NON-INVASIVE METHODS FOR OBTAINING OCCUPANCY PROBABILITIES AND DENSITY ESTIMATES OF INTERIOR ALASKA'S MESOCARNIVORE POPULATIONS

By

Casey Pozzanghera

RECOMMENDED:

Dr. Mark Lindberg

Dr. Kris Hundertmark

Dr. Laura Prugh
Advisory Committee Chair

Dr. Kris Hundertmark
Chair, Wildlife Biology and Conservation Program

APPROVED:

Paul W Layer
Dr. Paul Layer
Dean, Natural Science and Mathematics

John C Eichelberger
Dr. John Eichelberger
Dean of the Graduate School

20 November 2015
Date

NON-INVASIVE METHODS FOR OBTAINING OCCUPANCY PROBABILITIES AND DENSITY ESTIMATES OF INTERIOR ALASKA'S MESOCARNIVORE POPULATIONS

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Casey Pozzanghera, B.S.

Fairbanks, Alaska

DECEMBER 2015

ABSTRACT

Mesocarnivore species worldwide have been shown to be significant drivers of ecological communities. Changes in their abundance and distributions are known to cause cascading effects throughout ecosystems, and changes to the landscape and climate will likely lead to shifts in mesocarnivore population sizes and distributions. However, the current status of these species in some of the world's most susceptible landscapes is not known. I assessed the impacts of abiotic factors on the distributional patterns and abundance of boreal mesocarnivores and evaluated methods commonly used to estimate density and occupancy. I conducted non-invasive winter surveys of coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), lynx (*Lynx canadensis*), wolverines (*Gulo gulo*), and marten (*Martes americana*) in the interior of Alaska. Overall, mesocarnivore occupancy was most strongly influenced by snow depth and snow compaction as well as habitat type. Canid species used areas with shallow and compact snow while mustelid species used deeper and fluffier snow conditions most often, and lynx used areas with shallow and fluffy snow. Forested habitat types were used most commonly across all mesocarnivores. Prey abundance and the presence of human activity were less influential to mesocarnivore occupancy patterns than snow conditions and habitat, suggesting that a changing boreal climate may have a strong, direct influence on the distribution of these mesocarnivores. Estimating current population status of these species is particularly important in areas that are most susceptible to change, and I used two occupancy-modeling methods and a spatially explicit capture-recapture density estimator to assess coyote and red fox populations. Occupancy and density are two distinct parameters, however, the simplicity of occupancy (both in terms of sampling and modeling) makes its use as a proxy for density an appealing possibility. I found that occupancy and density estimates were not consistent and led to significantly different inference about coyote and red fox populations. Coyotes and red fox occupancy probabilities were similar to each other (range: 0.34-0.48), but red fox density was nearly four times greater than coyote density. While both methods produced precise parameter estimates, top-ranking occupancy and density models were different. I suggest that managers use caution when using occupancy as a proxy for density. Occupancy is best used to address questions related to spatial use, while density should be used to assess population size. Together, these findings provide valuable information about the current status of a previously unstudied mesocarnivore community and provide managers with useful insight into study design and management actions that should be taken to best protect this guild.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

Many people, organizations, and businesses were instrumental in the success of this research project. My major advisor, Laura Prugh, provided me with an unbelievable opportunity that most certainly changed my life. Her trust in me, continued encouragement and support, and endless enthusiasm guided me throughout this process, and for that I am truly grateful. Thank you to the members of my graduate committee, Mark Lindberg and Kris Hundertmark, for providing invaluable advice and expertise that I could always count on. I am also extremely grateful to all of the Prugh research lab members for creating an outstanding atmosphere of knowledge and friendship. Special thanks to Kelly Sivy, without whom this project would not have been possible; I could not have asked for a better partner to jump into the trenches with. Thanks to my other co-authors Kevin Colson, and Mathew Mumma for helping plan this research project, analyze data, and prepare manuscripts. Thanks to my two brave field technicians, Claude Bondy and Phillip Baigas, for enduring 3 months in the wilderness with me. Field and logistical support was provided by the Alpine Creek Lodge, ABR Inc., and Alaska Earth Sciences. Thanks to Brian Lawhead for help with reporting and funding administration. Primary funding for this research came from the Alaska Energy Authority. Thanks to the Alaska Department of Fish and Game for loaning field equipment and the University of Alaska Museum for loaning tissue samples for genetic analysis. Carol Piser and Jeff Baxter in the Biology and Wildlife office have been friendly and helpful since day one, and I thank them for all of the work that they do for our department. Thanks to all of my friends who have struggled with me throughout this process, and kept me in just the right amount of trouble during my time at UAF. Most importantly, I want to thank my family for all of their love and unwavering support. I

would not be where I am today without my sister, Emaline, and my parents, Steve and Betsy; I love you all.

CHAPTER 1. GENERAL INTRODUCTION

Mesocarnivores make up a diverse and wide ranging guild that has been shown to drive community structure and play a key role in shaping ecosystems (Roemer, Gompper & Van Valkenburgh 2009). A mesocarnivore can be defined as any carnivore species that is subordinate and physically smaller than the apex predator species in a community. The term mesocarnivore is therefore relative, and the criteria for what defines a mesocarnivore can vary among ecosystems (Prugh *et al.* 2009). Though these species are far more numerous than larger and more charismatic apex predator species, they have been somewhat neglected in the conservation and research community until fairly recently (Roemer, Gompper & Van Valkenburgh 2009). Significant declines in apex predator numbers across the world may be the primary reason that attention has started to shift to these smaller predators (Ripple *et al.* 2014).

With declines in apex predator species, primarily brought on by human-caused habitat loss and persecution (Ripple *et al.* 2014), mesocarnivores have taken the place atop the food chain in many parts of their range. Mesocarnivores that were previously suppressed by large apex species can experience dramatic population growth in the absence of those dominant species in a phenomenon called mesopredator release (Soulé *et al.* 1988). As mesocarnivores are released from suppression, they begin to exert more pressure on their primary prey resources leading to top-down trophic cascades (Ritchie & Johnson 2009). Examples of the mesocarnivore release phenomenon can be found worldwide, most commonly in terrestrial systems (Prugh *et al.* 2009; Ritchie & Johnson 2009). In areas where both apex- and mesocarnivores coexist, there is much debate over the role that each plays within the community and how interactions between species dictate those roles (Gehrt & Clark 2003; Mech 2012; Allen *et al.* 2014). These questions arise due to the recognized importance of these species to ecosystem structure and function, and the impact that changes to predator populations can have (Ritchie & Johnson 2009; Estes *et al.* 2011; Ripple *et al.* 2014).

Understanding the resource needs and current population status of mesocarnivores is key to better predicting community-wide impacts that could occur due to changes at the top of the food chain. The same threats that have led to the decline of apex predators may also be impacting mesocarnivores across the world. Areas in northern latitudes are particularly vulnerable to landscape-level changes (Travis 2003; Tape, Sturm & Racine 2006; Nikiforuk 2010), yet few studies have examined mesocarnivore communities in these areas. Climate change is one of the biggest threats to ecosystems in northern environments (Olsson 2009; Chapin *et al.* 2014), driving the need to examine habitat requirements for northern and boreal species. Increased anthropogenic activity and development may also cause shifts in mesocarnivore populations (Ordeñana *et al.* 2010; Bateman & Fleming 2012; Savory *et al.* 2014). Not only are northern boreal areas some of the most vulnerable, but areas such as Alaska still contain large and viable apex predator populations as well as numerous mesocarnivore species, all living in sympatry. Gaining a baseline of information on current resource needs and populations levels will allow researchers to manage mesocarnivore species in these areas as changes continue to occur, and will lead to further understanding of the role of these species in the boreal ecosystem and interactions among species.

Monitoring carnivore species can be an extremely challenging task. Many species are wide ranging and often times found at low densities (e.g., Karanth & Nichols 1998; Mowat & Strobeck 2000; Long *et al.* 2011). In addition, monitoring sensitive or vulnerable species may require that researchers prevent any harm or unnecessary stress to an animal, something that can be nearly impossible with traditional capture or trapping survey techniques (Arnemo *et al.* 2006).

For these reasons, non-invasive survey techniques have become increasingly popular for carnivore research (Long *et al.* 2008). Non-invasive techniques allow for the collection of data without the need to tag, collar, or handle the animal of interest. Although there is some information that can only be obtained through the use of radio collars, body measurements, or blood samples, the majority of population demographic information of interest to researchers and managers today can be obtained using non-invasive approaches (Long *et al.* 2008). Most non-invasive surveys can be conducted at a fraction of the cost of a more traditional capture-type survey, and these surveys are often safer (Arnemo *et al.* 2006) and can provide more data than traditional approaches (Prugh 2005). Many non-invasive carnivore surveys have been conducted using motion-sensitive camera traps, hair rub pads, aerial and ground-based track surveys, scat collections, and tracking plates (e.g., Gompper *et al.* 2006; McKelvey *et al.* 2006; Pauli *et al.* 2008; Sarmento *et al.* 2009; Whittington *et al.* 2014). Many traditional statistical analyses can accommodate data from non-invasive surveys, and a suite of newer analytical approaches have also been developed specifically for the use with non-invasive data (MacKenzie *et al.* 2006; Borchers *et al.* 2014). These tools make it more logistically and financially feasible to monitor mesocarnivores, especially in regions with challenging conditions like those encountered in interior Alaska.

Interior Alaska harbors a unique guild of mesocarnivores found few other places in the world. Two of the most common species include coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*). The red fox is the most widely distributed canid in the world and has been the subject of extensive research (Larivière & Pasitschniak-Arts 1996). Coyotes are also extremely abundant and adaptable throughout North America, but they are relatively new to Alaska, having only inhabited the state since the turn of the 20th century (Young & Jackson 1951). While these two canids live in sympatry in many regions, they rarely co-occur with mesopredators such as wolverine (*Gulo gulo*) and marten (*Martes americana*) as they do in Alaska. The wolverine is the largest terrestrial mustelid species and is well known for its dependence on snow-covered high elevation environments, making it a relatively common species in the Alaska Range (Kilström 2004). Marten are far more abundant across North America, but are restricted to heavily timbered regions like those found in the boreal forest of interior Alaska (Zielinski *et al.* 2005). Another forest specialist found in the interior is the Canada lynx (*Lynx canadensis*). This felid is one of the most famous examples of a dietary specialist due to its dependence on snowshoe hares (*Lepus americanus*) throughout its range (Ruggiero *et al.* 2000). These five species share a majority of the landscape in Alaska's interior, yet little information is known about how they use that landscape or about the current status of their populations.

In Chapter 2 I evaluated current patterns in mesocarnivore occupancy in the interior of Alaska. I collected presence-absence data on coyote, red fox, lynx, wolverine, and marten populations by performing snow tracking surveys during two winter field seasons. My goal was to estimate current occupancy probabilities of these species. Occupancy modeling is a tool that allows researchers to predict spatial use patterns of a target animal species, while simultaneously accounting for imperfect detection of that species during surveys (MacKenzie *et al.* 2006). I tested the influence that habitat type, prey abundance, snow conditions, and anthropogenic activity had on each species' occupancy in the study region. I predicted that these different landscape factors would have different influences on the mesocarnivore species of interest. It is expected that through climate change and increasing levels of anthropogenic activity and development, the landscape in northern boreal regions will change dramatically in the near future (Winfree *et al.* 2014; Marcot *et al.* 2015). The results from Chapter 2 provide important baseline data that can be used to manage mesocarnivore species by highlighting key resources that each species relies on in this region.

In Chapter 3 I evaluated two distinct non-invasive survey and modeling methods. I focused on gaining information on current coyote and red fox population dynamics in the interior of Alaska using dynamic occupancy models that included additional parameters to calculate site colonization and extinction (MacKenzie *et al.* 2003). In addition, I used a scat collection survey to procure genetic samples from these canid species and used a spatially explicit capture-recapture model to estimate population density (Borchers & Efford 2008). My goal with this chapter was to compare the modeling techniques and assess the consistency between results. While these methods each allow for non-invasive sampling, collecting data to estimate density is often a more labor intensive and expensive process. For that reason, it has been proposed that occupancy probability can be used as a less expensive index of density (Clare, Anderson & MacFarland 2015). I assessed the consistency between these two methods, and in doing so provided new data about Alaska's coyote and red fox populations.

CHAPTER 2. BOTTOM-UP DRIVERS OF BOREAL MESOCARNIVORE OCCUPANCY: VARIABLE EFFECTS OF SNOW CONDITIONS ACROSS SPECIES[1]

2.1. ABSTRACT

1. Mesocarnivores in northern regions are facing dramatic landscape alterations due to climate change and increasing levels of anthropogenic activity. Shifts in carnivore community structure can lead to cascading effects throughout entire ecosystems, but impacts of climate and landscape perturbations on mesocarnivore communities remain poorly understood.
2. We used snow-tracking surveys of five sympatric mesocarnivores over two winters in interior Alaska, U.S.A to identify primary factors affecting their occupancy. We evaluated the effects of snow depth and compaction, anthropogenic activity, prey abundance, and habitat type on occupancy of each species while accounting for detectability.
3. Snow depth and snow compaction were the best predictors of mesocarnivore occupancy, receiving over 90% AIC support in our model set. Coyotes (*Canis latrans*) and red fox (*Vulpes vulpes*) occurred in areas of shallow, compact snow, lynx (*Lynx canadensis*) occurred in areas of shallow, fluffy snow, and wolverines (*Gulo gulo*) and marten (*Martes americana*) occurred in areas of deep, fluffy snow.

---

[1] Prepared for submission in the Journal of Animal Ecology as Pozzanghera, C.P., Sivy, K.J., Lindberg, M.S., and Prugh, L.R. 2015.Bottom-up drivers of boreal mesocarnivore occupancy: variable effects of snow conditions across species.

4. Habitat had a strong influence on guild-wide occupancy, with most species showing similar patterns of use across broad habitat types. Prey abundance and levels of anthropogenic activity were relatively poor predictors of mesocarnivore occupancy.
5. Altered snow conditions due to climate change may have strong direct effects on the distribution of northern mesocarnivores. As the climate continues to warm, snow depth in northern boreal regions is likely to become more variable in space and time, and warmer temperatures should increase snow compaction. Distribution of mesocarnivores in northern regions may begin to mirror those currently found in more southern populations, with widely distributed canid populations and more isolated mustelid and lynx ranges.

2.2. INTRODUCTION

Mesocarnivores have a central role in ecosystems (Roemer, Gompper & Van Valkenburgh 2009). Interspecific interactions between meso- and apex predator species, and the resulting impacts on lower trophic levels, have been well documented and highlight the profound impact carnivores can have at a community scale (e.g., Crooks & Soule 1999; Prugh *et al.* 2009; Levi & Wilmers 2012). Most studies of mesocarnivores have focused on these intraguild interactions, whereas fewer studies (e.g., Rose & Polis 1998, Riley *et al.* 2003; Bateman & Fleming 2012) have investigated the effects of bottom-up and abiotic factors, such as climate change and human development, on their dynamics. However, mesocarnivores inhabiting northern boreal environments are affected by many landscape level factors likely to experience significant changes into the foreseeable future and therefore it is important to better understand the effects of these factors on mesocarnivore distribution.

The boreal ecosystem represents the world's largest terrestrial biome and makes up 38% of the world's forest cover (Olsson 2009). This region has also experienced some of the most dramatic climate-change impacts around the world (Post *et al.* 2009). Current climate predictions indicate that boreal regions will experience temperature rises in both winter and summer, and increases in precipitation throughout most of the year (Olsson 2009; SNAP 2015). In areas where winter warming is projected to result in above freezing average temperatures, this could result in less total snow accumulation and more rain. However, in areas where temperatures are still expected to stay below freezing, the increases in precipitation will likely result in deeper and more frequent snow. With these changes, it is expected that the composition and distribution of many habitats will shift. Russia's boreal forest is expected to undergo a massive shift from deciduous to coniferous tree species over the next 200-500 years; a shift that is creating a feedback loop and accelerating the warming process (Shuman, Shugart & O'Halloran 2011). In North America, increasing temperatures are expected to steadily decrease boreal forest habitat due to increases in wildfire frequency and severity and insect infestations (U.S. Environmental Protection Agency 2013). In addition, shrub species are experiencing both latitudinal and elevational range expansion and are encroaching on tundra habitats (U.S. Environmental Protection Agency 2013). Many small mammal and ungulate populations, which mesocarnivores depend on as a food source, are also likely to change as a result of boreal climate shifts (Marcot *et al.* 2015).

In addition to a changing climate, increased human development and anthropogenic activities are changing northern ecosystems (Johnson *et al.* 2005). The conversion of boreal forest into agricultural or developed areas has been well documented across northern latitudes (Östlund, Zackrisson & Axelsson 1997; Hobson, Bayne & Van Wilgenburg 2002). Boreal regions also contain important reservoirs of fossil fuels and are home to some of the largest energy production facilities in the world (Economides & Wood 2009; Nikiforuk 2010). Pressure to find alternative forms of energy have resulted in an increase in hydroelectric, wind, and solar energy exploration projects, all of which result in changes to the landscape through construction of roads and habitat loss or alteration. While landscape changes may be necessary to accommodate growing human populations, impacts on wildlife can be significant (Cameron *et al.* 1992; Amstrup 1993). These changes could directly impact mesocarnivore species by allowing greater access for hunting and trapping activity, fragmenting important habitat patches, or supplementing mesocarnivore diets with anthropogenic food sources (Savory *et al.* 2014).

We examined how snow conditions, prey abundance, habitat type, and current levels of anthropogenic activity influenced winter occupancy of coyotes (*Canis latrans*), red fox (*Vulpes vulpes)*, lynx (*Lynx canadensis)*, wolverine (*Gulo gulo)*, and marten (*Martes americana)* in Alaska's boreal forest. Winter is a critical period for mesocarnivores; coyotes, red fox and lynx generally breed between January and April, and parturition occurs during late winter for wolverine and marten (Buskirk 1983; Kilström 2004; Perrine 2005; Fanson *et al.* 2010). Food is most limiting in winter, and climate change is predicted to have especially strong effects on winter conditions in Alaska (SNAP 2015). Large-scale energy development is also on the rise in this region, and projects such as the proposed Susitna-Watana Hydroelectric Dam may alter the landscape in the near future (Alaska Energy Authority 2014). Understanding current mesocarnivore responses to bottom-up forces and establishing baseline population dynamics is key to monitoring shifts in this guild over time as landscapes continue to change.

Although the diet and space use of sympatric species within mesocarnivore guilds can overlap substantially (Ruggiero *at al.* 1994; Riley *et al.* 2003; Schuette *et al.* 2013; Goad *et al.*

2014), interspecific differences may lead to divergent effects of climate or land use change on each species. Species like the coyote and red fox are considered "human commensal"; they are highly adaptable and able to benefit from activities such as road construction and development (Young & Jackson 1951). Coyotes and red foxes, along with wolverine, are considered habitat and foraging generalists in northern regions, which aids in their adaptability to a variety of environments and environmental conditions (Kamler & Gipson 2000; Grinder & Krausman 2001; Kilström 2004; Perrine 2005). Marten are also able to exploit a wide range of prey resources but are fairly restricted to mature forest habitat (Zielinski *et al.* 2005). Lynx, perhaps one of the best examples of a predatory specialist, are well known for their dietary dependence on snowshoe hare (*Lepus americanus*) and are therefore associated with mature or mixed-age forest and tall shrub habitats that support hares (Ruggiero *et al.* 2000). The desirability of these species for their fur also may play a role in how land use changes can impact mesocarnivore distributions. If increased anthropogenic activity leads to increased access into new areas for trappers, valuable species like marten, lynx, and wolverine may be more susceptible to harvest.

We used occupancy modeling, which uses repeated presence-absence survey data to estimate detectability and spatial use patterns, to address four main predictions about the effects of bottom-up factors on mesocarnivores (MacKenzie *et al.* 2002). First, we predicted that snow conditions (depth and compaction) would have a strong influence on mesocarnivore occupancy. We expected snow depth to negatively affect all species except lynx. Increasing snow depth can hinder most species' ability to effectively move and forage, but the low foot-load of lynx (4.1-8.8 times less than that of coyotes) enables them to move on top of the snow where other species will sink in (Halpin & Bissonette 1988; Murray & Boutin 1991). Because small mammal prey such as snowshoe hares are also able to stay on top of the snow, species like coyotes are forced to change their hunting behavior from chasing to a less familiar ambushing approach in deep snow, whereas lynx have a more adaptable hunting approach and can effectively hunt with a chasing or ambushing strategy (Murray & Boutin 1991, Murray *et al.* 1995). Further, we expected snow compaction to positively affect coyotes and foxes. Compact snow allows canids to move across the landscape quickly, aiding in their ability to avoid competitors and increasing their effectiveness at catching prey in a traditional chasing manner.

