University of Alberta

Niche partitioning and spatial variation in abundance of Rock (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucura*): a case of habitat selection at multiple scales

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of

Master of Science

in

Department of Biological Sciences

Spring 2010
Edmonton, Alberta

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ABSTRACT

Climate change can affect habitat availability and species interactions at several spatial and temporal scales. I explored niche partitioning and spatial variation of Rock (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucura*) in southwest Yukon. I examined habitat selection of foraging areas within a population and patches within foraging areas in a sympatric population of Rock and White-tailed Ptarmigan. At the larger foraging area scale, Rock Ptarmigan used areas with greater shrub cover compared to White-tailed Ptarmigan. At the smaller patch scale, both species selected patches with greater rock cover, but differed in other patch features. Second, I examined spatial variation in abundance of both ptarmigan species between the Ruby and Kluane Ranges using pellet count and transect surveys. Relative abundance was lower in the Kluane Range based on pellet counts, but transect surveys proved inadequate as a measure of population density. The Kluane Range also had fewer positive degree days above 0 ºC and a greater mean standard deviation of NDVI, and was composed of finer textured colluvium compared to the Ruby Range, which could influence relative abundance of ptarmigan.

Acknowledgements

There are many individuals and organizations that helped make this research project possible. First, I would like to thank my supervisor Dr. David Hik for taking me on as a student, and for providing me with the freedom to run this project and the opportunity to study in the Kluane Lake region. Thank you to my committee members Dr. Colleen St. Clair and Dr. Mark Boyce for providing helpful suggestions and ideas over the course of this project with additional thanks to Dr. Kathy Martin and Dr. Susan Hannon for their added help and insights. A special thanks to Dr. Scott Wilson for allowing me to use a portion of his data set and helping me along the way.

Thank you to everyone I spent time with in the field and in the lab, particularly, Pika Camp, who made my experience fun and memorable: Saewan Koh, Ryan Danby, Shawn Morrison, Scott Williamson, Sabine Nouvet, Amy Wilson, Sarah Trefry, James Hudson, Kieran O’Donovan, Graham Pelchat, Isla Myers-Smith, Helen Wheeler, Vijay Patil, Francoise Cardou, Jolene Swain, Jodi Pongracz, Sylvie Mitford, Jade Laramie and Sheila Holmes. Thanks to the friends and researchers at the Kluane Lake Research Station for the entertainment, and the family and friends in Edmonton for an unforgettable two years.

Financial and logistic support was provided by the Arctic Institute of North America with special thanks to Andy Williams, Sian Williams, Lance Goodwin, Bronwyn Goodwin, Donjek Upton and Raffles. Further financial support was provided by Natural Sciences and Engineering Research Council of Canada (NSERC), and Northern Scientific Training Program (NSTP). Kluane First Nation gave permission to conduct research on their traditional lands, and Parks Canada gave permission to conduct research in Kluane National Park.

Finally, I would like to thank my family, Lester, Donna, and Sarah Wong, Rob Ronconi, and the Clason Clan for their encouragement and support. I could not have completed this project without the love, support and hard work of my partner and research assistant Alana Clason.

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Chapter 1: Introduction to habitat selection and interspecific competition – setting the context for ptarmigan distribution in southwest Yukon

Habitat Use and Selection

A central theme to the study of ecology is how an animal uses its environment, especially the food sources it consumes and the habitat types it occupies (Johnson 1980). Animals require adequate quantities of suitable resources in order to sustain healthy populations (Manly et al. 2002). Individuals of a particular species will select resources that best enable them to satisfy their requirements, while differential selection of resources allows species to coexist in similar habitats (Rosenzweig 1981). As a result, certain resources will be of higher quality to a particular species. Biologists aim to identify and monitor the availability of these key resources in order to address questions related to both research and management (Manly et al. 2002).

In the past, terminologies used in habitat use and habitat selection studies have been unclear. The environmental factors that species use for survival and reproduction are referred to as their *habitat* (Block and Brennan 1993 in Jones 2001). *Habitat use* describes the actual distribution of individuals across habitat types and how habitat types are used to meet life history needs (Hutto 1985). *Habitat selection* refers to a decision-making process or behaviour in which an animal chooses a resource, resulting in a disproportionate use of habitats (Jones 2001, Manly et al. 2002). On the other hand, *preference* is the likelihood of choosing an item at equal availability with others (Ellis et al. 1976, Johnson 1980). In short, *habitat use* patterns are the end result of *habitat selection* processes (Jones 2001). Furthermore, presence in a habitat is not indicative of habitat quality (Van Horne 1983, Pulliam 1988), so habitat selection is more informative as it infers individual or species choice.

