrality ranged from 1 to 21 with a mean of 2.79 (± 2.79 SD), degree centrality ranged from 1 to 13 with a mean of 2.49 (± 1.18 SD) and closeness centrality ranged from 46.63 to 135.75 with a mean of 90.08 (± 15.69 SD).

Permuted networks were also run to determine the effect of density on alpha centrality (Figure S4.4.1). The initial generalized linear models (GLMs) were not significant (Table S4.3.3), however we present the permuted network results here.

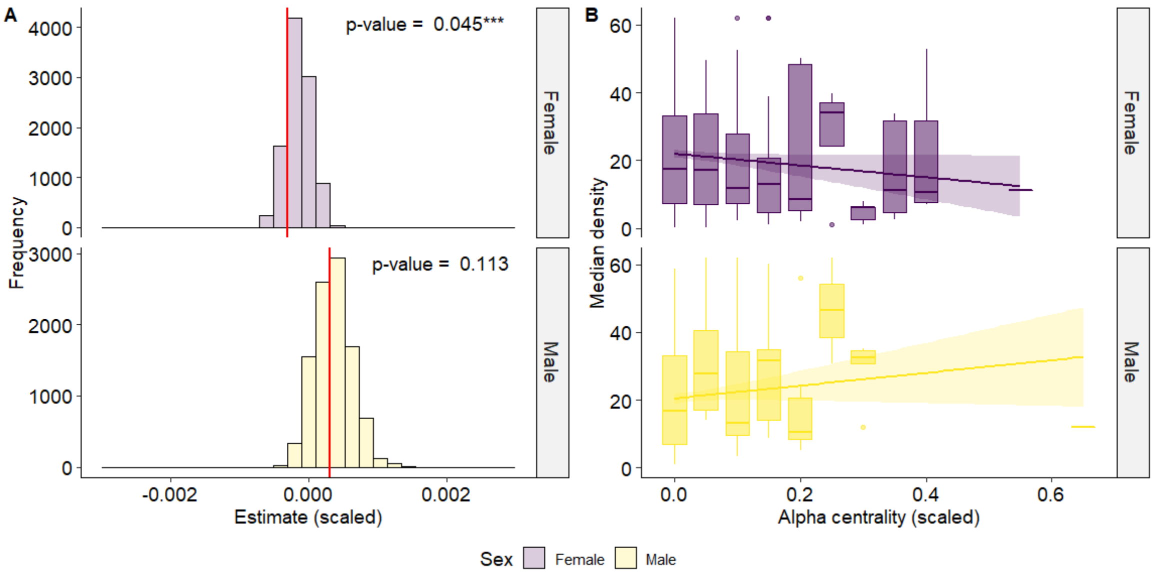

FIGURE S4.4.1: Sex-specific results of the effect of density on individual alpha centrality: both sexes (not significant), females (significant), and males (not significant). (A) Histogram comparing alpha centrality of the real network to randomized networks, showing the observed model estimate of the actual network (vertical line) compared to 10,000 randomized networks. Significant p-values shown in red. (B) Distribution of alpha centrality versus median density per individual.

APPENDIX 4.5: REPRODUCTIVE STATUS AND PREGNANCY

In all analyses, the number of offspring was transformed into binary format (0 = no offspring, 1 = one or more offspring). More than 75% of sampled females and males did not have any offspring (Figure S4.5.1). When including the inferred individuals from the pedigree reconstruction, more than 50% of females and males did not have any offspring (Figure S4.5.2).

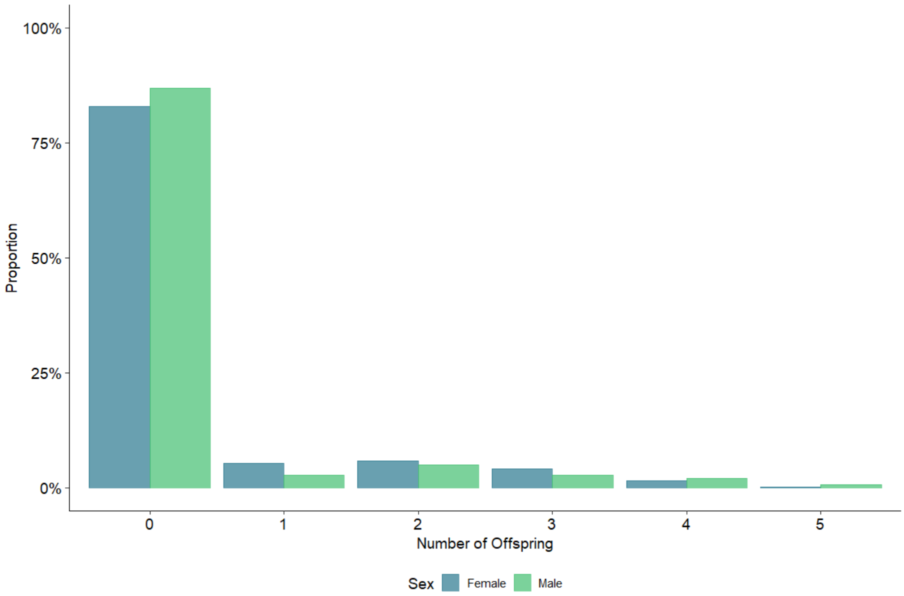

FIGURE S4.5.1: Number of offspring per sampled individual by frequency of females and frequency of males.