Second, we predicted that habitat would strongly influence mesocarnivore occupancy at the guild level, and that species-specific differences in habitat affiliation would occur based on individual species' behavior. For specialist species (lynx and marten), we expected relatively high occupancy probabilities in forested habitats based on their prey requirements and species behavior (Ruggiero *et al.* 2000; Zielinski *et al.* 2005). For generalist species (wolverine, coyote and fox), we did not expect to find differences in occupancy based on habitat type because these species are well adapted to a variety of habitats. Third, we predicted that prey abundance would be a strong predictor of overall mesocarnivore occupancy, and that individual mesocarnivore species would all have positive responses to areas with high prey abundance.

Finally, we predicted that anthropogenic activity would have a neutral or positive effect on occupancy for coyote and red fox and a negative effect on the remaining species. Valuable fur or a dependence on contiguous habitat tracts may reduce the probability of wolverine, marten, and lynx occupancy in heavily populated human areas, whereas canid pelt prices are far lower (Dorendorf 2015) and canids have been shown to thrive in human-dominated landscapes (Bateman & Fleming 2012). We expected canids to use snowmachine trails and established recreational areas to take advantage of anthropogenic food sources and pre-packed trails for easy traveling (Grinder & Krausman 2001; Goad *et al.* 2014).

2.3. MATERIALS AND METHODS

2.3.1. Study Region

Our study region included two study sites (hereafter, “Denali” and “Susitna”) within the central Alaska Range of interior Alaska (Fig. 2.1). Boreal forest (including spruce *Picea spp.*, aspen *Populus spp.* and birch *Betula spp.*), deciduous shrub, and tundra habitats dominate the landscape across both sites. This region is characterized by short summers and long, cold winters with ground-covering snow that can last from September until May (Shulski & Wendler 2007). Wolves (*Canis lupus),* black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) were present in the region, as well as caribou (*Rangifer tarandus*) and moose (*Alces alces*). The Denali study site was a 2000-km^2 area made up of federal, state, and private lands including the northeastern portion of Denali National Park and Preserve (DNPP) along with portions of the Stampede corridor, a 470-km^2 parcel of state and private land. DNPP represented an ecosystem that was relatively undisturbed and lacked anthropogenic habitat alterations and hunting or trapping pressures. Transportation within DNPP during the winter was restricted to ski and dog team. In contrast, the Stampede corridor, located outside of DNPP, was used for hunting, trapping, and motorized recreation vehicles and home to several hundred year-round residents. The Susitna study site was approximately 145 km southeast of the Denali study site and consisted of 1800 km^2 of primarily public (state and Bureau of Land Management) or Alaska Native corporation lands. Although this area did not include any protected areas and harvest of all five target species of mesocarnivores was allowed, it was less developed and less traveled than the Stampede corridor portions of the Denali study area. However, the proposed Susitna-Watana hydroelectric dam site was located in the southwest corner of the study area, and proposed transmission lines and new road corridors would span the entire latitudinal range of the study area (Alaska Energy Authoity 2014).

2.3.2. Survey Methods

We used a grid-based sampling design to collect data on mesocarnivore presence, prey abundance, snow depth and compaction, and habitat characteristics within our study region. We used ArcGIS (version 10.1, ESRI, Redlands, California) to overlay each study area with a grid of 2x2-km cells. This cell size (4 km^2) was chosen because it most closely matched marten home range size, the smallest of our target species (Buskirk 1983). Analysis at this spatial scale represents true occupancy probability for marten, but the assumption of spatial closure was likely violated for the other species. Thus, "occupancy probabilities" correspond to probabilities of use for foxes, coyotes, lynx, and wolverine. For simplicity, however, we refer to these as "occupancy probabilities" for all species. We assigned each grid cell one of three habitat types (forest, shrub, or tundra) based on the dominant vegetation cover type within the cell, as calculated from satellite imagery (Homer *et al.* 2007). Fine-scale habitat data (percent cover and composition of trees and shrubs) were also collected within each cell during winter surveys. Preliminary analyses revealed that fine-scale habitat data did not improve the occupancy models, and we therefore used the broad categorical habitat classifications in final model sets.

A stratified random sample of cells was selected from each study site based on the proportion of cells within each habitat classification. Each cell was further classified as either an area of high or low anthropogenic activity, relative to the surrounding region (Fig. 2.1). This distinction was made based on the sample cell's proximity to human residences and development, ease of access (based on road and/or trail density), and land ownership. Cells within DNPP were classified as low activity cells, and all cells within the Stampede Corridor were classified as high activity. Cells in the Susitna area were classified as high activity if they were found along the Denali highway or along the main winter trapping and hunting snowmachine trail. High activity areas were relative to our study region only and were not comparable to large metropolitan areas or other urbanized regions.

Surveys were conducted by two researchers within each study site from January to March, 2013 - 2014. In 2013, we evaluated the efficacy of three survey techniques: linear transects (n = 51 cells), square transects (n = 39 cells), and remote cameras (n = 45 cells). Cameras provided too few photos, and these cells were excluded from analyses. The linear transect method used temporal replication to estimate detection probabilities, whereas the square transects used spatial replication, which eliminated the need for return visits to the cell (MacKenzie *et al.* 2006). Where terrain allowed and snowmachine use was permitted, cells were surveyed by snowmachine. Where snowmachine use was prohibited (i.e., designated wilderness areas in DNPP) or impractical due to terrain, we surveyed linear transects by dog team or on foot. Areas surveyed by dog team were frequented by other dog mushers as well. Square transects were 1 km on each side and surveyed in a single visit. Linear transects were 1.87 km long on average (SE = 0.063), and they were surveyed repeatedly throughout the winter (range = 2-10 repeats, mean = 3.88). In 2014, we re-surveyed the randomly generated cells from 2013 and also surveyed those cells that we travelled through en route to the random cells (Fig. 2.1). All cells in 2014 (n=210) were surveyed using linear transects with temporal replication. This allowed us to increase our sample size and survey efficiency.

For all transects, we recorded all target mesocarnivore tracks encountered during the survey. We also recorded snow depth and snow compaction at the start of each transect and every 500 m thereafter. Snow compaction was indexed by measuring the sink depth of a 198-g tuna can (diameter = 8.2 cm and height = 4.2 cm), dropped from 50 cm above the ground. Snow conditions were also recorded at each encountered mesocarnivore track, and we also recorded the sink depth of a randomly-selected paw print (measured from the center of the pad) to assess the relationship between snow conditions and each species' sinking depth. We tallied the number of ptarmigan and grouse (Phasianidae family), snowshoe hare, red squirrel (*Tamiasciurus hudsonicus*) and vole (Cricetidae family) tracks encountered at 500-m intervals. For each carnivore track encountered, we identified it to species and marked the location on a handheld GPS unit (Garmin eTrex30, Garmin Ltd.). Because snow conditions can affect detection probability, we conducted surveys after a minimum of 24 h since the last track-obliterating snowfall to allow adequate time for tracks to accumulate, and no more than 7 days after a snowfall to prevent tracks from becoming too melted out, windblown, or otherwise disrupted.

2.3.3. Occupancy Analysis

We used single-season, single-species occupancy models to estimate occurrence (use) probabilities of the target mesocarnivore species. The single-season occupancy model provides estimates of two response parameters: probability of site occupancy (ψ), and detection probability (p), which is the probability that the target species is detected given that it is present (MacKenzie *et al.* 2002). Although two seasons of data were included in our analysis, we used a single-season model framework and included year as a covariate in our candidate model set because we were most interested in factors affecting use, not occupancy dynamics that would require estimation of colonization and extinction parameters. Similarly, species was included as a covariate, which allowed us to combine data from all species into one database and develop models to examine species-specific differences as well as guild-wide patterns. All analyses were performed in program R version 3.1.0 (R Development Core Team 2014) using packages unmarked (Fiske & Chandler 2011) and AICcmodavg (Mazerolle 2015).

We included two survey-specific covariates and nine site-specific covariates in our models using a logit link function. Survey covariates were: number of days since the last snowfall (DSLS) and total distance (km) surveyed within a sample cell (DIST). Site-specific covariates were: study year (YEAR), survey method (METHOD), study area (AREA), habitat type (HABITAT), species (SPECIES), level of anthropogenic activity (ACTIVITY), average snow depth over all survey occasions (DEPTH), average snow compaction over all survey occasions (COMPACTION), and average total combined prey species abundance per km surveyed, adjusted for days since last snowfall (PREY). We calculated average snow depth, snow compaction, and prey abundance within each habitat type and used a Pearson's correlation matrix to test for correlation between continuous covariates. DSLS, DIST, DEPTH, COMPACTION, and PREY were standardized for analyses.

We used a three-step process to develop a finalized candidate model set that was both biologically relevant and analytically feasible. We ranked all models based on AICc and QAICc (Burnham & Anderson 2002). First, we constructed models to estimate p while holding ψ constant (Schuette *et al.* 2013), using all combinations of DSLS, DIST, YEAR, METHOD, AREA, and SPECIES. The top-ranking model contained DSLS, DIST, AREA, and SPECIES, and received 37% AICc weight. The next best model contained DSLS, DIST, YEAR, AREA, and SPECIES and received 32% AICc weight. Both models received significant support (Δ AICc < 1), therefore we used all covariates from the more parameterized model, p(DSLS+DIST+YEAR+AREA+SPECIES), in the next steps in order to account for all relevant predictors of p.

In the second step, all combinations of YEAR, AREA, HABITAT, SPECIES, ACTIVITY, DEPTH, COMPACTION, and PREY were used to build models that estimated ψ while p was modeled as a function of covariates from step one. This resulted in a full candidate set of 256 additive models. We used this full set of models to calculate summed individual covariate weights to assess the relative importance of each predictive covariate on guild-wide occupancy. Covariates with weights > 50% were considered important (Burnham & Anderson 2002). In step three, we used a Δ AICc ≤ 2 cutoff to reduce the full candidate set down to the top 10 models. We supplemented this model set with seven interaction models and a null model, for a final candidate model set of 18 models. Each of these seven models contained an interaction term between SPECIES and one of the other seven covariates used to model occupancy. These models were developed in order to directly address our species-specific predictions about the influence of snow, habitat type, prey, and anthropogenic activity on occupancy.

We assessed fit of the data by evaluating the most complex model in the candidate set using a Pearson χ^2 goodness-of-fit test (MacKenzie & Bailey 2004) using package AICcmodavg with 1000 bootstrapped simulations. We used an estimate of the overdispersion factor ($\hat{c}$) to evaluate the dataset and identify potential overdispersion or independence violations. Violating the assumption of independence can lead to spatial autocorrelation issues and result in overly precise variance estimates (MacKenzie *et al.* 2006). We found a $\hat{c}$ value of 1.87, suggesting reasonable fit, and we therefore used the quasi-corrected AICc (QAICc) to rank the final 18-model set. In addition, we used the estimate of $\hat{c}$ to inflate standard errors to account for overdispersion (Burnham & Anderson 2002).

Species-specific occupancy and detection probability estimates were generated from the best-supported model (lowest QAICc) in the final 18-model set. We addressed our predictions by describing the influence of each explanatory covariate on guild-wide mesocarnivore occupancy using summed AICc weights from the full, additive model set, and we addressed species-specific occupancy predictions using the final model set with interaction terms.

2.4. RESULTS

Both snow conditions, DEPTH and COMPACTION, strongly influenced guild-wide mesocarnivore occupancy as well as species-specific occupancy probabilities. Snow DEPTH and COMPACTION received 55.5% and 68.2% AICc support weight in the additive model set (Table 2.1) and the top two ranking models based on the final 18-model set (which had a combined 92.0% QAICc weight) both estimated occupancy as a function of species and snow condition interactions (Table 2.2).

Overall occupancy (i.e., the proportion of survey cells across both areas that were occupied or used; (ψ ± SE)) was highest for wolverines (0.62 ± 0.09) and lowest for marten (0.19 ± 0.04). Coyotes (0.36 ± 0.05), red foxes (0.50 ± 0.05), and lynx (0.45 ± 0.07) had similar, intermediate occupancy probabilities. We used our top-ranking model (ψ(SPECIES*COMPACTION) to produce these estimates while holding COMPACTION at its mean value. Detection probabilities (p ± SE) from this top-ranking model were greatest for red fox in Susitna during 2013 (0.40 ± 0.05) and lowest for wolverine in Denali in 2014 (0.13 ± 0.03). Overall, detection probabilities were lower in the Denali site than the Susitna site (Fig. 2.2). Although survey effort increased during the 2014 season, detection (logit-transformed model coefficients ± SE) decreased during that year ($\beta = -0.13 \pm 0.13$).

We predicted that snow depth would negatively impact all species except lynx. However, areas with deeper snow were less likely to be occupied by coyotes ($\beta = -0.28 \pm 0.20$), red fox ($\beta = -0.21 \pm 0.27$), and lynx ($\beta = -0.57 \pm 0.37$), and more likely to be occupied by wolverine ($\beta =$

0.96 ± 0.33) and marten (β = 1.27 ± 0.36) (Fig. 3.3 A). Coyotes (β = -0.23 ± 0.19) and red foxes (β = -0.16 ± 0.27) had higher occupancy probabilities in areas with compact snow, whereas lynx (β = 0.83 ± 0.33), wolverine (β = 0.88 ± 0.33), and marten (β = 1.44 ± 0.37) had higher occupancy probabilities in areas with fluffy snow (Fig. 3.3 B). Average (mean ± SE) sink depth of snow tracks was greatest for lynx (6.3 cm ± 0.3) and wolverine (6.5 cm ± 0.3) and lower for coyote (4.5 cm ± 0.2), fox (4.1 cm ± 0.2), and marten (4.4 cm ± 0.2). Snow depths (mean ± SE) were similar in shrub (44.2 ± 1.8) and forest (39.0 ± 2.1) habitats and lowest in tundra (28.4 ± 2.2). Compaction was greatest (least penetrable snow) in the tundra (4.9 ± 0.3) and least (most penetrable snow) in the forest (8.0 ± 0.3). There was low correlation between snow (DEPTH and COMPACTION) and total prey species abundance (-0.19 and -0.22, respectively). Prey abundance was highest in forest habitats (7.6 ± 1.5 tracks per km*day), moderate in shrubs (3.2 ± 0.4), and lowest in tundra (1.8 ± 0.2).

We predicted HABITAT would be an important explanatory covariate of guild-wide as well as species-specific mesocarnivore occupancy. Our full model set indicated that HABITAT was indeed the most influential variable on guild-wide occupancy (Table 2.1). Based on model ψ(HABITAT+SPECIES), probability of occupancy (logit-transformed model coefficients ± SE) was highest in the forest (β = -0.05 ± 0.28) and lowest in the open tundra landscapes (β = -1.27 ± 0.27) across all species. We also predicted that specialist species would prefer forested habitats whereas generalists would show little preference among the three major habitat types. Model ψ(HABITAT*SPECIES) revealed that lynx and marten (known habitat specialists) indeed had highest occupancy probabilities in forested habitat and the remaining species (habitat generalists) had more equally distributed occupancy probabilities among the three habitat categories, but patterns of habitat use across all species were quite similar (Fig 3.4). Although habitat strongly influenced guild-wide mesocarnivore occupancy, the ψ(HABITAT*SPECIES) model had little support (Δ QAICc > 12.0), indicating that other factors had more effect on use.

Total prey species abundance was a poor predictor of guild-wide mesocarnivore occupancy (Table 2.1). The influence of PREY on mesocarnivores at the species-specific level was assessed in model ψ(SPECIES*PREY) (Table 2.2). Probability of occupancy (logit-transformed model coefficients ± SE) increased in areas of greater prey abundance for coyotes ($\beta = 0.71 \pm 0.33$), lynx ($\beta = 5.52 \pm 2.83$), and wolverine ($\beta = 2.21 \pm 1.70$), and decreased with greater prey abundance for red fox ($\beta = -0.90 \pm 0.38$) and marten ($\beta = -1.33 \pm 0.53$). However, this model received little support (QAICc weight = 3%).

Lastly, we predicted that occupancy would be negatively impacted by areas of high anthropogenic activity for all species other than coyotes and red foxes. In high activity areas, marten had very low occupancy probabilities, and coyotes and lynx had the highest probabilities of occupancy (Fig. 3.5), but we found little support to suggest that species-specific occupancy probabilities were influenced by ACTIVITY (Table 2.2). Similarly, guild-wide mesocarnivore occupancy was not strongly affected by anthropogenic activity (Table 2.1).

2.5. DISCUSSION

Our analysis of northern mesocarnivore occupancy indicates that abiotic factors strongly affect this important guild and the potential effects of future climate-induced change may be profound. Understanding how abiotic and bottom-up forces drive species distributions is vital. Landscape level changes, including those brought on by climate and anthropogenic factors, are imminent across much of the northern boreal regions and we have shown the importance of several landscape factors on mesocarnivores. Snow depth and compaction were the most influential predictors of mesocarnivore occupancy that we tested. The negative response to increasing snow depth shown by coyotes and red foxes matched our predictions. Likewise, we found that these species were more likely to occur in areas of more compact snow. Wind-blown regions, river corridors, existing animal travel routes, roads, and trails are all areas that could produce highly compacted and relatively shallow snow conditions, and these areas can allow canids to more successfully chase prey, escape predators by using familiar travel routes, and increase visibility to aid in hunting and predator avoidance (Murray & Boutin 1991; Murray, Boutin & O'Donoghue 1994).

We predicted that lynx, unlike canids, would be more tolerant of deep snow conditions due to their low foot loading (Murray & Boutin 1991; Murray, Boutin & O'Donoghue 1994). Surprisingly, lynx occupancy was lowest among all study species in areas of deep snow. However, their high occupancy probability in areas of less compact (fluffy) snow suggests that overall lynx are most frequently using areas with shallow, but fluffy snow. Lynx may use shallow snow for similar reasons described for canids, to reduce energetic costs, and they may be avoiding travel routes with compact snow that are frequented by canids to avoid competitive interactions (Ruggiero *et al.* 2000). On average we found that lynx sunk into snow more deeply than either canid species, contrary to our predictions and previous findings about foot-load ratios (Murray & Boutin 1991; Murray, Boutin & O'Donoghue 1994). However, the high probability of lynx use in areas with fluffy snow could lead to a deeper sink depth than canids without increasing energetic costs. Similarly, canid sink depth was likely reduced relative to lynx due to their higher use of compacted snow areas.

We found that snow was a better predictor of landscape-scale occupancy than either prey abundance or habitat type, although we recognize that we measured snow conditions and prey abundance at a different resolution than habitat type. Lynx are generally thought to use areas where they can most successfully access their primary prey source, with snow conditions playing a minimal role in use patterns (Ruggiero *et al.* 2000). The highest prey abundance during our study occurred in forested areas with fluffy snow, two conditions that were associated with high probabilities of lynx use. However, there was no direct correlation between snow conditions and prey abundance, and snow depths did not differ between forest and shrub habitats. In addition, lynx spatial use patterns may be determined primarily by snow conditions when there is an increased need for long distance daily travel. This can occur during periods of low snowshoe hare abundance (Ward & Krebs 1985), as was the case during our study.

Mustelids (wolverine and marten) also had highest probabilities of occupancy in areas of fluffy snow, but they were more likely to occur in areas with deeper snow. A previous study of marten in Manitoba found that they occurred across a range of snow depths and were seemingly unaffected by deep snow, possibly using subnivean travel routes under deep snowpack for thermal cover, predator avoidance, and increased access to prey species such as voles (Raine 1983). Similarly, wolverine are known to require persistent spring snow for denning (McKelvey *et al.* 2011), which may explain their occurrence in deep snow areas throughout the winter leading up to the denning period.

Snow conditions strongly affected occupancy of all mesocarnivores in our study, and yet those effects varied substantially among species. Climate change may directly impact these species' space use patterns, and ultimately their distribution. Snow conditions in northern boreal regions of Alaska, and worldwide, are predicted to change dramatically over the next century (Chapin *et al.* 2014; Winfree *et al.* 2014). Warmer temperatures and increased precipitation throughout the winter months may increase the variability of climatic conditions across the boreal regions. Areas projected to warm above freezing may experience more rain, less total snow accumulation and wetter snow that more easily becomes compacted. In those regions, species that use areas with shallow, compacted snow (i.e. canids) may become more widespread and abundant due in part to energetically efficient travel, increased hunting opportunities, and easier predator avoidance. In areas projected to remain below freezing, increases in winter precipitation could increase snow depth, which may favor mustelids by increasing access to spring denning areas and allowing for more consistent subnivean travel corridors. Snow conditions in boreal regions are projected to become similar to current conditions in areas such as the northwestern United States, where mid-elevation mountainous regions experience more winter precipitation as snow, and lower or more coastal regions receive more rain (McKelvey *et al.* 2011; SNAP 2015).

Our study was conducted near the northern edge of the region that harbors all five of our studied mesocarnivore species, with the southern edge of this region extending into the Northwestern United States (US). Although the Northwestern US does contain viable wolverine, marten, and lynx populations, these populations are generally restricted to isolated boreal regions with deep, persistent snow cover (Ruggiero *et al.* 1994). In contrast, coyotes and red foxes are widespread throughout North America, including areas that receive little or no snow (Riley *et al.* 2003). Canids in northern boreal regions may therefore continue to persist and thrive in areas that receive less snowfall, whereas mustelids may become restricted to areas that maintain sub-freezing temperatures consistently through the winter.

Surprisingly, habitat was a poorer predictor of species-specific occupancy probabilities than snow conditions. Thus, the effect of habitat type on occupancy does not appear to vary substantially among species. However, habitat was a strong predictor of occupancy when examining all mesocarnivores together, and we found forest habitat types to be areas of highest occupancy probabilities. The latter results are consistent with previous findings, especially those that describe lynx and mustelid habitat use (e.g., Ruggiero *et al.* 1994; Kilström 2004; Squires *et al.* 2010). We found highest numbers of prey in forest habitats, which could explain higher levels of mesocarnivore use in forested areas. However, we did not find prey abundance to be a strong predictor of occupancy in any analyses. It is possible that prey tracks are a poor index of abundance, especially for species such as voles that can travel below the snow, and ptarmigan that may fly through an area or perch in vegetation, rendering them undetectable via track surveys. Precise, spatially explicit estimates of prey abundance can be difficult to obtain across large study areas required for carnivore studies. Using track counts is one way to easily produce a spatially explicit abundance index, but validation of this method is needed before strong conclusions can be drawn.

Although the generalist species did occur in all habitats, we found strong guild-wide association with forested habitats and fairly weak differences in habitat use between generalist and specialists (Fig 2.4). Climate change may increase shrub and forest cover in some regions (Tape, Sturm & Racine 2006), which we have shown should broadly benefit mesocarnivores. Energy projects such as the Susitna-Watana hydroelectric dam, which is proposed for development in one of our study areas, may have habitat-mediated impacts on mesocarnivores at localized scales. The proposed dam would create a 9,500-hectare inundation reservoir in an area that is currently dominated by mature spruce forest, thereby removing prime habitat for forest specialists such as marten and lynx as well as habitat used by the generalist mesocarnivores. However, local extirpation of forest dependent species is unlikely due to the availability of boreal forest in the outlying regions beyond the inundation zone.

Energy development in boreal regions could affect mesocarnivores by increasing disturbance levels in addition to removing habitat. Levels of anthropogenic activity across our study region had minimal influence on species-specific occupancy and no influence on guild-wide mesocarnivore occupancy. We suggest this finding was due to the relatively low levels of activity in our study region. Our study region experiences very little habitat fragmentation and has a small human population, with the two nearest towns (Healy and Cantwell, AK) containing only 1,240 yearly residents (U.S. Census Bureau, 2010). This area is similar to many other boreal systems, and the low human population density may facilitate avoidance of areas with intensive human activity by mesocarnivores. Our results indicate that current levels of anthropogenic activity in rural boreal areas do not strongly affect mesocarnivore occupancy. However, a marked increase in activity or a large-scale disturbance associated with energy infrastructure could produce different results. If construction of the Susitna-Watana dam moves forward, mesocarnivore occupancy should continue to be monitored to improve our understanding of how mesocarnivores respond to increased anthropogenic activity in boreal regions.

In conclusion, our study indicates that snow conditions likely play a large role in determining guild-wide and species-specific patterns of mesocarnivore occupancy in northern boreal regions. It is likely that there will be winners and losers when it comes to adapting to landscape level changes, and we have shown that snow conditions, which are likely to change dramatically in the near future, may be one of the most significant factors determining who wins and who loses. In turn, the shifting mesocarnivore guild may lead to further community-wide cascading events. Future work should explore the impact of snow conditions on mesocarnivore occupancy over time and across a wider range of boreal environments to assess how patterns of use change with a changing climate. In addition, addressing the link between these abiotic drivers and interspecific interactions may help further explain spatial use patterns.

2.6. ACKNOWLEDGEMENTS

Funding was provided by the Alaska Energy Authority (RSA # 1331 to L.R.P.), a Discover Denali Fellowship to K.J.S., and a National Science Foundation Graduate Research Fellowship (#2012136814) to K.J.S. Administrative and logistical field support was provided by the Alpine Creek Lodge, Alaska Earth Sciences, Alaska Biological Research, Inc., the Murie Science Learning Center, Alaska Geographic, and Denali National Park and Preserve. Earlier drafts of this manuscript were improved by comments from K. Hundertmark, A. Powell, and K. Mulder. We thank field technicians C. Bondy, P. Baigas, and J. Reppert for their hard work and dedication.

2.7. FIGURES

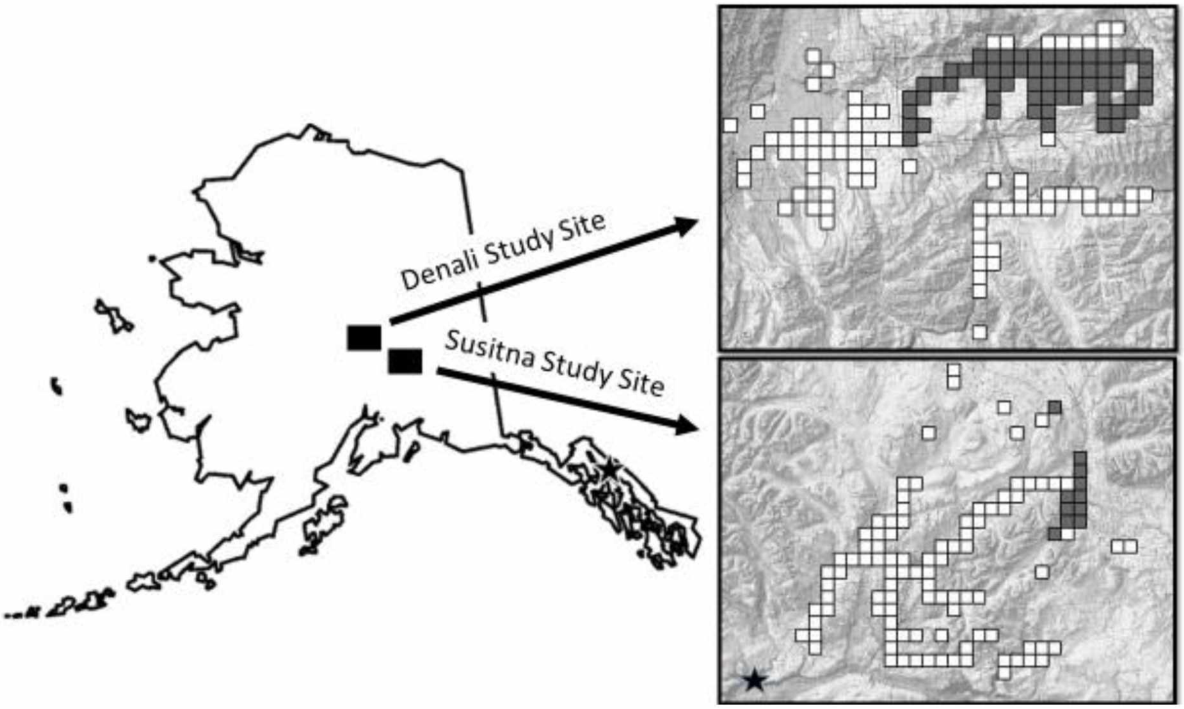

Figure. 2.1. Study area map
Interior Alaska mesocarnivore study region and survey locations including individual 2 x 2 km survey cells (n = 300). Black cells had relatively high levels of anthropogenic activity and white cells had relatively low levels of activity. Cells were surveyed during winters of 2013 and 2014. Black star shows approximate location of proposed Susitna-Watana hydro dam site.

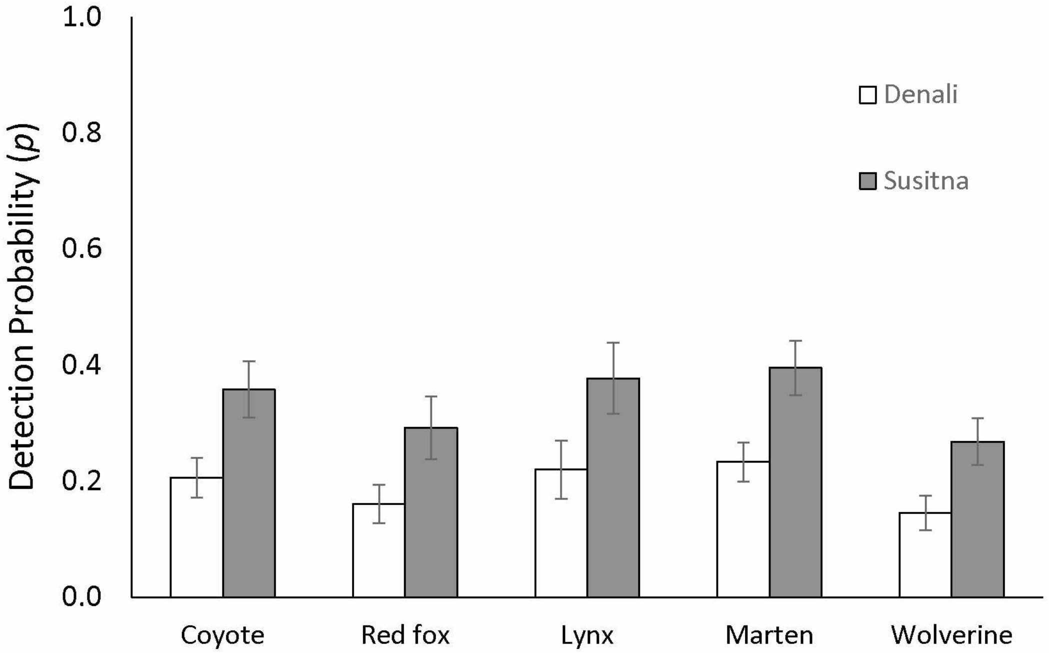

Figure. 2.2. Mesocarnivore detection probabilities
Detection probability estimates with standard errors for each target species by study site in 2013. Estimates were derived from the top ranking overall model: ψ(SPECIES*COMPACTION) p(AREA+DIST+DSLS+SPECIES+YEAR). DIST and DSLS were held at their mean value.

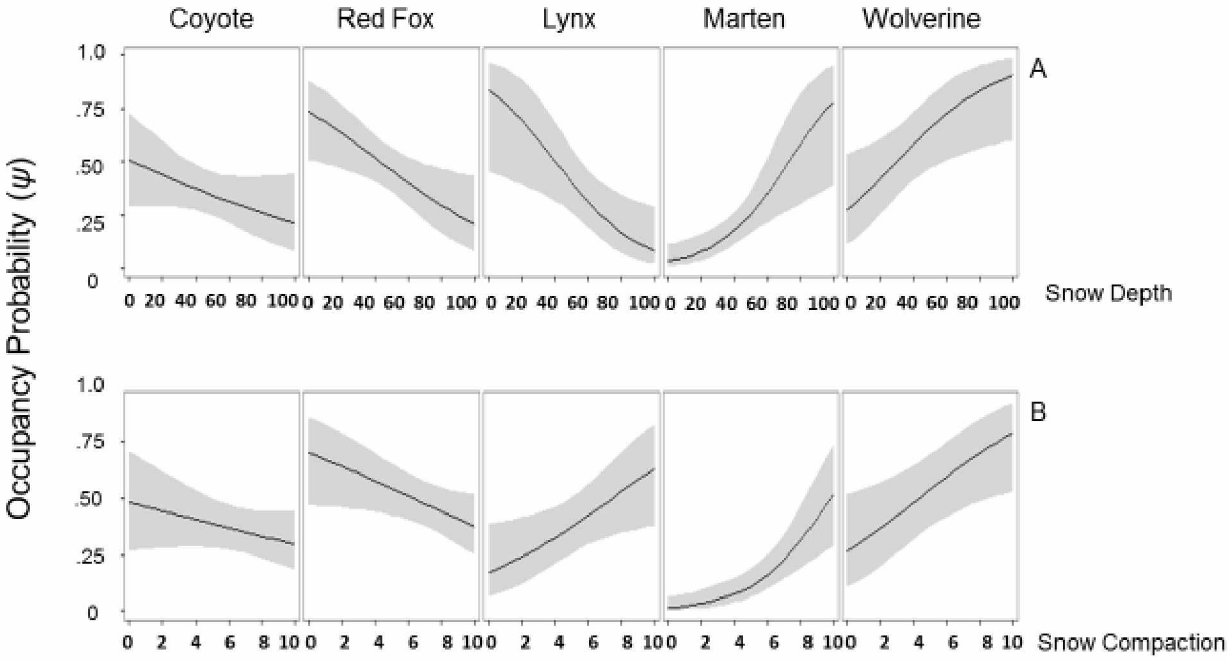

Figure. 2.3. Mesocarnivore occupancy probabilities by snow conditions
Occupancy probability for each target species based on snow conditions within the interior Alaska study region, 2013-2014. Snow depth (panel A) and snow compaction (panel B) are measured in cm. Snow compaction ranges from highly compact (0) to fluffy (10). Error bands represent 95% confidence intervals.

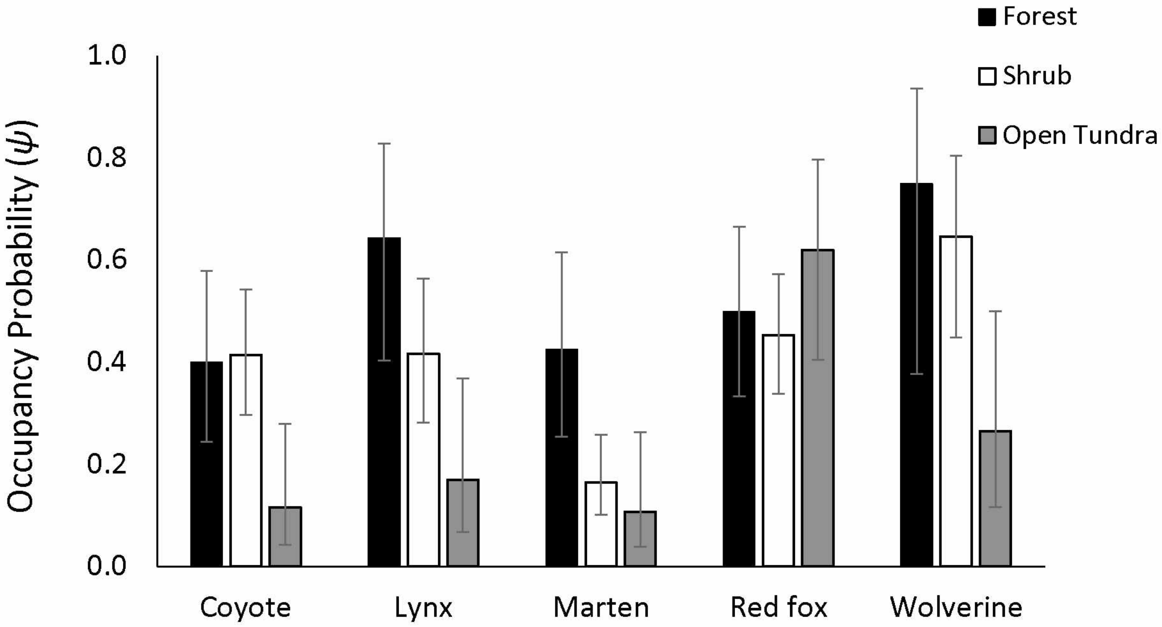

Figure. 2.4. Mesocarnivore occupancy probabilities by habitat type
Species-specific occupancy probabilities across major habitat categories within the interior Alaska study region, 2013-2014. Error bars represent 95% confidence intervals.

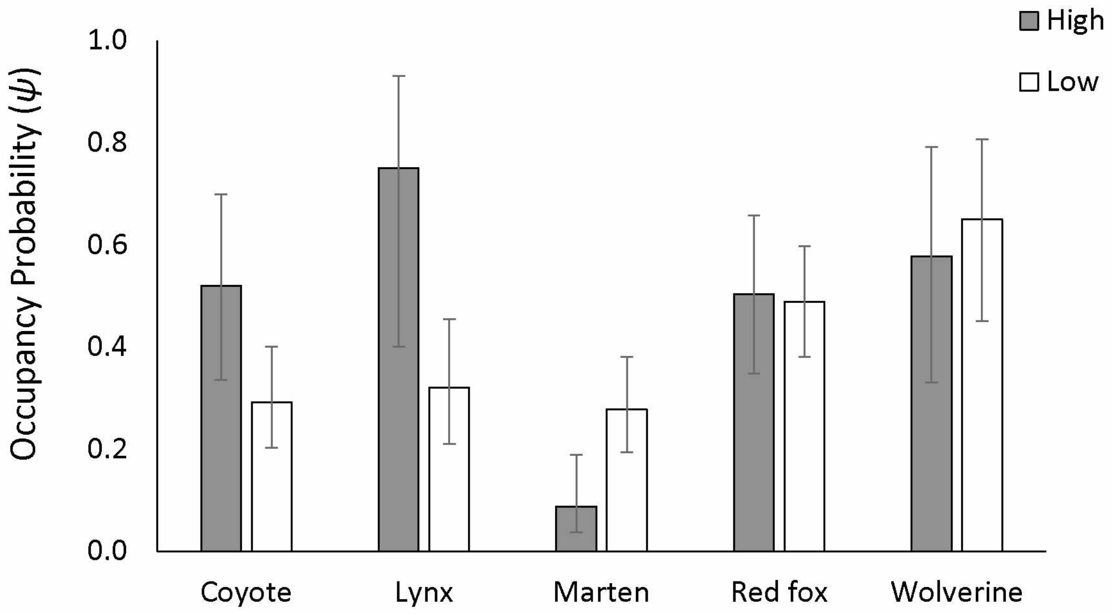

Figure. 2.5. Mesocarnivore occupancy probabilities by levels of anthropogenic activity Influence of high and low levels of anthropogenic activity on occupancy probabilities of interior Alaska's mesocarnivore species, 2013-2014. Error bars represent 95% confidence intervals.

2.8. TABLES

Table 2.1. Predictive covariate summed model weights
Influence of covariates (summed AICc weight) on mesocarnivore occupancy probabilities in interior Alaska, 2013-2014. Levels of each categorical covariate are listed in the description.

Covariate Name	Description	AICc Weight (%)
SPECIES	Target species (coyote, lynx, marten, red fox, wolverine)	99.9
HABITAT	Major habitat type within sample cell (forest, shrub, tundra)	99.2
COMPACTION	Survey cell average snow compaction. Standardized to mean of 0	68.2
DEPTH	Survey cell average snow depth. Standardized to mean of 0	55.5
PREY	Average prey species abundance per cell. Standardized to mean of 0	40.5
AREA	Study site (Denali or Susitna)	34.7
ACTIVITY	Level of anthropogenic activity within cell (high or low)	29.2
YEAR	Study year (2013 or 2014)	27.8

Table 2.2. Occupancy model selection table

Top ranked models explaining mesocarnivore occupancy in interior Alaska, 2013-2014. Models are described by the number of parameters (K), Quasi-Akaike Information Criterion value corrected for sample size (QAICc), change in QAICc (ΔQAICc) and overall model weight (QAICcWt). Models represent the subset with Δ QAICc < 10 from the final set of 18 models. The detection probability, *p,* was modeled as *p*(AREA+DIST+DSLS+SPECIES+YEAR) for all 8 models.

Model Description	K	QAICc	ΔQAICc	QAICcWt
ψ(SPECIES*COMPACTION)	20	1537.39	0.00	0.58
ψ(SPECIES*DEPTH)	20	1538.48	1.09	0.34
ψ(SPECIES*PREY)	20	1543.15	5.76	0.03
ψ(HABITAT+SPECIES)	17	1545.40	8.01	0.01
ψ(HABITAT+SPECIES+COMPACTION)	18	1546.02	8.63	0.01
ψ(HABITAT+SPECIES+SNOW)	18	1546.71	9.31	0.01
ψ(SPECIES*AREA)	20	1546.71	9.32	0.01
ψ(HABITAT+SPECIES+SNOW+COMPACTION)	19	1546.84	9.45	0.01

2.9. REFERENCES

Alaska Energy Authority (2014) Susitna-Watana Hydro. 16 February, 2015. http://www.susitna-watanahydro.org/.

Amstrup, S.C. (1993) Human disturbances of denning polar bears in Alaska. *Arctic,* **46,** 246-250.

Bateman, P.W. & Fleming, P.A. (2012) Big city life: carnivores in urban environments. *Journal of Zoology,* **287,** 1-23.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach,* 2nd edn. Springer Verlag, New York, U.S.A.

Buskirk, S.W. (1983) The ecology of marten in southcentral Alaska. PhD thesis, University of Alaska Fairbanks, U.S.A.

Cameron, R.D., Reed, D.J., Dau, J.R. & Smith, W.T. (1992) Redistribution of calving caribou in response to oil field development on the arctic slope of Alaska. *Arctic,* **45,** 338-342.