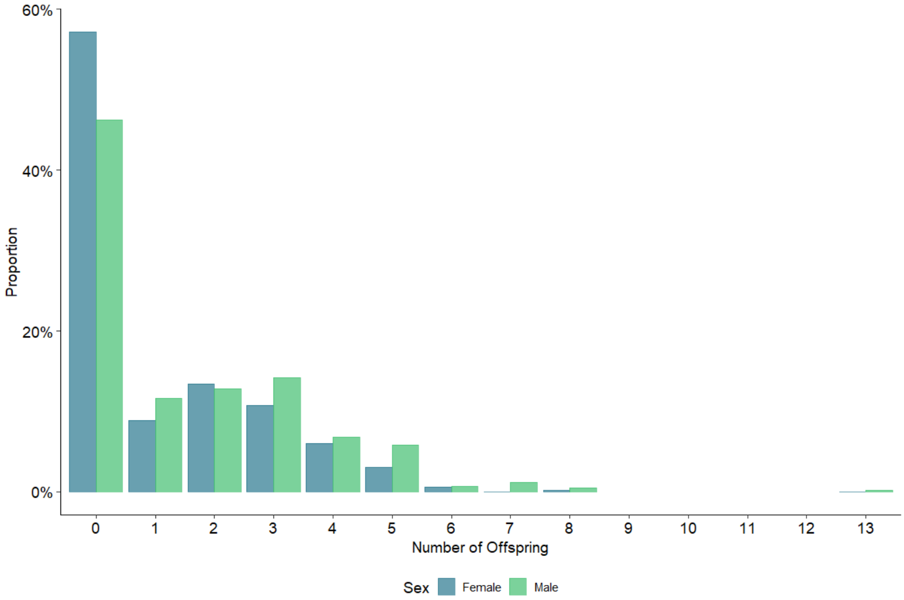

FIGURE S4.5.2: Number of offspring per individual (sampled and inferred individuals) by frequency of females and frequency of males.

Part III

CONCLUSION

5

Conclusion

The general objective of my thesis was to further our understanding of the spatial distribution and individual-level demographic parameters of boreal caribou. To do so, in Chapter 2, I first investigated methods for estimating population density of seven populations of boreal caribou and determined the precision and bias of these analyses, to aid in expanding this work to other populations and other researchers. In Chapter 3, I investigated familial networks of boreal caribou and analyzed these networks spatially, determining that boreal caribou in Saskatchewan form a complex, interconnected familial network, and identifying spatial local areas with higher fitness levels and family cohesion. In Chapter 4, I brought the work from Chapters 2 and 3 together to investigate the effects of population density on several demographic parameters and on familial networks of boreal caribou. By creating a spatially-explicit representation of density across the Saskatchewan Boreal Plains, I was then able to determine the effect of density on the network centrality, dispersal, and reproductive success of individual female and male boreal caribou.

5.1 FUTURE RESEARCH

There are several avenues of future research that have been illuminated by my dissertation. Using genetic data allows researchers to address numerous research questions, and I have identified several interesting avenues for future research:

Expanding the spatially-explicit density analyses presented in Chapter 4 by creating and assessing new methods for extrapolating density results to a broader area, potentially to a provincial or subspecies level. There is incredible potential for the spatially-explicit density analyses I implemented in this dissertation for the management and recovery of boreal caribou. Obtaining spatially-explicit density estimates for boreal caribou has not been done before. I have shown in this dissertation that density is highly variable within a population and across the landscape, varying with landscape features and disturbance, and not accounting for this heterogeneity can lead to incorrect assumptions about population parameters or the status of a population. This work shows how dependent boreal caribou density and distribution is on habitat availability, habitat quality, and anthropogenic disturbance. Creating statistical techniques for extrapolating density results to broader landscapes could create spatial density estimates for a larger proportion of the boreal caribou range within Canada, and contribute to future conservation and recovery efforts of the species. Extrapolating to larger areas can be challenging; I experienced this firsthand with the analysis in Chapter 4. I first completed the density modeling for Chapter 4 with only two years of data from SK2 Central, prior to data collection in SK2 Central in 2019 and SK2 West and SK2 East in 2020. I experienced challenges in extrapolating the results to the SK Boreal Plains until I included the additional study areas of SK2 West and East. Being able to extrapolate the density results (and therefore the density-covariate relationships) to a broader area could be immensely helpful for conservation and recovery work of boreal caribou, and this could be applied to other species as well – very few studies so far have incorporated spatial covariates into their spatial capture-recapture density estimates (but see Lamb et al. 2018; Morrell et al. 2021). The R package *secr* (Efford 2018) has the capability for extrapolating to a slightly larger study area, but it is beyond the scope of this package to identify the best methods for extrapolating.