Chapin, F.S., III, S. F. Trainor, P. Cochran, H. Huntington, C. Markon, M. McCammon, A. D. McGuire & Serreze, M. (2014) Climate Change Impacts in the United States: The Third National Climate Assessment. (eds J. M. Melillo, T.C. Richmond & T.W. Yohe), pp. 514-536. United States Global Change Research Program, Washington, D.C.

Crooks, K.R. & Soulé M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature,* **400,** 563-566.

Dorendorf, R.R. (2015) Motivations and drivers of interior Alaskan trappers. MS thesis, University of Alaska Fairbanks, U.S.A.

Economides, M.J. & Wood, D.A. (2009) The state of natural gas. *Journal of Natural Gas Science and Engineering,* **1,** 1-13.

Fanson, K.V., Wielebnowski, N.C., Shenk, T.M., Vashon, J.H., Squires, J.R. & Lucas, J.R. (2010) Patterns of ovarian and tueal activity in captive and wild Canada lynx (*Lynx canadensis*). *General and Comparative Endochinology*, **169**, 217-224.

Fiske, I. & Chandler, R. (2011) unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software,* **43,** 1-23.

Goad, E.H., Pejchar, L., Reed, S.E. & Knight, R.L. (2014) Habitat use by mammals varies along an exurban development gradient in northern Colorado. *Biological Conservation,* **176,** 172-182.

Grinder, M.I. & Krausman, P.R. (2001) Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *Journal of Wildlife Management,* **65,** 887-898.

Halpin, M.A. & Bissonette, J.A. (1988) Influence of snow depth on prey availability and habitat use by red fox. *Canadian Journal of Zoology,* **66,** 587-592.

Hobson, K.A., Bayne, E.M. & Van Wilgenburg, S.L. (2002) Large-Scale Conversion of Forest to Agriculture in the Boreal Plains of Saskatchewan. *Conservation Biology,* **16,** 1530-1541.

Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., VanDriel, J.N., and Wickham, J. 2007. Completion of the 2001 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing,* **73**, 337-341.

Johnson, C.J., Boyce, M.S., Case, R.L., Cluff, H.D., Gau, R.J., Gunn, A. & Mulders, R. (2005) Cumulative effects of human developments on arctic wildlife. *Wildlife Monographs,* **160,** 1-36.

Kamler, J.F. & Gipson, P.S. (2000) Space and habitat use by resident and transient coyotes. *Canadian Journal of Zoology,* **78,** 2106-2111.

Kilström, Å. (2004) The wolverine population in the boreal forest area. PhD thesis, Uppsala University, Sweden.

Levi, T. & Wilmers, C.C. (2012) Wolves-coyotes-foxes: a cascade among carnivores. *Ecology,* **93,** 921-929.

MacKenzie, D.I. & Bailey, L.L. (2004) Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics,* **9,** 300-318.

MacKenzie, D.I., Nichols, J., Royle, J., Pollock, K., Bailey, L. & Hines, J. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurence*. Elsevier Academic Press, Oxford, UK.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology,* **83,** 2248-2255.

Marcot, B., Jorgenson, M.T., Lawler, J., Handel, C. & DeGange, A. (2015) Projected changes in wildlife habitats in Arctic natural areas of northwest Alaska. *Climatic Change,* **130,** 145-154.

Mazerolle, M.J. (2015) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3. http://CRAN.R-project.org/package=AICcmodavg.

McKelvey, K.S., Copeland, J.P., Schwartz, M.K., Littell, J.S., Aubry, K.B., Squires, J.R., Parks, S.A., Elsner, M.M. & Mauger, G.S. (2011) Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications,* **21,** 2882-2897.

Murray, D.L. & Boutin, S. (1991) The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia,* **88,** 463-469.

Murray, D.L., Boutin, S. & O'Donoghue, M. (1994) Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology,* **72,** 1444-1451.

Murray, D.L., Boutin, S., O'Donoghue, M., & Nams, V.O. (1995) Hunting behaviour of a sympatric felid and canid in relation to vegetative cover. *Animal Behaviour,* **50,** 1203-1210.

Nikiforuk, A. (2010) *Tar sands: Dirty oil and the future of a continent.* Greystone Books Ltd, Vancouver, BC, Canada.

Olsson, R. (2009) Boreal Forest and Climate Change. *Air Pollution and Climate Series 23.* Air Pollution & Climate Secretariat & Taiga Rescue Network, Göteborg, Sweden.

Östlund, L., Zackrisson, O. & Axelsson, A.-L. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian journal of forest research,* **27,** 1198-1206.

Perrine, J.D. (2005) Ecology of red fox (*Vulpes vulpes*) in the Lassen Peak region of California, USA. PhD thesis, University of California, Berkeley, U.S.A.

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., Fox, A.D., Gilg, O., Hik, D.S., Hoye, T.T., Ims, R.A., Jeppesen, E., Klein, D.R., Madsen, J., McGuire, A.D., Rysgaard, S., Schindler, D.E., Stirling, I., Tamstorf, M.P., Tyler, N.J., van der Wal, R., Welker, J., Wookey, P.A., Schmidt, N.M. & Aastrup, P. (2009) Ecological dynamics across the Arctic associated with recent climate change. *Science,* **325,** 1355-1358.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The rise of the mesopredator. *Bioscience,* **59,** 779-791.

Raine, R.M. (1983) Winter habitat use and responses to snow cover of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. *Canadian Journal of Zoology,* **61,** 25-34.

Riley, S.P.D., Sauvajot, R.M., Fuller, T.K., York, E.C., Kamradt, D.A., Bromley, C. & Wayne, R.K. (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology,* **17,** 566-576.

Roemer, G.W., Gompper, M.E. & Van Valkenburgh, B. (2009) The ecological role of the mammalian mesocarnivore. *Bioscience,* **59,** 165-173.

Rose, M.D. & Polis, G.A. (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology,* **79,** 998-1007.

Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J. & Zielinski, W.J. (1994) The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. *General Technical Report RM-254,* pp. 184. United States Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, U.S.A.

Ruggiero, L.F., Squires, J.R., Buskirk, S.W., Aubry, K.B., McKelvey, K.S., Koehler, G. & Krebs, C.J. (2000) *Ecology and conservation of lynx in the United States*. University Press of Colorado Boulder, U.S.A.

Savory, G.A., Hunter, C.M., Wooller, M.J. & O'Brien, D.M. (2014) Anthropogenic food use and diet overlap between red foxes (Vulpes vulpes) and arctic foxes (Vulpes lagopus) in Prudhoe Bay, Alaska. *Canadian Journal of Zoology,* **92,** 657-663.

Schuette, P., Wagner, A.P., Wagner, M.E. & Creel, S. (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation,* **158,** 301-312.

Shulski, M. & Wendler, G. (2007) *The Climate of Alaska.* University of Alaska Press, Fairbanks, AK, U.S.A.

Shuman, J.K., Shugart, H.H. & O'Halloran, T.L. (2011) Sensitivity of Siberian larch forests to climate change. *Global Change Biology,* **17,** 2370-2384.

SNAP (2015) Scenarios Network for Alaska + Arctic Planning. 1 May, 2015. www.snap.uaf.edu.

Squires, J.R., Decesare, N.J., Kolbe, J.A. & Ruggiero, L.F. (2010) Seasonal resource selection of Canada lynx in managed forests of the Northern Rocky Mountains. *Journal of Wildlife Management,* **74,** 1648-1660.

Tape, K.D., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology*, **12**, 686-702.

U.S. Census Bureau (2010) Census of Population and Housing, *Population and Housing Unit Counts*, CPH-2-3, Alaska. U.S. Government Printing Office, Washington, DC, 2012. 1 October, 2015. https://www.census.gov/prod/cen2010/cph-2-3.pdf.

U.S. Environental Protection Agency (2013) Climate Impacts in Alaska. 1 May, 2015. http://www.epa.gov/climatechange/impacts-adaptation/alaska.html.

Ward, R.M.P. & Krebs, C.J. (1985) Behavioural responses of lynx to declining snowshoe hare abundance. *Canadian Journal of Zoology,* **63,** 2817-2824.

Winfree, R., Rice, B., Fresco, N., Krutikov, L., Morris, J., Callaway, D., Mow, J. & Swanton, N. (2014) Climate change scenario planning for central Alaska parks: Yukon-Charley, Wrangell-St. Elias, and Denali. *Natural Resource Report NPS/AKSO/NRR-2014/829*. National Park Service, Fort Collins, Colorado, U.S.A.

Young, S. & Jackson, H. (1951) The clever coyote. *The Stackpole Co., Harrisburg, Pa., and The Wildlife Management Institute,* Washington, DC.

Zielinski, W.J., Truex, R.L., Schlexer, F.V., Campbell, L.A. & Carroll, C. (2005) Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. *Journal of Biogeography,* **32,** 1385-1407.

CHAPTER 3. EVALUATING MESOCARNIVORE POPULATION STATUS USING OCCUPANCY AND DENSITY MODELING[2]

3.1. ABSTRACT

1. Interspecific interactions among carnivore species can shape community dynamics through phenomena such as mesocarnivore release and carnivore cascades. Although many studies have shown that apex predators can strongly impact ecosystems, their effects on mesocarnivores vary substantially among studies. Inconsistencies among studies may arise from the use of different survey and analytical methodologies. Multiple non-invasive survey methods have been established to monitor elusive mesocarnivore species, and parameters such as occupancy and density are widely used to evaluate population trends. However, the ability of relatively inexpensive and simple methods, such as occupancy, to accurately represent trends in carnivore population size has not been well examined.
2. We used non-invasive track and scat surveys of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in the interior of Alaska to estimate occupancy probabilities and densities of these two species. We compared occupancy and density estimations using three methods: single-season occupancy models, dynamic occupancy models, and spatially explicit capture-recapture models.
3. We found that occupancy estimates derived from single-season and dynamic occupancy models produced nearly identical results for coyote and red fox populations. Current

---

[2] Prepared for submission in the Journal of Animal Ecology as Pozzanghera, C.P., Sivy, K.J., Lindberg, M.S., Mumma, M.A., Colson, K., and Prugh, L.R. (2015) Evaluating mesocarnivore population status using occupancy and density modeling.

occupancy probabilities were similar for both species and strongly influenced by habitat type. Red fox densities were higher than coyote densities, but densities for both species were far lower than those reported from studies in lower latitudes.

4. We found that estimates of occupancy and density each provided different information about our study populations, suggesting that occupancy (based on track distribution) was not a good proxy for density. Top ranking occupancy and density models varied about highly influential predictor variables, and parameter estimates of comparable models did not follow similar trends.
5. The low cost of occupancy study designs relative to density surveys may not warrant their use as a density proxy. Occupancy should be used to assess habitat use patterns, spatial partitioning of landscapes, and year to year changes in distributions, as it was originally designed to do.

3.2. INTRODUCTION

Apex and mesopredators play a key role in ecological communities, and global declines in apex predator populations have resulted in an increased interest and need for carnivore research (Miller *et al.* 2012). Direct and indirect interactions between apex and mesocarnivores can ripple through ecosystems, and the loss of apex species has begun to shift the role of mesocarnivores (Prugh *et al.* 2009). Many studies have documented mesocarnivore release and carnivore cascades in a variety of populations (Ritchie & Johnson 2009), but other studies have failed to document mesocarnivore release, and the response of small carnivores to the presence of large carnivores remains controversial (e.g., Gehrt & Clark 2003; Squires *et al.* 2012; Allen *et al.* 2014). Discrepancies among carnivore studies may arise in part because of different methodologies. Many studies use indirect measures of carnivore activity or distribution, or provide correlative information to examine interspecific interactions between carnivores (e.g., Chamberlain & Leopold 2005; Levi & Wilmers 2012; Miller *et al.* 2012; Sollmann *et al.* 2012). Few studies use experimental manipulations or estimate true animal density to compare population sizes and assess these community dynamics (Henke & Bryant 1999; Berger & Gese 2007). Although some studies have compared the relative efficiency of various survey designs (Gompper *et al.* 2006), fewer studies have assessed the consistency of inference across different methods commonly used to examine carnivore population dynamics (but see Clare, Anderson & MacFarland 2015).

Due to the elusive nature of many carnivores, data hungry population parameters such as density and abundance can be logistically difficult and prohibitively expensive to obtain (Garshelis 1992). For that reason, the use of density and abundance proxies has grown in popularity (Pollock *et al.* 2002; Jhala, Qureshi & Gopal 2011). Analyses such as occupancy modeling produce population-level metrics that describe the probabilities that a species occupies or uses predefined areas (MacKenzie *et al.* 2006). While traditional occupancy models are not designed to be direct surrogates for density, they can be used to describe spatial partitioning of the landscape among carnivores (Schuette *et al.* 2013; Steinmetz, Seuaturien & Chutipong 2013), and some studies have shown a positive relationship between occupancy and population size (Gaston *et al.* 2000; Bailey, Simons & Pollock 2004; Clare, Anderson & MacFarland 2015). However, movement patterns of carnivores can change dramatically in response to changes in prey, climate, or interspecific interactions, and these changes may strongly affect occupancy patterns and complicate the use of occupancy as a direct proxy for carnivore abundance (Murray & Boutin 1991; Kamler & Gipson 2000; Chamberlain & Leopold 2005; Prugh 2005; Randa *et al.*

2009). Dynamic occupancy models extend traditional models by including parameters to estimate colonization and extinction of study sites by a species of interest, allowing more accurate inferences to be made about the changes in occupancy from year to year and in response to a variety of factors (MacKenzie *et al.* 2003). Including a spatial and temporal component to occupancy increases the power of this model, but it is still unclear whether occupancy can or should be used as a density surrogate.

Studies that estimate carnivore density have typically used standard capture-mark-recapture (CMR) models (Mowat & Strobeck 2000; Boersen, Clark & King 2003; Mulders, Boulanger & Paetkau 2007), but these models generate abundance estimates that must be converted to density based on post-hoc trapping area designations and thus result in heterogeneity in capture probabilities due to edge effects (Karanth & Nichols 1998). Improvements from traditional density estimators have been made through the recent development of spatial CMR models that estimate density directly by combining the location data provided by trap or capture coordinates with the encounter histories of marked individuals (Borchers & Efford 2008; Royle & Young 2008; Thompson, Royle & Garner 2012). Spatially explicit capture-recapture (Borchers & Efford 2008) is a recently developed method for spatial density estimation that is based on a maximum likelihood framework. Flexibility in these models allows for non-invasive survey designs to be used; however, the need for individual identification presents an added challenge compared to presence/absence surveys like occupancy.

In this paper, we compare the consistency of inference using multiple survey and modeling techniques that are used increasingly to study carnivores: spatially explicit capture-mark-recapture (SECR), traditional occupancy modeling, and dynamic occupancy modeling.

Surveying for carnivores presents unique challenges and requires researchers to weigh the pros and cons of many decisions. Clear management goals or study objectives should be the driving force behind choosing a study design, but as is often the case, limitations on time, money, and qualified field technicians may end up guiding many project decisions. With that in mind, it is critical to understand what options are available and what questions can be answered with the resources available to each study.

Both of the above outlined modeling techniques (occupancy and spatial capture-mark-recapture) can be used with a non-invasive survey design. Non-invasive survey methods including remote cameras, track surveys, scat and hair collections, and tracking plates are often used to monitor carnivore populations (Soulé *et al.* 1988; Long *et al.* 2011; Sollmann *et al.* 2012; Whittington *et al.* 2014). Non-invasive surveys are safer, often require fewer bureaucratic hurdles, and can provide similar or superior information as surveys that require capture and handling of study animals (Gompper *et al.* 2006; Long *et al.* 2008). Occupancy surveys are possibly the most logistically feasible population level survey. Presence/absence data can be collected with observational surveys, sound surveys, sign surveys, motion activated camera traps, or species specific markings of a target species, and depending on the survey design, researchers may only need to conduct a single survey (Long *et al.* 2011; Sollmann *et al.* 2012; Whittington *et al.* 2014). These features, along with the limited amount of laboratory analysis required, makes occupancy studies flexible and inexpensive.

Survey designs for SECR density estimation can be equally as flexible but require a way for the researcher to assign each “sample” collected to a specific individual. This is most commonly done through collection of genetic material, but can also be done using photos of species with uniquely marked individuals (Karanth 1995). This process likely will result in more time and money invested into SECR surveys and laboratory processing than required for occupancy studies, but may be necessary if density is the parameter of interest. By combining winter scat collection with snow tracking surveys, we simultaneously collected data required for SECR and occupancy modeling, respectively, to assess current populations of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in two study areas in interior Alaska and to assess the relationships between these two modeling methods as well as the relationships between animal density and track density.

Mesocarnivores have been shown to play a key role in the boreal ecosystem in the interior of Alaska (Prugh 2005), yet little is known about their current population size and distribution in this region. Changes to the landscape brought on by increased anthropogenic development and climate shifts will likely alter coyote and red fox distributions (Alaska Energy Authority 2014; Winfree *et al.* 2014). In addition, state predator control efforts targeting wolves (*Canis lupus*) and bears (*Ursus americanus* and *U. arctos*) can result in patchy and fluctuating apex predator distributions that have unknown impacts on smaller canid species (Van Ballenberghe 2006; Alaska Department of Fish and Game 2015a). We provide the first non-invasive density and occupancy estimates of sympatric red fox and coyotes in areas of interior Alaska with and without wolf control, creating a population baseline that can be referred to for future management of these species. We generated red fox and coyote population estimates from different modeling methods to compare the inference that could be drawn from each. We examined the efficacy of using occupancy as a surrogate for density by comparing patterns in these population metrics between species and study areas. We predicted that occupancy estimates from traditional and dynamic occupancy models would be similar, and that occupancy and density estimates would have the same trends. Specifically, we predicted that within-species estimates of occupancy probability and density would be best estimated as a function of the same predictive covariates. Overall, we expected red fox densities and occupancy probabilities to be significantly higher than coyotes due to smaller home range requirements for foxes (Peters 1986; Sargeant, Allen & Hastings 1987; Harrison, Bissonette & Sherburne 1989). We also predicted the existence of a carnivore cascade and expected that low wolf abundance in the study area with wolf control would result in higher coyote density and lower red fox densities than in the study area where wolves were at natural densities (Levi & Wilmers 2012; Newsome & Ripple 2015).

3.3. MATERIALS AND METHODS

3.3.1. Study Region

Our study region included two study sites (hereafter, “Denali” and “Susitna”) within the central Alaska Range of interior Alaska (Fig 3.1). Boreal forest (including spruce *Picea spp.*, aspen *Populus spp.* and birch *Betula spp.*), deciduous shrub, and tundra habitats dominate the landscape across both sites. This region is characterized by short summers and long, cold winters (Shulski & Wendler 2007). Black bears (*Ursus americanus*), grizzly bears (*Ursus arctos*), Canada lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), American marten (*Martes americana*), ermine (*Mustela erminea*), and least weasel (*Mustela nivalis*) were also present in the region, as well as two aquatic mesocarnivores, mink (*Mustela vison*) and river otter (*Lutra canadensis*). Common prey species included voles (Cricetidae family), ptarmigan (*Lagopus* spp.), grouse (*Bonasa umbellus* and *Falcipennis canadensis*), snowshoe hares (*Lepus americanus)*, red squirrels (*Tamiasciurus hunsonicus*), ground squirrels (*Spermophilus parryii*), caribou (*Rangifer tarandus*), and moose (*Alces alces*). The Denali study site was a roughly 2000-km^2 area that included the northeastern portion of Denali National Park and Preserve (DNPP) along with portions of the Stampede corridor, a 470-km^2 parcel of state and private land. All species within the DNPP border were protected from harvest, and general-season hunting and trapping of coyotes and foxes was legal in the Stampede corridor. The Susitna study site was approximately 145 km southeast of the Denali study site and consisted of 1800 km^2 of primarily public (state and Bureau of Land Management) or Alaska Native corporation lands. General season harvest of coyotes and red fox was also legal throughout the Susitna study area. In addition, this site has been included in the Intensive Management predator control program since 2000, resulting in a reduced wolf abundance in this area (Alaska Department of Fish and Game 2015b). Differences between study areas (i.e. weather, amount of human disturbance, prey abundance) did exist beyond wolf abundance, and we recognize that our models do not include all potentially relevant covariates to determine causes for potential population differences between study areas. Our focus is on comparing model results given consistent predictor variables, and we use study area comparisons as a way to directly compare the population level inference that we obtain from occupancy and density estimations.

3.3.2. Track surveys and sample collection

Scat samples were collected in each study site from January to March in 2013 and 2014 for use in spatially explicit density estimations. Collection of samples coincided with mesocarnivore track surveys that used a grid-based survey design to estimate species occupancy probabilities. In 2013, each site was overlaid with a grid of 2x2-km cells using ArcGIS (version 10.1, ESRI, Redlands, California), and cells in each study area were randomly selected for occupancy surveys (Fig 3.1). We assigned each grid cell one of three habitat types (forest, shrub, or tundra) based on the dominant vegetation cover type within the cell, as calculated from satellite imagery (Homer *et al.* 2007). We surveyed a total of 300 cells across both years and study areas, 90 cells in 2013 and 210 cells in 2014. Fifty-one of these cells were surveyed during both seasons and used in the dynamic occupancy analysis. We used either linear transects or track squares to survey each cell. The linear transect method used temporal replication to estimate detection probabilities, whereas the square transects used spatial replication, which eliminated the need for return visits to the cell (MacKenzie *et al.* 2006). Where snowmobile use was prohibited (i.e., designated wilderness areas in DNPP) or impractical due to terrain, we surveyed by dog team or on foot. Because snow conditions can affect detection probability, we conducted surveys after a minimum of 24 h since the last track-obliterating snowfall to allow adequate time for tracks to accumulate, and no more than 7 days after a snowfall to prevent tracks from becoming too melted out, windblown, or otherwise disrupted. We recorded all mesocarnivore tracks encountered during each survey.

We connected the randomly selected survey cells in each study area with trails that resulted in a network of travel routes spread across each study site. These travel routes made up the primary scat survey areas in 2013 and 2014, and were also included in 2014 occupancy surveys to increase sample size (Fig 3.1). Scats that were encountered along travel routes were collected with a Ziplock plastic bag that was then placed inside an autoclave bag or Whirlpak. GPS coordinates, date, and estimated age of the scat were recorded. During daily surveys, any coyote or red fox tracks encountered along travel routes were marked and a fresh set of tracks was chosen at the end of the survey day to follow in order to find additional scat samples. We started these backtracking surveys at the point where canid tracks crossed our travel route, and followed them backwards until a scat was located. Backtracking surveys greatly increased sample size and expanded the search area. In addition to the collection of scats along established travel routes and backtracking trails, all scats that were opportunistically encountered during non-survey periods (i.e., when moving base camp locations, bringing in camp supplies, or exploring new regions of the study sites) were also collected. All scat samples were kept frozen to slow the degradation of fecal DNA.

3.3.3. DNA extraction and species verification

To extract DNA, scats were removed from the -80°C freezer and placed on ice to slowly defrost. After the outer surface of each scat had thawed (~ 30 minutes), we rubbed the outer surface of each scat with the end of a wooden craft stick. We broke off the end of the craft stick that contained the sample into a 1.5 ml tube so that no part of the stick extended above the top of the tube. DNA was then extracted using Qiagen DNA Investigator Kits (Qiagen Inc., Valencia, CA, USA) with a negative control included in each batch to monitor for contamination.

Each sample was identified to species using a modification of a previously developed mitochondrial DNA test (De Barba *et al.* 2014). Primer pair DL1F and DL5R (Palomares *et al.* 2002) and a forward primer, Gulo1F (Dalen, Gotherstrom & Angerbjorn 2004), were combined with the primers SIDL (Murphy, Waits & Kendall 2000), H3R (Dalen, Gotherstrom & Angerbjorn 2004), and H16145 (Murphy, Waits & Kendall 2000), to amplify DNA fragments of species-specific lengths. Red fox and coyote scats were verified via DNA fragments of ~346 base pairs (bps) and ~363 bps, respectively, whereas scats that failed to amplify or were from non-target species were excluded from further analyses. The conditions for our original 15 μL reaction were 0.2 μM DL1F, 0.2 μM DL5R, 0.2 μM Gulo1F, 0.4 μM SIDL, 0.4 μM H3R, 0.2 μM H161453, 3 μL H20, 1.26 μL TE buffer, 7.5 μL 1x Qiagen Master Mix, 1.5 μL Q solution, and 1.5 μL of DNA extract. We later scaled down this reaction to 7 μL to reduce costs. We maintained primer concentrations while adjusting the remaining solution volumes to 0.69 μL dH_20, 0 μL TE buffer, 3.5 μL 1x Qiagen Master Mix, 0.7 μL 0.5x Qiagen Q solution, and 2 μL of DNA extract. The PCR profile for both the 15 and 7 μL reactions consisted of an initial denaturation step of 95˚C for 15 minutes followed by 30 cycles of 95˚C for 15 seconds, 46˚C for 90 seconds, 72˚C for 60 seconds with a final elongation step of 72˚C for 15 minutes. Fragment sizes were determined using an Applied Biosystems 3730xl Genetic Analyzer (Applied Biosystems Inc., Foster City, CA, USA) and associated GENEMAPPER 3.7 software.

3.3.4. Individual identification

All scats verified as red fox or coyote were genotyped twice using a canid PCR multiplex (C1) consisting of 5 microsatellite primer pairs (FH2328, FH2054, FH2010, FH2088, and FH2001; Breen *et al.* 2001; Guyon *et al.* 2003; Moore, Brown & Sacks 2010). Similar to our species verification test, we maintained primer concentrations for C1 while reducing the PCR volume from 20 to 7 µL to limit costs. The concentrations of our 7 µL reaction were 0.22 µM FH2328, 0.18 µM FH2054, 0.2 µM FH2010, 0.22 µM FH2088, and 0.22 µM FH2001, along with 0.65 µL dH_2O, 3.5 µL 1x Qiagen Master Mix, 0.7 µL 0.5x Qiagen Q solution, and 2 µL of DNA extract. Samples that failed to produce matching genotypes at ≥3 loci were considered degraded and excluded from further analyses.

High quality coyote samples (≥3 matching loci) were genotyped up to 2 additional times for C1 and up to 4 times for a second canid multiplex (C2) depending upon how many loci amplified consistently. C2 included 5 additional primer pairs (FH2137, FH2140, FH2159, FH2096, and CXX2235; Breen *et al.* 2001; Guyon *et al.* 2003) combined in a 7 µL multiplex, scaled down from 20 µL, that included control and sex identification primer pairs (DBX and DBY; Seddon 2005). The conditions for the 7 µL reaction were 0.2 µM FH2137, 0.2 µM FH2140, 0.2 µM FH2159, 0.22 µM FH2096, 0.18 µM CXX2235, 0.2 µM DBX, 0.2 µM DBY, 0.6 µL dH_2O, 3.5 µL 1x Qiagen Master Mix, 0.7 µL 0.5x Qiagen Q solution, and 2 µL of DNA extract. High quality fox samples (≥3 matching loci) were genotyped up to 2 additional times for

C1 and up to 4 times for a fox multiplex (V2), which we designed after we found that fox samples failed to amplify at certain loci contained in C2. V2 consisted of a 7 μL reaction that had been scaled down from 20 μL and included 4 primers pairs (INU055, FH2140, REN105L03, and CXX2235; Breen *et al.* 2001; Guyon *et al.* 2003; Moore, Brown & Sacks 2010) and 2 sex determining loci (CF-hprt and VV-sry; Berry *et al.* 2007). The conditions of the 7 μL reaction were 0.2 μM INU055, 0.2 μM FH2140, 0.2 μM REN105L03, 0.2 μM CXX2235, 0.2 μM CF-hprt, 0.07 μM VV-sry, 0.65 μL dH2O, 3.5 μL 1x Qiagen Master Mix, 0.7 μL 0.5x Qiagen Q Solution, and 2 μL of DNA extract. The PCR profile for all 3 individual identification multiplexes began with a denaturation step of 95°C for 15 minutes followed by a touchdown of 10 cycles at 94°C for 30 seconds, 68°C for 30 seconds (annealing), and 72°C for 45 seconds with a 1°C decrease in the annealing temperature at each cycle followed by 25 cycles at 94°C for 30 seconds, 58°C for 30 seconds, and 72°C for 45 seconds and a final elongation step of 60°C for 15 minutes. We included a negative control for each batch of PCR reactions. Allele sizes were determined using an Applied Biosystems 3730xl Genetic Analyzer (Foster City, CA, USA) and GENEMAPPER 3.7 software.

We determined consensus genotypes for each locus by comparing replicate PCRs for each sample and required ≥2 matching PCRs for heterozygous and ≥3 matching PCRs for homozygous loci because the probability of an allelic dropout is greater than the probability of a false allele. To construct reliable multi-locus genotypes for each sample, we required consensus genotypes at ≥6 loci for each fox and ≥7 loci for each coyote sample after first determining the minimum number of loci necessary to assure a low probability of misidentifying 2 first-order relatives as the same individual (probability of identity siblings ≤0.01; (Waits, Luikart & Taberlet 2001) using the software GENALEX6 (Peakall & Smouse 2006). We then used

GENALEX6 to identify individuals by matching our completed samples based on the consensus multi-locus genotypes. We categorized samples that had matching genotypes or a mismatch at only 1 locus as being from the same individual. Grouping samples with single mismatches avoided falsely inflating the number of individuals, because it was more likely that single locus mismatches would occur from allelic dropouts or false alleles than it was for the samples to represent 2 unique individuals (Peakall & Smouse 2006).

3.3.5. Statistical analyses

3.3.5.1. Occupancy

We used single-season, single-species occupancy models and dynamic occupancy models to estimate coyote and red fox occupancy probabilities. The single-season occupancy model provides estimates of two response parameters: probability of site occupancy (ψ), and detection probability (p), which is the probability that the target species is detected given that it is present (MacKenzie *et al.* 2002). Dynamic occupancy models include 2 additional parameters, colonization probability (γ) and local extinction probability (ε), to estimate population changes over time (MacKenzie *et al.* 2003). We included two survey-specific covariates and four site-specific covariates in our models using a logit link function. Covariates were: number of days since the last snowfall (DSLS), total distance surveyed within a sample cell (DIST), study year (YEAR; only included in single-season models), survey method (METHOD), study area (AREA), and habitat type (HABITAT). All analyses were performed in program R version 3.1.0 (R Development Core Team 2014) using packages unmarked (Fiske & Chandler 2011) and AICcmodavg (Mazerolle 2015).

We used a two-step process to develop finalized candidate model sets that were both biologically relevant and analytically feasible for each species and each occupancy model technique. We report the following steps based on dynamic occupancy modeling, but note that our single-season analysis followed identical steps while ignoring the steps related to γ and ε. We ranked all models based on AICc and QAICc (Burnham & Anderson 2002). First, we constructed models to estimate p while holding ψ, ε, and γ constant (Schuette *et al.* 2013), using all combinations of DSLS, DIST, METHOD, and AREA. In the second step, all additive combinations of HABITAT and AREA were used to build a candidate model set for each species that estimated ψ while p was modeled using the top-ranked detection model identified in step one and γ and ε were fixed as either a function of AREA or HABITAT. Because we only had two study years, we were unable to model the colonization and extinction parameters as a function of year. This resulted in a full candidate set of nine single-season models and 10 dynamic occupancy models for each species (1 null model was included with each analysis).

We assessed fit of the data for single season occupancy models by evaluating the most global model in the candidate set for each species using a Pearson χ^2 goodness-of-fit test (MacKenzie & Bailey 2004) using package AICcmodavg with 1,000 bootstrapped simulations. We used an estimate of the overdispersion factor ($\hat{c}$) to evaluate the dataset and identify potential overdispersion or independence violations. Violating the assumption of independence (e.g., due to spatial autocorrelation) can result in overly precise variance estimates (MacKenzie *et al.* 2006). We found a $\hat{c}$ value of 2.46 for our coyote data and 1.59 for our red fox data, suggesting both had reasonable fit, and we therefore used the quasi-corrected AICc (QAICc) to rank the final 9 models for each species. In addition, we used the estimate of $\hat{c}$ to inflate standard errors to account for overdispersion (Burnham & Anderson 2002). A similar approach to assess goodness-of-fit for dynamic occupancy models has not been developed in available software packages, and package AICcmodavg does not support a correction for overdispersion in dynamic occupancy models. Therefore, we did not correct for any potential lack of fit in these models.

3.3.5.2. Density

We used spatially explicit capture-recapture models implemented with the R package secr to estimate coyote and red fox density (Borchers & Efford 2008). This model uses the spatial location of traps across the study area along with spatial records for every capture event to produce density estimates based on theoretical home range locations within the study area. The package secr allows a variety of trap (or detector) techniques to be implemented, including those used in non-invasive sampling. We used the “count” detector option which is designed for studies that capture animals using traps that do not restrict animal’s movements, and which allows multiple individuals to be captured at one location during the same occasion, making it ideal for scat collection studies. This method assumes that captures (detections) occur at a specified location within a sampling grid cell. Therefore, we created a grid of 1x1-km cells over each study region and specified the center of each cell as the “trap location”. The relatively small cell size ensured good spatial coverage of the study area and allowed us to map individual home ranges at a scale that produced more precise density estimates than the larger 2x2-km cells we used for occupancy surveys. We used ArcGIS (version 10.1, ESRI, Redlands, California) to identify the cell associated with each genotyped scat. In addition, we categorized each cell across both study sites based on the level of survey effort (termed “usage” in secr). Cells that intersected our primary scat travel routes were classified as high usage, cells located within areas that were accessible during backtracking surveys or opportunistic collections were classified as low usage, and cells that were never searched or inaccessible were considered unused.

SECR models estimate three response parameters: density (D), the probability of detection for a detector at the center of the home range (g0), and a scaling parameter (σ). Together, g0 and σ define the model for detection probability as a function of location. Models may be constructed to estimate parameters based on automatically generated predictor variables such as survey occasion (t; the discrete sampling event) and survey session. A survey session in secr is defined as a set of occasions over which a population is considered closed to immigration, emigration, births, and deaths. We used study area (AREA) and survey year (YEAR) to break our study into a maximum of four sessions (Denali 2013, Denali 2014, Susitna 2013, and Susitna 2014) or a minimum of two sessions where only AREA was evaluated (Denali and Susitna). We divided our surveys into two occasions each session (T), the first spanning from January through February, and the second consisting of March and early April. Occasions were set up to divide the survey season in half, both in terms of timing and survey effort. We chose not to separate our occasions by month (January, February, March) because January often produced fewer scat samples due to lack of daylight available for searching. We first used the above two predictors (session and occasion) to create 8 models for each species to estimate g0 and σ while holding D constant. We then used AICc to identify the most parsimonious detection model for both coyote and fox. We then constructed models for D, the true parameter of interest, while maintaining a fixed set of detection parameters.

When modeling D, user-defined covariates and habitat masks may be used to estimate density across a group or landscape gradient. We included a habitat mask using 3 broad habitat categories that matched our occupancy habitat covariate: forest, shrub, and open tundra. We used the habitat mask to create models that estimated density as a function of habitat type (HABITAT). We also modeled density differences between sessions and occasions. We built a set of 9 models to estimate coyote density. The top-ranking model was then used to create a coyote density surface that described coyote activity centers across the study area. We modeled red fox density using the same habitat mask and session argument, and we also included the coyote density surface as a user-defined covariate in the red fox models to assess the effect that coyote density had on red fox density. Eleven fox models were created. All models were ranked using AICc. We did not correct for potential lack of fit in these models due to the large amount of computational power required to run fit tests in secr and the lack of any current support in the literature to suggest that such a test is useful to estimate overdispersion.

3.3.6. Model evaluation and comparison

We used the top-ranking models for each species and method, along with the best supported models that held either the density or occupancy parameters constant, to evaluate the consistency of inference among methods. Top ranking models were used to provide baseline data on current red fox and coyote population status. We compared parameter estimates between species from models holding ψ and D constant and considered estimates to be significantly different between species if 95% confidence intervals did not overlap. We looked for similar trends in population estimates across our three models to signify consensus between modeling methods. In addition, we used well-supported models that estimated density and occupancy as functions of AREA or HABITAT to compare the influence of these covariates on our parameters of interest. We evaluated the precision of occupancy and density estimates by comparing coefficient of variation (CV) values for reported models (standard errors divided by parameter estimates).

3.4. RESULTS

3.4.1. Species and individual identification

We successfully identified species of 84% of scats collected in winters 2013 and 2014 (*n* = 875) and obtained reliable multi-locus genotypes from 82% of the coyote scats (*n* = 150 genotyped scats from 36 individual coyotes) and 70% of fox scats (*n* = 355 genotyped scats from 86 individual foxes).

3.4.2. Single-season occupancy models

Detection probabilities were estimated from the top-ranking model evaluated for each species when ψ was held constant. The top-ranking model for coyotes contained DIST, DSLS, METHOD, and YEAR. Detection probabilities (p ± SE) were higher in 2014 (0.575 ± 0.155) than in 2013 (0.133 ± 0.044). Detection (logit transformed model coefficients ± SE) increased with DSLS (β = 0.253 ± 0.139) and DIST (β = 0.895 ± 0.199). The top-ranking model for fox contained DIST, DSLS, and YEAR. In contrast to coyotes, detection probabilities (p ± SE) were higher in 2013 (0.359 ± 0.054) than 2014 (0.237 ± 0.033). Detection (logit-transformed model coefficients ± SE) increased with DSLS (β = 0.574 ± 0.119) and DIST (β = 0.399 ± 0.145).

Occupancy for coyotes was best explained as a function of habitat type (Table 3.1): model p(DIST+DSLS+YEAR+METHOD) ψ(HABITAT). Coyote occupancy (ψ± SE) was highest in shrub habitats (0.51 ± 0.08), intermediate in forest (0.43 ± 0.09), and lowest in open tundra (0.16 ± 0.06). Overall coyote occupancy when holding ψ constant was 0.40 ± 0.05. AREA was an influential covariate on occupancy (ΔQAICc = 1.81) when modeled with HABITAT (Table 3.1), and occupancy (logit-transformed model coefficients ± SE) was greater in Denali (β = -0.21 ± 0.39) than Susitna (β = -0.42 ± 0.47). Fox occupancy was best described when held constant (0.50 ± 0.05) or modeled as a function of YEAR, or YEAR and AREA (Table 3.1).

Occupancy probabilities were greater in 2014 (0.65 ± 0.11) than in 2013 (0.40 ± 0.06) using model p(DIST+DSLS+YEAR) ψ(YEAR). Occupancy probabilities were nearly identical between Denali (0.50 ± .06) and Susitna (0.49 ± 0.07) when looking at study area differences alone.

3.4.3. Dynamic occupancy models

Detection probabilities for coyotes were best modeled as a function of DIST, DSLS, and AREA. Detection (logit-transformed model coefficients ± SE) increased with DSLS ($\beta = 0.18 \pm 0.29$) and DIST ($\beta = 0.46 \pm 0.26$). Detection probabilities (p ± SE) were greater in the Denali study area (0.45 ± 0.09) than the Susitna study area (0.14 ± 0.06). Fox detection was best modeled as a function of DIST, DSLS, and METHOD. Detection probability (logit-transformed model coefficients ± SE) increased with DIST ($\beta = 0.24 \pm 0.18$) but decreased with DSLS ($\beta = -0.09 \pm 0.25$). Covariates included in these top-ranking detection models for each species were included for modeling of the occupancy, colonization, and extinction parameters.

Occupancy probability of coyotes using dynamic occupancy models was best explained as a function of habitat type when γ and ε were held constant (Table 3.2). Coyote occupancy (ψ ± SE) was highest in shrub habitats (0.56 ± 0.17), intermediate in forest (0.46 ± 0.16), and lowest in open tundra (0.10 ± 0.10). Site colonization probability (γ ± SE) was 0.23 ± 0.12 and local extinction probability (ε ± SE) was 0.363 ± 0.19. Overall coyote occupancy when holding ψ constant was 0.34 ± 0.08. AREA was again an influential covariate when modeled with HABITAT (Table 3.2), and occupancy (logit-transformed model coefficients ± SE) was greater in the Denali study area ($\beta = 0.17 \pm 0.72$) than the Susitna area ($\beta = -1.78 \pm 1.30$).

The best-fitting fox model estimated occupancy as a function of habitat type while colonization and extinction were estimated as a function of AREA (Table 3.2). Fox occupancy

(ψ ± SE) was highest in open tundra habitats (0.93 ± 0.18), intermediate in shrub (0.42 ± 0.12), and low in forested areas (0.3 ± 0.14). Site colonization probability (logit-transformed model coefficients ± SE) was greater in Denali (β = 3.12 ± 5.55) than Susitna (β = -2.18 ± 1.52) and local extinction probability was greater in Susitna (β = -0.29 ± 1.14) than Denali (β = -0.76 ± 0.99). Overall fox occupancy when holding ψ constant was 0.49 ± 0.09.

3.4.4. Spatially explicit capture-recapture models

Coyote detectability (log-transformed model coefficients ± SE) was best modeled as a function of AREA and YEAR. Detection probability at the home range center (g0) was greatest in Denali during 2013 (β = -1.37 ± 0.29) and lowest in Susitna 2013 (β = -2.96 ± 0.57). Fox detection was best modeled as a function of AREA alone and was greater in Susitna (β = -1.63 ± 0.24) than in Denali (β = -2.18 ± 0.19).

The top-ranking model from our candidate model set (Table 3.3) estimated coyote density as a constant (6.02 ± 1.15 coyotes/1000km^2) while the detection parameters were both estimated as functions of AREA and YEAR. We used this top-ranking model to produce a surface of coyote activity centers (Fig 3.2). Our second ranking, and well supported (ΔAIC = 1.65), model estimated density as a function of AREA and YEAR and showed that coyote density was greatest in Denali during 2014 (19.7 ± 11.4 coyotes/1000km^2) and lowest in Susitna during 2013 (3.0 ± 1.3 coyotes/1000km^2). When estimating density as a function of HABITAT alone, coyote densities were greatest in forest habitats (20.8 ± 9.65 coyotes/1000km^2), intermediate in shrubs (4.81 ± 1.41 coyotes/1000km^2) and lowest in open tundra (2.2 ± NA coyotes/1000km^2), however precision of these estimates was poor (Fig 3.3).