Another future project could involve creating mating networks from female-male (mating) pairs rather than familial pedigree networks from parent-offspring pairs, and assess how individual heterogeneity, demographic populations parameters, and spatial landscape variables may influence mating dynamics of boreal caribou. Caribou are a highly polygynous species with a short mating season, forming temporary mating groups for a few weeks in late autumn (Røed et al. 2002). As shown in Chapter 4 and in McFarlane et al. 2018, there is large reproductive skew for both males and female caribou, with most individuals not successfully reproducing calves that survive until fall. Creating a mating network could elucidate potential individual or spatial variables that may be contributing to the highly skewed reproductive success of female and male boreal caribou.

Another area of research that is not addressed in this dissertation, but is a research interest of mine, is analyzing genetic data from mountain caribou populations in the Rocky Mountains. Our research group has analyzed thousands of samples from the Jasper, A la Peche, Narraway, and Redrock-Prairie Creek populations. Extending the analyses done in this dissertation to a different ecotype of caribou could further highlight differences between the ecotypes, or identify similarities. Initial familial network analysis was completed on the caribou populations in Jasper National Park during my Master's thesis [@McFarlane2018], and I have continued to analyze the mountain caribou populations throughout my dissertation but have not included these analyses in my dissertation. Expanding analyses to another ecotype could further provide proof that familial network analyses can be widely used to address questions about demographic parameters across the species.

5.2 CONSERVATION IMPLICATIONS

This work highlights the importance of accounting for heterogeneity in individual and spatial population parameters. For most species, not accounting for heterogeneity across the range can result in incorrect inferences about ecological processes and patterns, leading to incorrect interpretations (Badger et al. 2020; Cam et al. 2002; Nussey et al. 2008; Paterson et al. 2018; Plard et al. 2014; Service 2000; Weladji et al. 2008). In Chapter 2, I looked at population parameters and showed that population density can vary considerably between neighbouring populations of the same subspecies. Accurately estimating population size or density is a critical component of effective conservation and recovery strategies for endangered species (Reed et al. 2003). In Chapter 3, I identified finer-scale differences in population parameters by identifying spatial variation in familial network parameters in boreal caribou with a continuous distribution. The spatial application of the familial networks identified individuals presenting different fitness levels, short-and long-distance dispersing ability across the range in support of population monitoring and recovery efforts. In Chapter 4, I looked at sex-specific individual differences in population parameters of boreal caribou. The work in this chapter builds off the analyses from the first two chapters, and represents a cohesive analysis bringing together individual-level demographic parameters and the spatial distribution of the species.

5.3 RECOMMENDATIONS FOR DOING THIS KIND OF WORK

The primary recommendation from my dissertation research is to make genetic data the primary data source of a research or management program. Boreal caribou have traditionally been monitored through aerial surveys (e.g. Larter et al. 2017; Serrouya et al. 2017; Courtois et al. 2007) or female-biased telemetry studies (e.g. Beauchesne et al. 2014; Avgar et al. 2012). Genetic surveys can accurately estimate abundance (Carr et al. 2012), and can also provide numerous demographic parameters for both sexes (e.g. Hettinga et al. 2012). Telemetry studies are biased towards females as only female caribou are collared (such as Beauchesne et al. 2014; Leclerc et al. 2014; Briand et al. 2009; Hins et al. 2009; Courtois et al. 2007, leading to inferences about resource selection and lambda rates from only females. However, males are generally considered to be the dispersing sex in many polygynous species (Dobson 1982; Lehmann and Perrin 2003), and there can be substantial differences between male and female demographic parameters, as highlighted in Chapter 4.

A second recommendation is to collect samples from a wide geographic area or in multiple populations. My dissertation illustrates the heterogeneity within and across populations. Chapter 2 illustrates how density differs considerably between populations, even populations that border each other. Although boreal caribou are considered the more sedentary subspecies (COSEWIC 2011), Chapter 3 and 4 highlight that boreal caribou move throughout their range and there are some long-distance dispersal events.

A third recommendation is to survey a population multiple times. Density is a critical population parameter for conservation and management, and requires a minimum of two surveys within the same year (roughly a month apart) to estimate density and abundance (Hettinga et al. 2012; Pollock 1982). The advantage of collecting genetic data over other sources of data is that genetic data can be used for numerous other analyses and can determine numerous other demographic parameters that cannot be determined from other types of data.

A fourth recommendation is to consider multiple parameters together and how they may influence each other. In Chapter 4 I illustrate how density influences network centrality, dispersal and individual fitness of both female and male caribou. By only focusing on one of these parameters, other critical information that completes the story would not be accounted for.

Finally, a fifth recommendation is to do individual-based analyses. Genetic data allows for individual-level data, and Chapter 3 and 4 highlight the variability between individuals in the same population. These differences would not be accounted for if only considering population-level demographic parameters.

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Appendix

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