The top-ranking model for red fox described density and both detection parameters as a function of AREA (Table 3.3). This model suggested red fox densities were greater in Susitna

(23.5 ± 3.4 foxes/1000km^2) than in Denali (14.8 ± 3.1 foxes/1000km^2). A model that held density constant and estimated the detection parameters as a function of AREA was also well-supported (ΔAICc = 1.07) and produced precise estimates of fox density (19.9 ± 2.4 foxes/1000km^2). Although there was some support for the model that estimated fox densities as a function of current coyote activity centers (ΔAICc = 3.3), there did not appear to be a strong response of foxes to coyotes. At low coyote density (1 coyote/1000km^2), fox density was estimated at 20.1 foxes/1000km^2, and with a 20-fold increase in coyote density (21.0 coyotes/1000km^2), fox density decreased by only 1.5% (19.8 foxes/1000km^2).

3.4.5. Model comparison

The top-ranking single-season and dynamic occupancy models for coyotes both estimated ψ as a function of habitat (Tables 3.1 and 3.2), while the best SECR model estimated coyote density as a constant (Table 3.1). Occupancy estimates were consistent between modeling methods (Fig 3.3), suggesting highest occupancy probabilities in shrub habitats. In contrast, density estimates indicated that coyote densities were higher in forest habitats compared to shrub and tundra, but these estimates had poor precision (Fig 3.3). The top-ranking models from the three different methods each suggested that different factors affected fox populations. The top-ranked single-season occupancy model estimated ψ as a function of study year (Table 3.1), while dynamic occupancy models best estimated ψ as a function of habitat type (Table 3.2), and density was best estimated as a function of study area (Table 3.3). Comparing estimates between models estimating ψ or D as a function of AREA alone (all of which had reasonable support) shows consistency between dynamic and single-season occupancy estimates, but a different trend in density. Density estimates showed significantly higher coyote abundance in Denali compared to Susitna, whereas occupancy estimates were similar between the two areas (Fig 3.4). When comparing constant estimates of ψ or D for coyotes and foxes, both occupancy analyses showed consistent and non-significant trends of slightly higher fox than coyote occupancy, and the SECR analysis indicated fox densities were significantly higher than coyote densities (Fig 3.5). Estimates of ψ or D in the constant model were more precise for foxes than coyotes using single-season occupancy models (CV= 0.10 and 0.13 for foxes and coyotes, respectively), dynamic occupancy models (CV= 0.18 and 0.24), and SECR density models (CV= 0.12 and 0.19).

3.5. DISCUSSION

Our study of mesocarnivores in the interior of Alaska provided an important evaluation of non-invasive survey methods and modeling techniques for carnivore research. We have shown that scat collection and snow tracking can be effective survey methods for coyotes and red fox in northern, boreal environments and that modeling techniques to estimate occupancy probability and density may provide useful but different information on mesocarnivore populations. These results suggest that inconsistent findings among mesocarnivore studies may be partially explained by methodological differences.

Our study has shown that both occupancy modeling and SECR density estimation can be useful tools, but based on our findings we caution against using occupancy as a surrogate for density in systems with similar species and sampling conditions (Gaston *et al.* 2000; Clare, Anderson & MacFarland 2015). We predicted that results from our two occupancy analyses (dynamic and single-season) would be similar and lead to the same population level inference. Although we did not use dynamic occupancy models to assess long term population level trends (MacKenzie *et al.* 2003), we showed that estimates between the models were consistent and that the dynamic occupancy models are robust and held up well to relatively small sample sizes. We used only the subset of survey cells that were surveyed during both years of our study for the dynamic occupancy models, resulting in a sample size less than one quarter the size of our single-season analysis (n = 51 cells vs 295 cells, respectively). Precision was worse, as expected, for the dynamic occupancy models; however, the inference drawn from both analyses were nearly identical between the two forms of occupancy models. We included a small number of covariates in our models, and there was general consensus that habitat type was the primary predictor of coyote occupancy. Although coyotes are considered habitat generalists across much of their range, in northern regions they are tied to snowshoe hares and may therefore be more dependent on habitat types that support high hare abundance (Murray, Boutin & O'Donoghue 1994; Prugh 2005). Indeed, we found highest coyote occupancy in shrub and forest habitats. The single-season analysis for red fox best predicted occupancy as a function of survey year while the dynamic model predicted habitat to be the most influential parameter, however we were not able to include year in our dynamic occupancy analysis. Overall our analyses indicate that dynamic and single-season occupancy models can provide consistent results for occupancy probability, but acknowledge that in other settings these models might appropriately indicate different dynamics (e.g., stable occupancy with high, but balanced rates of extinction and colonization).

When comparing results between density estimates and occupancy estimates for both mesocarnivore species in our study, we found more inconsistencies than agreement. Density models seemed to perform well with the level of precision somewhere between that of the single-season and dynamic occupancy models, and even in instances with extremely low sample sizes (e.g., zero coyote tracks were found in tundra habitats in the Susitna area), all models converged and produced usable point estimates. The inconsistency between occupancy and density models was evident in two ways, however. First, top-ranking models from SECR analysis and those from the occupancy analyses did not include any of the same predictive covariates on their parameters of interest (density and occupancy, respectively). While coyote occupancy varied strongly by habitat type, the best-ranked density models held habitat, study area and study years constant. Similarly, fox density varied most strongly by study area, while study area had minimal influence on occupancy probabilities. Second, when we examined comparable models for both coyotes and foxes, we found strong inconsistencies between point estimates from SECR compared to occupancy. Coyote densities were significantly higher in forested areas compared to shrub lands, while occupancy estimates were higher in shrub than forest. In addition, coyote densities were significantly higher in Denali than Susitna, yet occupancy probabilities were similar between the two study areas. Clare, Anderson & MacFarland (2015) estimated bobcat occupancy and density using camera traps across a large area and regressed occupancy estimates from multiple survey sites as functions of density and found a strong positive relationship between occupancy and density. We surveyed an area less than one third the size of this bobcat study and were unable to produce similar functions to directly compare occupancy and density, which could partially explain some of the discrepancies in our findings.

We recognize that our comparison between occupancy modeling and SECR density estimation used different sampling approaches, and it is possible that occupancy and density estimates could be more comparable in situations when identical data are used. Nonetheless, these comparisons offer useful insights because carnivore researchers often use fecal genotyping to estimate density and use cameras or track surveys to estimate occupancy. In future studies, the collection of scats could be used to create a presence/absence encounter history so that occupancy modeling as well as SECR modeling could be done with the same data. In addition, occupancy may be more likely to accurately represent density in situations when the target species is territorial and survey cells can approximately match the size of an average animal's home range. In this way, it can be assumed that occupied cells represent a single animal's home range, and the proportion of occupied cells in a study area more closely approximates overall abundance rather than use. However this analysis represents the first one of its kind for these species and we suggest that density and occupancy estimates should not be used interchangeably for population inference without further examination of the relationship between these two parameters.

Both occupancy modeling and SECR analyses are important for carnivore research. Occupancy modeling provides an inexpensive and informative way of looking at spatial use patterns, changes in distribution of a species over time, and even interspecific-interactions (Sollmann *et al.* 2012; Richmond, Hines & Beissinger 2013; Schuette *et al.* 2013). Managers should be cautious about using occupancy as a proxy or index for abundance, as spatial use patterns may easily change due to a variety of factors unrelated to population size including prey abundance, habitat quality, or climate patterns (Murray & Boutin 1991; Kamler & Gipson 2000; Chamberlain & Leopold 2005; Prugh 2005; Randa *et al.* 2009). Our analysis suggests that occupancy is most appropriate to examine current use patterns of different levels of landscape scale factors such as habitat. Although we were unable to examine the relationships of occupancy and density in areas with high carnivore densities, occupancy is bounded at 1 whereas density is not, creating no way to identify occupancy differences between regions of high density (Clare, Anderson & MacFarland 2015). Density models allow for more precise population monitoring related to population size and have direct benefits for species that are subject to harvest pressure by trapping and hunting. Obtaining density, even using non-invasive survey methods, is a more costly endevour than occupancy analyses and can be highly variable when using genetic information (Mumma *et al.* 2015). Costs of non-invasive genetic analyses can range between $25-150 per sample depending on sample sizes, complexity of analyses, and labor costs (Stenglein *et al.* 2010; Mumma *et al.* 2015), in addition to the costs of fieldwork to collect samples. In contrast, costs of occupancy estimation consisted solely of fieldwork expenses.

Although we have shown that little consensus can be drawn between occupancy and density estimation, our results provide an informative baseline for boreal Alaska canid populations. Overall we predicted that red fox would have greater densities and occupancy probabilities across our study region than coyotes. Red foxes are smaller bodied, require less overall prey biomass, and can therefore maintain smaller home ranges (Peters 1986; Sargeant, Allen & Hastings 1987; Harrison, Bissonette & Sherburne 1989). Indeed, our spatially explicit density estimates for red fox were more than three times higher than estimates for coyotes (19.9 foxes vs 6.03 coyotes per 1,000 km^2). While consistent with our predictions, these estimates were dramatically lower than reported densities from other parts of their distributions, which are as high as 910 foxes and 710 coyotes per 1,000 km^2 (Hein & Andelt 1995; Henke & Bryant 1999; Heydon, Reynolds & Short 2000; Sarmento *et al.* 2009). Low densities may be partly related to low snowshoe hare numbers during our study, but large red fox home ranges reported in other northern boreal regions may be an indication that these mesocarnivores continually persist at low densities in this ecosystem (Jones & Theberge 1982). Indeed, our low-density estimates were similar to estimates of coyote abundance from a previous study in interior Alaska (Prugh *et al.* 2005).

Results from our density analysis seem to suggest a clear difference in population size between these canids, yet our occupancy analyses suggested that there was an equal distribution of used landscape in our study region. Estimates from both dynamic and single season occupancy analyses indicated that foxes had similar occupancy probabilities to coyotes. Many studies have shown spatial partitioning of sympatric coyotes and red foxes (Sargeant, Allen & Hastings 1987; Harrison, Bissonette & Sherburne 1989; Gosselink *et al.* 2003). Taking into account our density estimates, we suggest that coyotes exist at a lower density yet require larger home ranges and end up using an equal amount of the landscape as the more numerous red foxes across the boreal regions of interior Alaska. Using both density and occupancy provides a more complete picture of the current status of these populations, but these results suggests that relying on one method alone may lead to incomplete inference if the study goal is to examine space use and population size, especially when comparing two species with different home range sizes.

Finally, we predicted that current coyote and red fox populations would be impacted by the Alaska state-sponsored wolf control program and that our analyses would highlight the existence of a carnivore cascade. Our study was un-replicated and differences in density and occupancy estimates between our study areas could have been due to factors aside from wolf control, and we used this analysis as an example to explore the consistency of inference drawn between two analytical methods. We predicted that wolf control would release coyote populations and indirectly reduce red fox abundance, leading to higher coyote densities and occupancy probabilities in Susitna than in Denali and the opposite pattern for foxes (Roemer, Gompper & Van Valkenburgh 2009; Levi & Wilmers 2012). We found that in our high wolf study area (Denali), mesocarnivores had strikingly similar densities and occupancy probabilities to each other, and coyotes actually had higher densities in Denali than in the Susitna area, where wolf densities have been reduced by 35-80% per year for the past decade using aerial shooting (Alaska Department of Fish and Game 2015b). In addition, we predicted that coyotes would displace red fox, but we found that coyote density had little to no effect on red fox densities across the study region. Finally, in the Susitna area where low wolf abundance should have indirectly resulted in low red fox abundance by releasing coyotes, red fox densities were actually higher, and occupancy probabilities equal to those in Denali. These findings do not support the existence of a carnivore cascade between wolves, coyotes, and red fox in this region, and our multi-method approach for evaluating this hypothesis provides a useful example of how inconsistencies in current mesocarnivore research may arise due to differences in methodologies.

Assessing population trends at a landscape scale can provide an important overview of a population's status and provide insight into species interactions. Differences in cost, efficiency, efficacy, and survey logistics can make it difficult to decide which survey methods are most appropriate for a specific project. These differences may translate into discrepancies in research and interpretation of biological data. We have shown that occupancy modeling and density estimation can be successfully used to assess mesocarnivore populations in northern boreal regions, but we caution that these parameters should be treated independently and that occupancy may not be an appropriate proxy for true density estimates.

3.6. ACKNOWLEDGEMENTS

Funding was provided by the Alaska Energy Authority (RSA # 1331 to L.R.P.), a Discover Denali Fellowship to K.J.S., and a National Science Foundation Graduate Research Fellowship (#2012136814) to K.J.S. Administrative and logistical field support was provided by the Alpine Creek Lodge, Alaska Earth Sciences, Alaska Biological Research, Inc., the Murie Science Learning Center, Alaska Geographic, and Denali National Park and Preserve. Earlier drafts of this manuscript were improved by comments from K. Hundertmark. We thank field technicians C. Bondy, P. Baigas, and J. Reppert for their hard work and dedication. Laboratory work could not have been completed without the help of E. Magnuson and J.M. Acuna, we thank them for their tremendous contribution.

3.7. FIGURES

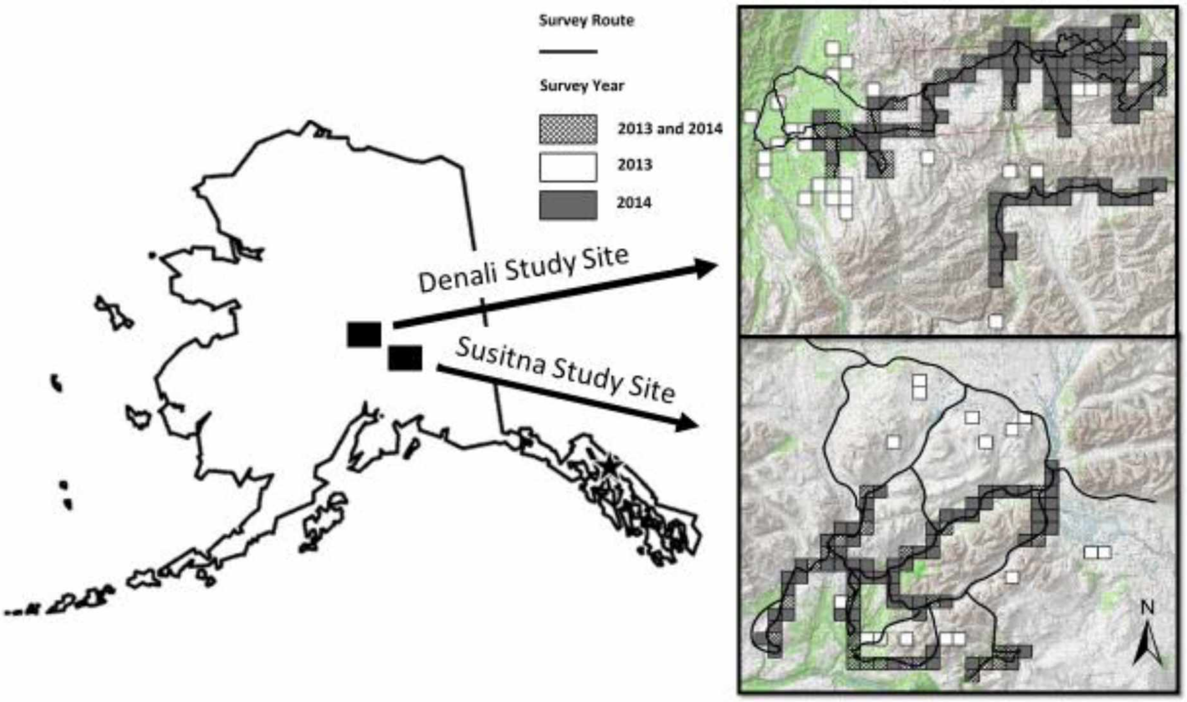

Figure. 3.1. Study area map
Interior Alaska mesocarnivore study areas showing individual 2 x 2 km survey cells (n = 300) used for occupancy analyses, and primary scat collection survey routes through each study area.

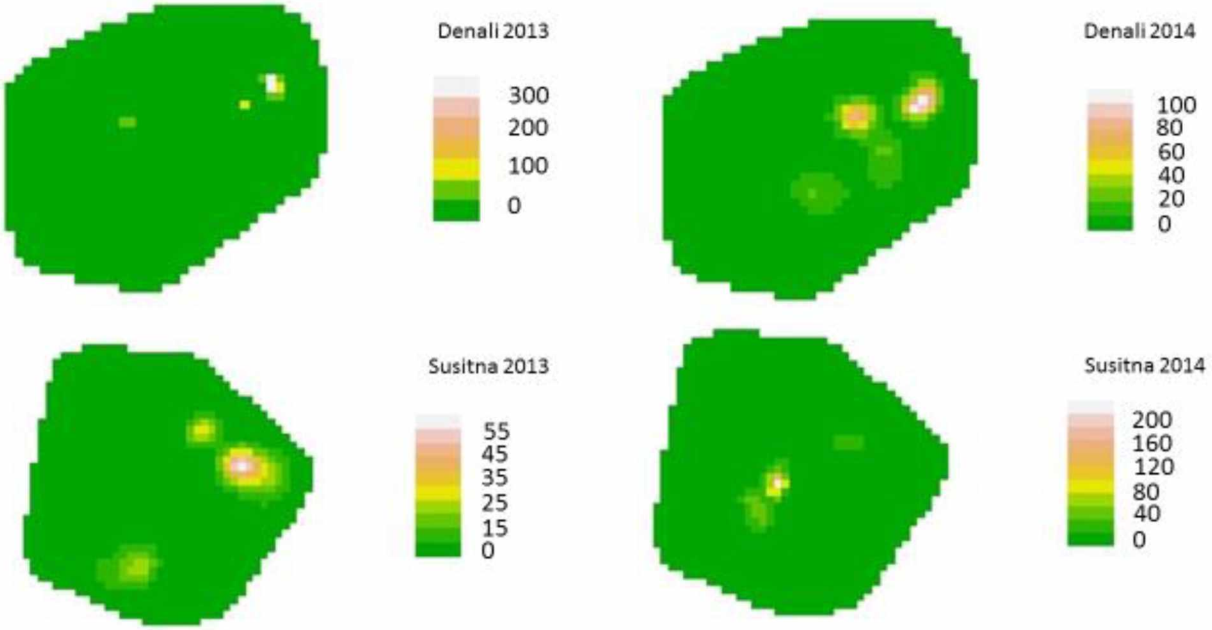

Figure. 3.2. Coyote density centers
Interior Alaska study areas showing coyote density for 2013 and 2014. Estimates (animals/1000km^2) are derived from model D(.)g0(SA+Y)σ(SA+Y).

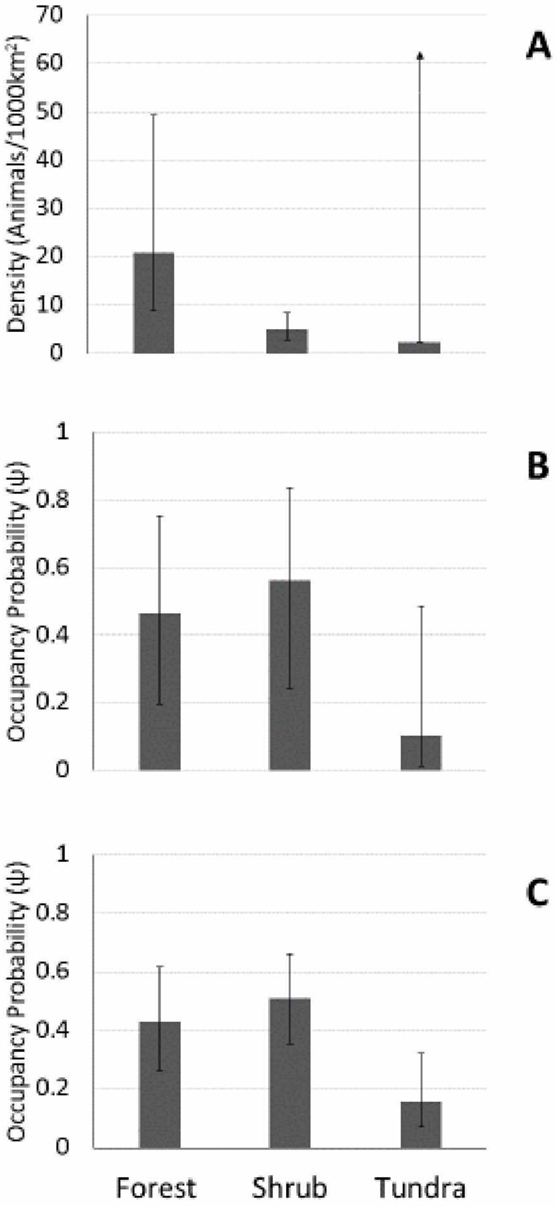

Figure. 3.3. Coyote occupancy and density estimates by habitat type
Interior Alaska coyote density estimates and occupancy probabilities. Estimates are derived from the top ranking spatially explicit capture-recapture (A) dynamic occupancy (B) and single-season occupancy (C) models that estimate D or ψ as a function of habitat type. Error bars represent 95% confidence intervals.

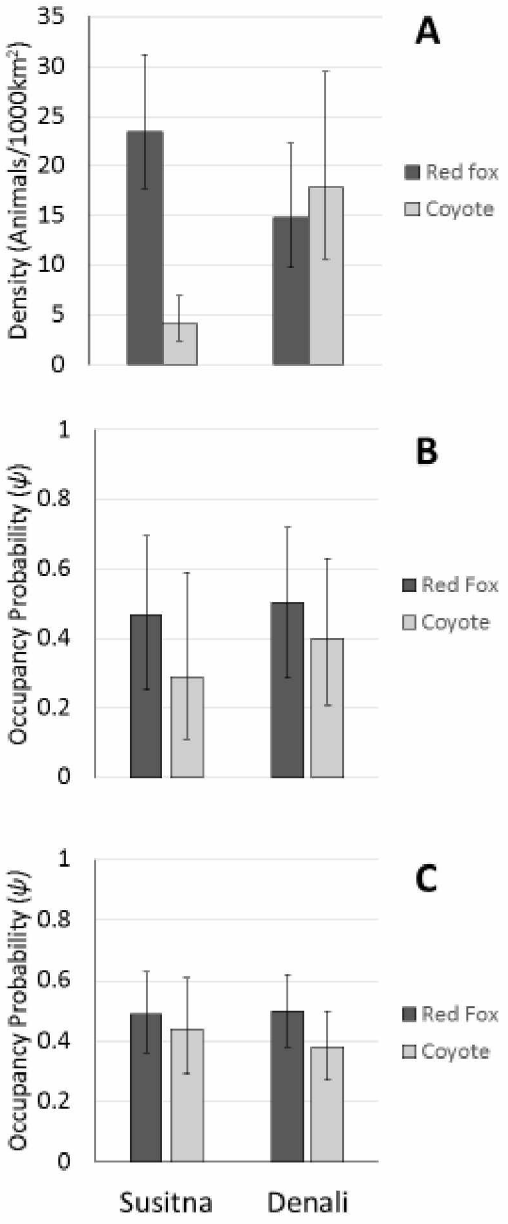

Figure. 3.4. Canid occupancy and density estimates by study area
Interior Alaska red fox and coyote density estimates and occupancy probabilities for the Susitna and Denali study areas. Estimates are derived from the top ranking spatially explicit capture-recapture (A) dynamic occupancy (B) and single-season occupancy (C) models that estimate D or ψ as a function of study area. Error bars represent 95% confidence intervals.

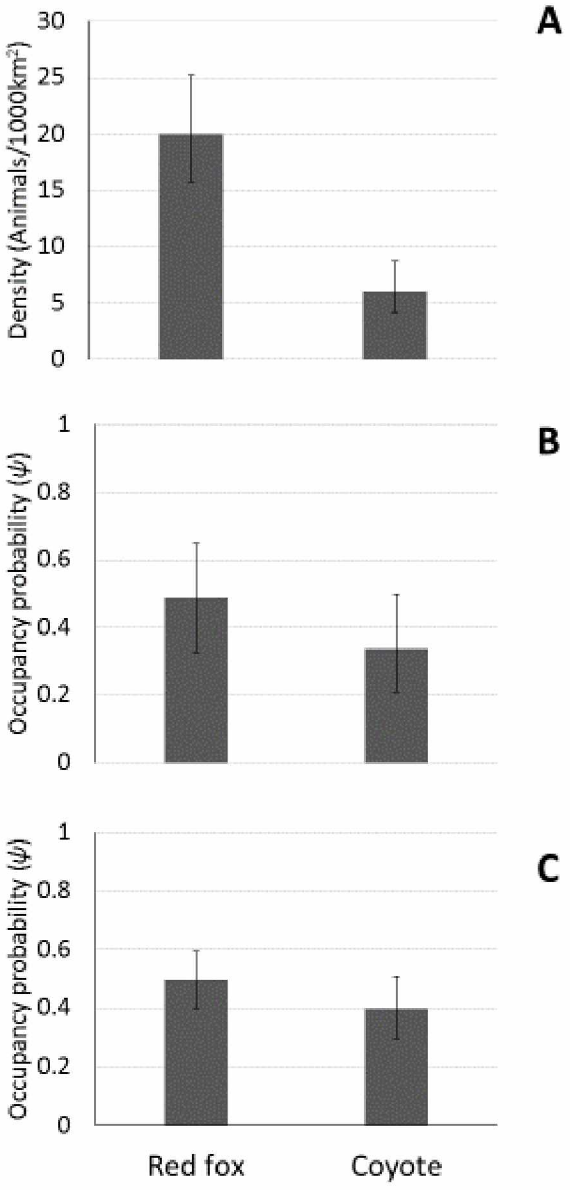

Figure. 3.5. Overall canid occupancy and density estimates
Interior Alaska red fox and coyote density estimates and occupancy probabilities. Estimates are derived from the top ranking spatially explicit capture-recapture (A) dynamic occupancy (B) and single-season occupancy (C) models that estimate D or ψ as a constant. Error bars represent 95% confidence intervals.

3.8. TABLES

Table 3.1. Single-season occupancy model selection table
Occupancy models for coyotes and red foxes in interior Alaska, 2013-2014. Models are described by the number of parameters (K), Quasi-Akaike Information Criterion value corrected for sample size (QAICc), change in QAICc (ΔQAICc) and overall model weight (QAICcWt). Models are ranked by QAICc. Parameters are held constant (.), or modeled as a function of survey distance (DIST), days since the last snowfall (DSLS), survey method (M), study area (SA), study year (Y), or habitat type (H).

Model	**K**	**QAICc**	**ΔQAICc**	**QAICcwt**
Coyote				
p(DIST+DSLS+M+Y) ψ(H)	9	242.53	0.00	0.26
p(DIST+DSLS+M+Y) ψ(.)	7	243.21	0.69	0.18
p(DIST+DSLS+M+Y) ψ(H+Y)	10	244.09	1.57	0.12
p(DIST+DSLS+M+Y) ψ(H+A)	10	244.33	1.81	0.11
p(DIST+DSLS+M+Y) ψ(Y)	8	244.71	2.19	0.09
p(.) ψ(.)	3	244.74	2.21	0.09
p(DIST+DSLS+M+Y) ψ(A)	8	245.10	2.58	0.07
p(DIST+DSLS+M+Y) ψ(H+Y+A)	11	245.54	3.01	0.06
p(DIST+DSLS+M+Y) ψ(Y+A)	9	246.76	4.23	0.03
Red fox				
p(DIST+DSLS+Y) ψ(Y)	7	462.20	0.00	0..40
p(DIST+DSLS+Y) ψ(.)	6	463.17	0.97	0..24
p(DIST+DSLS+Y) ψ(Y+A)	8	464.13	1.93	0.15
p(DIST+DSLS+Y) ψ(A)	7	465.26	3.06	0.09
p(DIST+DSLS+Y) ψ(H+Y)	9	466.23	4.03	0.05
p(DIST+DSLS+Y) ψ(H)	8	467.23	5.03	0.03
p(DIST+DSLS+Y) ψ(H+Y+A)	10	467.88	5.67	0.02
p(DIST+DSLS+Y) ψ(H+A)	9	469.35	7.15	0.01
p(.) ψ(.)	3	478.55	16.35	0.00

Table 3.2. Dynamic occupancy model selection table
Dynamic occupancy models for coyotes and red foxes in interior Alaska, 2013-2014. Models are described by the number of parameters (K), Akaike Information Criterion value (AIC), change in AIC (ΔAIC) and overall model weight (AICwt). Models are ranked by AIC. Parameters are held constant (.), or modeled as a function of survey distance (DIST), days since the last snowfall (DSLS), survey method (M), study area (SA), or habitat type (H).

Model	**K**	**AIC**	**ΔAIC**	**AICwt**
Coyote				
ψ(H) γ(.) ε(.) *p*(DIST+DSLS+A)	9	244.68	0.00	0.17
ψ(H+A) γ(A) ε(A) *p*(DIST+DSLS+A)	12	245.11	0.43	0.14
ψ(H+A) γ(.) ε(.) *p*(DIST+DSLS+A)	10	245.31	0.63	0.13
ψ(.) γ(.) ε(.) *p*(.)	4	245.57	0.89	0.11
ψ(H) γ(A) ε(A) *p*(DIST+DSLS+A)	11	245.67	0.98	0.11
ψ(.) γ(.) ε(.) *p*(DIST+DSLS+A)	7	245.74	1.06	0.10
ψ(.) γ(H) ε(H) *p*(DIST+DSLS+A)	9	245.96	1.28	0.09
ψ(A) γ(A) ε(A) *p*(DIST+DSLS+A)	10	247.60	2.92	0.04
ψ(A) γ(.) ε(.) *p*(DIST+DSLS+A)	8	247.69	3.0	0.04
ψ(H+A) γ(H) ε(H) *p*(DIST+DSLS+A)	14	247.72	3.04	0.04
ψ(H) γ(H) ε(H) *p*(DIST+DSLS+A)	13	250.00	5.32	0.01
ψ(.) γ(A) ε(A) *p*(DIST+DSLS+A)	11	250.23	5.55	0.01
ψ(A) γ(H) ε(H) *p*(DIST+DSLS+A)	12	251.37	6.69	0.00
Red fox				
ψ(H) γ(A) ε(A) *p*(DIST+DSLS+M)	11	306.79	0.00	0.45
ψ(H+A) γ(A) ε(A) *p*(DIST+DSLS+M)	12	307.29	0.50	0.35
ψ(.) γ(A) ε(A) *p*(DIST+DSLS+M)	9	310.30	3.51	0.08
ψ(H) γ(.) ε(.) *p*(DIST+DSLS+M)	9	311.38	4.59	0.04
ψ(H+A) γ(.) ε(.) *p*(DIST+DSLS+M)	10	311.71	4.92	0.04
ψ(A) γ(A) ε(A) *p*(DIST+DSLS+M)	10	312.26	5.47	0.03
ψ(.) γ(.) ε(.) *p*(DIST+DSLS+M)	7	315.04	8.25	0.01
ψ(H) γ(H) ε(H) *p*(DIST+DSLS+M)	13	316.29	9.50	0.00
ψ(H+A) γ(H) ε(H) *p*(DIST+DSLS+M)	14	316.60	9.81	0.00
ψ(A) γ(.) ε(.) *p*(DIST+DSLS+M)	8	317.04	10.25	0.00
ψ(.) γ(.) ε(.) *p*(.)	4	319.01	12.22	0.00
ψ(.) γ(H) ε(H) *p*(DIST+DSLS+M)	11	319.53	12.74	0.00
ψ(A) γ(H) ε(H) *p*(DIST+DSLS+M)	12	321.51	14.72	0.00

Table 3.3. Spatially explicit capture-recapture model selection table
Spatially explicit capture recapture models for coyotes and red foxes in interior Alaska, 2013-2014. Models are described by the number of parameters (K), Akaike Information Criterion value corrected for sample size (AICc), change in AICc (ΔAICc) and overall model weight (AICcwt). Models are ranked by AICc score. Parameters can be held constant (.), or modeled as a function of study area (SA), study year (Y), survey occasion (T), habitat type (H), or coyote density (CD).

Model	**K**	**AICc**	**ΔAICc**	**AICcwt**
Coyote				
D(.)g0(SA+Y)σ(SA+Y)	9	901.69	0.00	0.60
D(SA+Y)g0(SA+Y)σ(SA+Y)	12	903.34	1.66	0.26
D(h)g0(SA+Y)σ(SA+Y)	11	905.14	3.45	0.11
D(SA+Y+H)g0(SA+Y)σ(SA+Y)	14	907.38	5.70	0.03
D(SA+H)g0(SA)σ(SA)	8	914.45	12.76	0.00
D(SA)g0(SA)σ(SA)	6	915.76	14.07	0.00
D(.)g0(.)σ(.)	3	921.01	19.38	0.00
D(.)g0(SA)σ(SA)	5	928.03	26.35	0.00
D(h)g0(SA)σ(SA)	7	933.67	31.98	0.00
Red fox				
D(SA)g0(SA)σ(SA)	6	2265.13	0.00	0.49
D(.)g0(SA)σ(SA)	5	2266.21	1.07	0.29
D(CD)g0(SA)σ(SA)	6	2268.43	3.30	0.09
D(SA+H)g0(SA)σ(SA)	8	2268.55	3.42	0.09
D(H)g0(SA)σ(SA)	7	2270.35	5.22	0.04
D(.)g0(SA+Y)σ(T)	7	2278.82	13.69	0.00
D(CD)g0(SA+Y)σ(T)	8	2281.22	16.08	0.00
D(SA+Y)g0(SA+Y)σ(T)	10	2282.54	17.41	0.00
D(H)g0(SA+Y)σ(T)	9	2283.63	18.50	0.00
D(SA+Y+H)g0(SA+Y)σ(T)	12	2287.58	22.45	0.00
D(.)g0(.)σ(.)	3	2310.49	45.36	0.00

3.9. REFERENCES

Alaska Department of Fish and Game (2015a) Intensive Management in Alaska. 14 August, 2015. Alaska Depatment of Fish and Game, http://www.adfg.alaska.gov/index.cfm?adfg=intensivemanagement.main.

Alaska Department of Fish and Game (2015b) Annual Report to the Alaska Board of Game on Intensive Management for Moose with Wolf Predation Control in unit 13. 14 August, 2015. Alaska Depatment of Fish and Game, http://www.adfg.alaska.gov/static/research/programs/intensivemanagement/pdfs/2015_gmu_13_intensive_management_annual_report.pdf.

Alaska Energy Authority (2014) Susitna-Watana Hydro. 16 February, 2015 Alaska Energy Authority, http://www.susitna-watanahydro.org/.

Allen, B.L., Lundie-Jenkins, G., Burrows, N.D., Engeman, R.M., Fleming, P.J. & Leung, L.K.P. (2014) Does lethal control of top-predators release mesopredators? A re-evaluation of three Australian case studies. *Ecological Management & Restoration,* **15,** 191-195.

Bailey, L.L., Simons, T.R. & Pollock, K.H. (2004) Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications,* **14,** 692-702.

Berger, K.M. & Gese, E.M. (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? *Journal of Animal Ecology,* **76,** 1075-1085.

Berry, O., Sarre S.D., Farrington L., Aitken N. (2007) Faecal DNA detection of invasive species: the case of feral foxes in Tasmania. *Wildlife Research* **34**, 1-7.

Boersen, M.R., Clark, J.D. & King, T.L. (2003) Estimating Black Bear Population Density and Genetic Diversity at Tensas River, Louisiana Using Microsatellite DNA Markers. *Wildlife Society Bulletin (1973-2006),* **31,** 197-207.

Borchers, D.L. & Efford, M.G. (2008) Spatially Explicit Maximum Likelihood Methods for Capture–Recapture Studies. *Biometrics,* **64,** 377-385.

Breen, M., Jouquand, S., Renier, C., Mellersh, C.S., Hitte, C., Holmes, N.G., Cheron, A., Suter, N., Vignaux, F., Bristow, A.E., Priat, C., McCann, E., Andre, C., Boundy, S., Gitsham, P., Thomas, R., Bridge, W.L., Spriggs, H.F., Ryder, E.J., Curson, A., Sampson, J., Ostrander, E.A., Binns, M.M., and Galibert, F. (2001). Chromosome-Specific Single-Locus FISH Probes Allow Anchorage of an 1800-Marker Integrated Radiation-Hybrid/Linkage Map of the Domestic Dog Genome to All Chromosomes. *Genome Research* 11 **10**, 1784-1795.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach,* 2nd edn. Springer Verlag, New York, U.S.A.

Chamberlain, M.J. & Leopold, B.D. (2005) Overlap in space use among bobcats (Lynx rufus), coyotes (Canis latrans) and gray foxes (Urocyon cinereoargenteus). *American Midland Naturalist,* **153,** 171-179.

Clare, J.D.J., Anderson, E.M. & MacFarland, D.M. (2015) Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. *Journal of Wildlife Management,* **79,** 469-480.

Dalen, L., Gotherstrom, A., Angerbjorn, A. (2004) Identifying species from pieces of faeces. *Conservation Genetics* **5**, 109–111.

De barba, M., Adams, J.R., Goldberg, C.S., Stansbury, C.R., Arias, D., Cisneros, R., Waits, L.P. (2014) Molecular species identification for multiple carnivores. *Conservation Genetics* **6**, 821-824.

Garshelis, D. (1992) Mark-Recapture Density Estimation for Animals with Large Home Ranges. *Wildlife 2001: Populations* (eds D. McCullough & R. Barrett), pp. 1098-1111. Springer Netherlands.

Fiske, I. & Chandler, R. (2011) unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software,* **43,** 1-23.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000) Abundance–occupancy relationships. *Journal of Applied Ecology,* **37,** 39-59.

Gehrt, S.D. & Clark, W.R. (2003) Raccoons, Coyotes, and Reflections on the Mesopredator Release Hypothesis. *Wildlife Society Bulletin (1973-2006),* **31,** 836-842.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. (2006) A Comparison of Noninvasive Techniques to Survey Carnivore Communities in Northeastern North America. *Wildlife Society Bulletin,* **34,** 1142-1151.

Gosselink, T.E., Deelen, T.R.V., Warner, R.E. & Joselyn, M.G. (2003) Temporal Habitat Partitioning and Spatial Use of Coyotes and Red Foxes in East-Central Illinois. *Journal of Wildlife Management,* **67,** 90-103.

Guyon, R., Lorentzen, T.D., Hitte, C., Kim, L., Cadieu, E., Parker, H.G., Quignon, P., Lowe, J.K., Renier, C., Gelfenbeyn, B., Vignaux, F., DeFrance, H.B., Gloux, S., Mahairas, G.G., Andre, C., Galibert, F., & Ostander, E.A. (2003) A 1-MB resolution radiation hybrid map of the canine genome. *Proceedings of the National Academy of Sciences,* **100**, 5296–5301.

Harrison, D.J., Bissonette, J.A. & Sherburne, J.A. (1989) Spatial Relationships between Coyotes and Red Foxes in Eastern Maine. *Journal of Wildlife Management,* **53,** 181-185.

Hein, E.W. & Andelt, W.F. (1995) Estimating Coyote Density from Mark-Resight Surveys. *Journal of Wildlife Management,* **59,** 164-169.

Henke, S.E. & Bryant, F.C. (1999) Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management*, **63,** 1066-1081.

Heydon, M.J., Reynolds, J.C. & Short, M.J. (2000) Variation in abundance of foxes (Vulpes vulpes) between three regions of rural Britain, in relation to landscape and other variables. *Journal of Zoology,* **251,** 253-264.

Homer, C., Dewitz, J., Fry, J., Coan, M., Hossain, N., Larson, C., Herold, N., McKerrow, A., VanDriel, J.N., and Wickham, J. 2007. Completion of the 2001 National Land Cover Database for the Conterminous United States. *Photogrammetric Engineering and Remote Sensing,* **73**, 337-341.

Jhala, Y., Qureshi, Q. & Gopal, R. (2011) Can the abundance of tigers be assessed from their signs? *Journal of Applied Ecology,* **48,** 14-24.

Jones, D.M. & Theberge, J.B. (1982) Summer home range and habitat utilisation of the red fox (Vulpes vulpes) in a tundra habitat, northwest British Columbia. *Canadian Journal of Zoology,* **60,** 807-812.

Kamler, J.F. & Gipson, P.S. (2000) Space and habitat use by resident and transient coyotes. *Canadian Journal of Zoology,* **78,** 2106-2111.

Karanth, K.U. (1995) Estimating tiger Panthera tigris populations from camera-trap data using capture—recapture models. *Biological Conservation,* **71,** 333-338.

Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in india using photographic captures and recaptures. *Ecology,* **79,** 2852-2862.

Levi, T. & Wilmers, C.C. (2012) Wolves-coyotes-foxes: a cascade among carnivores. *Ecology,* **93,** 921-929.

Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J. & Buzas, J.S. (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape Ecology,* **26,** 327-340.

Long, R.A., MacKay, P., Ray, J. & Zielinski, W. (2008) *Noninvasive survey methods for carnivores*. Island Press, Washington, D.C., USA.

MacKenzie, D.I. & Bailey, L.L. (2004) Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics,* **9,** 300-318.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology,* **83,** 2248-2255.

MacKenzie, D.I., Nichols, J., Royle, J., Pollock, K., Bailey, L. & Hines, J. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurence*. Elsevier Academic Press, Oxford, UK.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology,* **84,** 2200-2207.

Mazerolle, M.J. (2015) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3. http://CRAN.R-project.org/package=AICcmodavg.

Miller, B.J., Harlow, H.J., Harlow, T.S., Biggins, D. & Ripple, W.J. (2012) Trophic cascades linking wolves (*Canis lupus*), coyotes (*Canis latrans*), and small mammals. *Canadian Journal of Zoology,* **90,** 70-78.

Moore, M., Brown, S.K., Sacks, B.N. (2010) Thirty-one short red fox (*Vulpes vulpes*) microsatellite markers. *Molecular Ecology Resources* **10**, 404-408.

Mowat, G. & Strobeck, C. (2000) Estimating Population Size of Grizzly Bears Using Hair Capture, DNA Profiling, and Mark-Recapture Analysis. *Journal of Wildlife Management,* **64,** 183-193.

Mulders, R., Boulanger, J. & Paetkau, D. (2007) Estimation of population size for wolverines Gulo gulo at Daring Lake, Northwest Territories, Using DNA based mark-recapture methods. *Wildlife Biology,* **13,** 38-51.

Mumma, M.A., Zieminski, C., Fuller, T.K., Mahoney, S.P. & Waits, L.P. (2015) Evaluating noninvasive genetic sampling techniques to estimate large carnivore abundance. *Molecular ecology resources,* **15**, 1133-1144.

Murphy, M.A., Waits, L.P., Kendall, K.C. (2000) Quantitative evaluation of fecal drying methods for brown bear DNA analysis. *Wildlife Society Bulletin,* **28**, 951–957.

Murray, D.L. & Boutin, S. (1991) The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia,* **88,** 463-469.

Murray, D.L., Boutin, S. & O'Donoghue, M. (1994) Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology,* **72,** 1444-1451.

Newsome, T.M. & Ripple, W.J. (2015) A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology,* **84,** 49-59.

Palomares, F., Godoy, J.A., Piriz, A., O'Brien, S.J., Johnson, W.E. (2002) Faecal genetic analysis to determine the presence and distribution of elusive carnivores: design and feasibility for the Iberian lynx. *Molecular Ecology*, **11**, 2171–2182.

Peters, R.H. (1986) *The ecological implications of body size*. Cambridge University Press.

Peakall, R.O.D, Smouse, P.E (2006) GENALEX 6: genetic analyses in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes,* **6**, 288-295.

Pollock, K.H., Nichols, J.D., Simons, T.R., Farnsworth, G.L., Bailey, L.L. & Sauer, J.R. (2002) Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics,* **13,** 105-119.

Prugh, L.R. (2005) Coyote prey selection and community stability during a decline in food supply. *Oikos,* **110,** 253-264.

Prugh, L.R., Ritland, C.E., Arthur, S.M. & Krebs, C.J. (2005) Monitoring coyote population dynamics by genotyping faeces. *Molecular Ecology,* **14,** 1585-1596.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The rise of the mesopredator. *Bioscience,* **59,** 779-791.

Randa, L.A., Cooper, D.M., Meserve, P.L. & Yunger, J.A. (2009) Prey switching of sympatric canids in response to variable prey abundance. *Journal of Mammalogy,* **90,** 594-603.

Richmond, O.M.W, Hines, J.E. & Beissinger, S.R. (2013) Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications,* **20,** 2036-2046.

Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters,* **12,** 982-998.

Roemer, G.W., Gompper, M.E. & Van Valkenburgh, B. (2009) The Ecological Role of the Mammalian Mesocarnivore. *Bioscience,* **59,** 165-173.

Royle, J.A. & Young, K.V. (2008) A hierarchical model for spatial capture–recapture data. *Ecology,* **89,** 2281-2289.

Sargeant, A.B., Allen, S.H. & Hastings, J.O. (1987) Spatial Relations between Sympatric Coyotes and Red Foxes in North Dakota. *Journal of Wildlife Management,* **51,** 285-293.

Sarmento, P., Cruz, J., Eira, C. & Fonseca, C. (2009) Evaluation of Camera Trapping for Estimating Red Fox Abundance. *Journal of Wildlife Management,* **73,** 1207-1212.

Schuette, P., Wagner, A.P., Wagner, M.E. & Creel, S. (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation,* **158,** 301-312.

Seddon, J.M. (2005) Canid-specific primers for molecular sexing using tissue or non-invasive samples. *Conservation Genetics,* **6**,147-149.

Shulski, M. & Wendler, G. (2007) *The Climate of Alaska.* University of Alaska Press, Fairbanks, AK.

Sollmann, R., Furtado, M.M., Hofer, H., Jacomo, A.T.A., Torres, N.M. & Silveira, L. (2012) Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology,* **77,** 41-46.

Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S. (1988) Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. *Conservation Biology,* **2,** 75-92.

Squires, J.R., DeCesare, N.J., Hebblewhite, M. & Berger, J. (2012) Missing lynx and trophic cascades in food webs: A reply to Ripple *et al. Wildlife Society Bulletin,* **36,** 567-571.

Steinmetz, R., Seuaturien, N. & Chutipong, W. (2013) Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation,* **163,** 68-78.

Stenglein, J.L., Waits, L.P., Ausband, D.E., Zager, P. & Mack, C.M. (2010) Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. *Journal of Wildlife Management*, **74**, 1050-1058.

Thompson, C.M., Royle, J.A. & Garner, J.D. (2012) A framework for inference about carnivore density from unstructured spatial sampling of scat using detector dogs. *Journal of Wildlife Management,* **76,** 863-871.

Van Ballenberghe, V. (2006) Predator control, politics, and wildlife conservation in Alaska. *Alces,* **42,** 1-11.

Waits, L.P., Luikart, G., Taberlet, P. (2001) Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. *Molecular Ecology,* **10**, 249-256.

Whittington, J., Heuer, K., Hunt, B., Hebblewhite, M. & Lukacs, P. (2014) Estimating occupancy using spatially and temporally replicated snow surveys. *Animal Conservation,* **18**, 92-101.

Winfree, R., Rice, B., Fresco, N., Krutikov, L., Morris, J., Callaway, D., Mow, J. & Swanton, N. (2014) Climate change scenario planning for central Alaska parks: Yukon-Charley, Wrangell-St. Elias, and Denali. *Natural Resource Report NPS/AKSO/NRR-2014/829.* National Park Service, Fort Collins, Colorado.

CHAPTER 4. GENERAL CONCLUSIONS

This study has revealed current trends in mesocarnivore space use patterns and population densities in interior Alaska. I have shown that landscape factors, including abiotic and bottom-up forces, play a key role in current occupancy patterns of coyotes, red foxes, lynx, marten, and wolverines. In addition, I have used multiple non-invasive survey techniques and modeling methods to produce current estimates of occupancy probabilities and canid densities while comparing two commonly used modeling techniques.

I examined the impacts that habitat type, prey abundance, snow conditions, and human activity had on the target mesocarnivore species. I found snow conditions, both average snow depth and snow penetrability, to be the most influential covariates for predicting occupancy probabilities. Coyotes and foxes had highest occupancy probabilities in areas of shallow and compacted snow. These findings matched my predictions and are well supported by other studies that suggest canids use areas for traveling and hunting that reduce the amount of energy required to move through the snow (Murray & Boutin 1991; Murray, Boutin & O'Donoghue 1994). Unlike canids, lynx have been shown to be more tolerant of deep snow conditions (Murray & Boutin 1991) and I predicted that they would have greater occupancy probabilities in deep and less compacted (fluffy) snow compared to other mesocarnivores. I did find that lynx used areas of fluffy snow, however, I was surprised to find that lynx occupancy in deep snow was the lowest of all mesocarnivores. Wolverines and marten had unique responses to snow conditions in that they both used deep and fluffy snow. This preference may be due to the need for snow covered denning areas (wolverine) and increase availability of subnivean travel routes (marten) used for predator avoidance, thermal cover, and access to prey (Raine 1983; McKelvey *et al.* 2011). Overall I have shown that climatic conditions may play an important role in determining how mesocarnivores are distributed. Snow conditions are likely to shift dramatically in boreal regions due to climate change (Chapin *et al.* 2014; Winfree *et al.* 2014), and these shifts could lead to changes in spatial distributions of mesocarnivores.

Although snow conditions were the most influential predictor of mesocarnivore occupancy during my study, I recognize that prey and habitat are also important (Murray, Boutin & O'Donoghue 1994; Prugh 2005) and that covariation among these predictors must be addressed. When assessing occupancy of all mesocarnivores together, habitat type was a strong predictor. This guild-wide analysis suggested that forest habitat types were used the most by the study species, and I also found that prey abundance was highest in these forested areas. However, I found that snow depths did not differ significantly between forest and shrub habitats and that there was no correlation between snow conditions and prey abundance. Prey covariate also received little support as a predictor of occupancy probability. Prey abundance was based on a count of tracks encountered during occupancy surveys, and it is possible that tracks are a poor index of prey abundance. These methods need to be validated further before strong conclusions about the impact of prey can be made. I also investigated the effect that human activity had on mesocarnivores and found a minimal impact in our study area. It is likely that the current levels of human influence in this rural boreal region are too low to be of significance at the scale that I examined (~4,000 km^2), however an increase in development and activity in the area could cause dramatic changes (Ordeñana *et al.* 2010; Bateman & Fleming 2012). I suggest that my results be used as a baseline and that follow up studies are conducted in the coming years to assess the impacts climate change and development projects such as the proposed Susitna-Watana hydroelectric dam may have on mesocarnivores.

The occupancy analysis presented in Chapter 1 highlights resources of particular importance and influence on mesocarnivore distribution. Occupancy analyses like the one I have conducted have become a staple for non-invasive research on habitat selection, impacts of urbanization on wildlife, and identifying resource needs and areas of importance for vulnerable species (Karanth *et al.* 2011; Sollmann *et al.* 2012; Schuette *et al.* 2013). The population level inference that can be derived from these models is extensive (MacKenzie *et al.* 2006), however the relationship between occupancy and density has not been well established. In Chapter 2 I evaluated the use of occupancy models and spatially explicit capture-recapture (SECR) models for mesocarnivore studies, and I compared the inference obtained from each.

I predicted that occupancy models (single-season and dynamic) would produce similar inference on canid population abundance as density estimates produced from SECR analysis. As expected, I found that single-season and dynamic occupancy models produced similar results. Overall, estimates suggested higher red fox occupancy than coyote occupancy and similar trends in both habitat use and study area occupancy. Precision was good in both models, and the slightly greater variance observed in the dynamic models is likely due to smaller survey-site sample sizes. However, I found inconsistencies between results from occupancy and SECR analyses, suggesting that methodological differences may explain some of the inconsistencies found in current mesocarnivore research regarding interspecific interactions (e.g., Gehrt & Clark 2003; Ritchie & Johnson 2009; Allen *et al.* 2014). In addition, my results do not support recent findings that occupancy is a strong index of density (Clare, Anderson & MacFarland 2015). I found that habitat was a strongly influential covariate for both coyote and fox occupancy, but was not well supported as a predictor of density. Overall precision was adequate with all models ($CV < 0.25$), suggesting that each is a viable option for mesocarnivore research, however managers should be cautious about using occupancy as a proxy for density. The differences I have shown between these modeling methods could partially be explained by differences in survey designs and data collection. Using scat collection to estimate density, and track surveys to estimate occupancy may have led to some of the differences between this study and that of Clare, Anderson & MacFarland (2015), and I recommend that further model comparisons be performed using data collected from a single survey method. While occupancy modeling provides an inexpensive and informative way to assess spatial patterns, it is likely most appropriate for assessing habitat use, changes in spatial distribution over time, or spatial relationships between co-occurring species (Sollmann *et al.* 2012; Richmond, Hines & Beissinger 2013; Schuette *et al.* 2013). Density estimation with SECR is a more suitable model if research goals revolve around monitoring population size for conservation purposes or harvest management.

My findings will improve management efforts and survey designs in boreal regions for these valuable furbearer species by establishing important resource needs and baseline population demographic information for these species. As conditions in boreal regions around the world continue to change, it is vital to understand how mesocarnivore species interact with their environment so that we can better understand how they interact with each other and how to continue to study them in the most efficient way possible.

4.1. REFERENCES

Allen, B.L., Lundie-Jenkins, G., Burrows, N.D., Engeman, R.M., Fleming, P.J. & Leung, L.K.P. (2014) Does lethal control of top-predators release mesopredators? A re-evaluation of three Australian case studies. *Ecological Management & Restoration,* **15,** 191-195.

Arnemo, J.M., Ahlqvist, P., Andersen, R., Berntsen, F., Ericsson, G., Odden, J., Brunberg, S., Segerström, P. & Swenson, J.E. (2006) Risk of capture-related mortality in large free-ranging mammals: experiences from Scandinavia. *Wildlife Biology,* **12,** 109-113.

Bateman, P.W. & Fleming, P.A. (2012) Big city life: carnivores in urban environments. *Journal of Zoology,* **287,** 1-23.

Borchers, D.L., Distiller, G., Foster, R., Harmsen, B. & Milazzo, L. (2014) Continuous-time spatially explicit capture–recapture models, with an application to a jaguar camera-trap survey. *Methods in Ecology and Evolution,* **5,** 656-665.

Borchers, D.L. & Efford, M.G. (2008) Spatially Explicit Maximum Likelihood Methods for Capture–Recapture Studies. *Biometrics,* **64,** 377-385.

Chapin, F.S., III, S. F. Trainor, P. Cochran, H. Huntington, C. Markon, M. McCammon, A. D. McGuire & Serreze, M. (2014) Climate Change Impacts in the United States: The Third National Climate Assessment. (eds J. M. Melillo, T.C. Richmond & T.W. Yohe), pp. 514-536. United States Global Change Research Program, Washington, D.C.

Clare, J.D.J., Anderson, E.M. & MacFarland, D.M. (2015) Predicting bobcat abundance at a landscape scale and evaluating occupancy as a density index in central Wisconsin. *Journal of Wildlife Management,* **79,** 469-480.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011) Trophic downgrading of planet earth. *Science,* **333,** 301-306.

Gehrt, S.D. & Clark, W.R. (2003) Raccoons, coyotes, and reflections on the mesopredator release hypothesis. *Wildlife Society Bulletin (1973-2006),* **31,** 836-842.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in Northeastern North America. *Wildlife Society Bulletin,* **34,** 1142-1151.

Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D. & MacKenzie, D.I. (2011) Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology,* **48,** 1048-1056.

Karanth, K.U. & Nichols, J.D. (1998) Estimation of tiger densities in india using photographic captures and recaptures. *Ecology,* **79,** 2852-2862.

Kilström, Å. (2004) The wolverine population in the boreal forest area. PhD thesis, Uppsala University, Sweden.

Larivière, S. & Pasitschniak-Arts, M. (1996) Vulpes vulpes. *Mammalian species***, 537**, 1-11.

Long, R.A., Donovan, T.M., MacKay, P., Zielinski, W.J. & Buzas, J.S. (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape Ecology,* **26,** 327-340.

Long, R.A., MacKay, P., Ray, J. & Zielinski, W. (2008) *Noninvasive survey methods for carnivores.* Island Press, Washington, D.C., USA.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology,* **84,** 2200-2207.

MacKenzie, D.I., Nichols, J.D., Royle, J., Pollock, K., Bailey, L. & Hines, J. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurence*. Elsevier Academic Press, Oxford, UK.

Marcot, B., Jorgenson, M.T., Lawler, J., Handel, C. & DeGange, A. (2015) Projected changes in wildlife habitats in Arctic natural areas of northwest Alaska. *Climatic Change,* **130,** 145-154.

McKelvey, K.S., Copeland, J.P., Schwartz, M.K., Littell, J.S., Aubry, K.B., Squires, J.R., Parks, S.A., Elsner, M.M. & Mauger, G.S. (2011) Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications,* **21,** 2882-2897.

McKelvey, K.S., Von Kienast, J., Aubry, K.B., Koehler, G.M., Maletzke, B.T., Squires, J.R., Lindquist, E.L., Loch, S. & Schwartz, M.K. (2006) DNA analysis of hair and scat collected along snow tracks to document the presence of Canada lynx. *Wildlife Society Bulletin,* **34,** 451-455.

Mech, L.D. (2012) Is science in danger of sanctifying the wolf? *Biological Conservation,* **150,** 143-149.

Mowat, G. & Strobeck, C. (2000) Estimating Population Size of Grizzly Bears Using Hair Capture, DNA Profiling, and Mark-Recapture Analysis. *Journal of Wildlife Management,* **64,** 183-193.

Murray, D.L. & Boutin, S. (1991) The influence of snow on lynx and coyote movements: does morphology affect behavior? *Oecologia,* **88,** 463-469.

Murray, D.L., Boutin, S. & O'Donoghue, M. (1994) Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Canadian Journal of Zoology,* **72,** 1444-1451.

Nikiforuk, A. (2010) *Tar sands: Dirty oil and the future of a continent*. Greystone Books Ltd. Vancouver, BC Canada.

Olsson, R. (2009) Boreal Forest and Climate Change. *Air Pollution and Climate Series 23.* Air Pollution & Climate Secretariat & Taiga Rescue Network, Göteborg, Sweden.

Ordeñana, M.A., Crooks, K.R., Boydston, E.E., Fisher, R.N., Lyren, L.M., Siudyla, S., Haas, C.D., Harris, S., Hathaway, S.A. & Turschak, G.M. (2010) Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy,* **91,** 1322-1331.

Pauli, J.N., Hamilton, M.B., Crain, E.B. & Buskirk, S.W. (2008) A single-sampling hair trap for mesocarnivores. *Journal of Wildlife Management,* **72,** 1650-1652.

Prugh, L.R. (2005) Coyote prey selection and community stability during a decline in food supply. *Oikos,* **110,** 253-264.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S. & Brashares, J.S. (2009) The rise of the mesopredator. *Bioscience,* **59,** 779-791.

Raine, R.M. (1983) Winter habitat use and responses to snow cover of fisher (*Martes pennanti*) and marten (*Martes americana*) in southeastern Manitoba. *Canadian Journal of Zoology,* **61,** 25-34.

Richmond, O.M.W., Hines, J.E. & Beissinger, S.R. (2013) Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications,* **20,** 2036-2046.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014) Status and Ecological Effects of the World's Largest Carnivores. *Science,* **343,** 1241484.

Ritchie, E.G. & Johnson, C.N. (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters,* **12,** 982-998.

Roemer, G.W., Gompper, M.E. & Van Valkenburgh, B. (2009) The ecological role of the mammalian mesocarnivore. *Bioscience,* **59,** 165-173.

Ruggiero, L.F., Squires, J.R., Buskirk, S.W., Aubry, K.B., McKelvey, K.S., Koehler, G. & Krebs, C.J. (2000) *Ecology and conservation of lynx in the United States*. University Press of Colorado Boulder, CO.

Sarmento, P., Cruz, J., Eira, C. & Fonseca, C. (2009) Evaluation of camera trapping for estimating red fox abundance. *Journal of Wildlife Management,* **73,** 1207-1212.

Savory, G.A., Hunter, C.M., Wooller, M.J. & O'Brien, D.M. (2014) Anthropogenic food use and diet overlap between red foxes (*Vulpes vulpes*) and arctic foxes (*Vulpes lagopus*) in Prudhoe Bay, Alaska. *Canadian Journal of Zoology,* **92,** 657-663.

Schuette, P., Wagner, A.P., Wagner, M.E. & Creel, S. (2013) Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation,* **158,** 301-312.

Sollmann, R., Furtado, M.M., Hofer, H., Jacomo, A.T.A., Torres, N.M. & Silveira, L. (2012) Using occupancy models to investigate space partitioning between two sympatric large predators, the jaguar and puma in central Brazil. *Mammalian Biology,* **77,** 41-46.

Soulé, M.E., Bolger, D.T., Alberts, A.C., Wrights, J., Sorice, M. & Hill, S. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conservation Biology,* **2,** 75-92.

Tape, K.E.N., Sturm, M. & Racine, C. (2006) The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology,* **12,** 686-702.

Travis, J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B: Biological Sciences,* **270,** 467-473.

Whittington, J., Heuer, K., Hunt, B., Hebblewhite, M. & Lukacs, P. (2014) Estimating occupancy using spatially and temporally replicated snow surveys. *Animal Conservation.*

Winfree, R., Rice, B., Fresco, N., Krutikov, L., Morris, J., Callaway, D., Mow, J. & Swanton, N. (2014) Climate change scenario planning for central Alaska parks: Yukon-Charley, Wrangell-St. Elias, and Denali. *Natural Resource Report NPS/AKSO/NRR-2014/829.* National Park Service, Fort Collins, Colorado.

Young, S. & Jackson, H. (1951) The clever coyote. *The Stackpole Co., Harrisburg, Pa., and The Wildlife Management Institute,* Washington, DC.

Zielinski, W.J., Truex, R.L., Schlexer, F.V., Campbell, L.A. & Carroll, C. (2005) Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. *Journal of Biogeography,* **32,** 1385-1407.