Early studies of habitat selection were closely linked to optimal foraging theory (MacArthur and Pianka 1966, Ellis et al. 1976) with focus on correlations between habitat characteristics and species abundance (Rosenzweig 1991). These observations led to ‘ideal-free distribution’ models (Fretwell and Lucas 1970) and their derivatives (Fretwell 1972), which stated that optimal habitats are selected first, while the use of marginal habitats fluctuate year to year (Haila et al. 1996). In other words, individuals must choose from an available set of resources, which change in time and space (Martin 1998). Several standard methods were devised to examine use-availability data (Johnson 1980), such as modified forage ratios (Jacobs 1974, Chesson 1978) and the index of electivity (based on Ivlev 1961). However, conclusions from usage-availability studies depended on what components were considered available to an animal (Johnson 1980). Many studies considered the entire study area to be available to an individual, but the extent of a study area is usually arbitrary and not all parts of the study area are equally available (Arthur et al. 1996, Spencer et al. 1996, Jones 2001).

Johnson (1980) introduced the hierarchical nature of habitat selection in an attempt to better define availability. These ideas were not new (see Owen 1972, Wiens 1973), but Johnson (1980) developed the natural ordering of the selection hierarchy. First-order selection referred to the geographic range of a species.

Second-order selection was a portion within the geographic range, such as the home range. Usage of components within the home range, such as feeding sites was considered third-order selection. And, finally, fourth-order selections were the food items selected within the feeding site. This hierarchical concept has been widely adopted and studies typically use several scales to identify habitat selection of an organism (Orians and Wittenberger 1991, Manly et al. 2002, Boyce et al. 2003).

Remote sensing techniques are powerful tools for investigating resource selection and predicting occurrence and abundance patterns of wildlife species (Boyce and McDonald 1999, Boyce et al. 2002, Gottschalk et al. 2005, Elith et al. 2006, Bellis et al. 2008). These data have become more readily available and cost effective over the past two decades and, as a result, published vegetation and land cover maps have been incorporated into habitat selection studies (Homer et al. 1993, Turner et al. 2003). However, remotely sensed habitat indices must be suitable for the particular study organism (Bellis et al. 2008). Combining remote sensing data with ground-truthed surveys and knowledge of the study species can greatly enhance the effectiveness, accuracy and value to habitat selection models (Homer et al. 1993, Bellis et al. 2008). Furthermore, choosing the appropriate grain size and habitat features at each hierarchical level are important to properly reflect the selection processes occurring at the various scales.

The geographic range of a species reflects the limit of its distribution and species can be found in a variety of habitats (Pulliam 1988, Brown et al. 1996).

Within a local geographical region, selection is thought to be heavily influenced by broad-scale biotic and abiotic factors, such as climate, topography, geomorphology, and habitat composition and structure (Brown et al. 1996, Carrascal and Seoane 2009). However, there are relatively few studies of spatial variation of abundance across the geographic range (Brown et al. 1995), likely due to the large amounts of time and effort required to survey large areas. Furthermore, ecologists infrequently examine fitness or reproductive success, which is important when assessing habitat quality and source or sink populations (Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991, Martin 1998). Identifying factors within the geographic range that affect abundance and fitness of a population is important for addressing the effects of large-scale environmental change, such as climate change (Peterson et al. 2001, Hughes 2003, Rondinini et al. 2005, Ritchie et al. 2008), and may provide information to guide conservation in large-scale geographic contexts (Carrascal and Seoane 2009).

Interspecific Competition and Niche Partitioning

While broad-scale biotic and abiotic factors play a large role in selection at the geographic range levels (Brown et al. 1996, Carrascal and Seoane 2009), other ecological factors, such as competition, have a larger influence on selection at finer scales (Cody and Walter 1976). Interspecific competition is the competition between different species for limited resources and the coexistence of competing species is achieved through niche partitioning (Colwell and Fuentes 1975). All species have “fundamental” and “realized” niches. The fundamental niche is the entire range of resources a species can use, while the realized niche is the range of resources that a species actually uses in the presence of competitors (Begon et al. 1996). The realized niche can change in the absence or presence of other species, so long as there is an overlap in the fundamental niche (Robertson 1972). Species will try to limit competition; the degree of competition depends on the amount of overlap in the fundamental niches and the competitive abilities of the competing species (Colwell and Fuentes 1975, Munday et al. 2001). If there is a large niche overlap and similar competitive abilities, both species are expected to show niche contraction (Colwell and Fuentes 1975). However, if one species is dominant over the other, then the subordinate species should display greater niche contraction (Colwell and Fuentes 1975, Munday et al. 2001).

Interspecific interactions change throughout the geographic range of a species and habitat distributions of species can expand or retract in the presence or absence of other species (Alatalo et al. 1985). In regions of sympatry, species can live in coexistence at finer scales with or without territorial overlap (Kumstatova et al. 2004, Wilson and Martin 2008). In the case of territorial overlap, species generally partition resources within the same habitat as a means to limit competition (Haila and Hanski 1987, Kumstatova et al. 2004). In non-overlapping territories, species can limit competition by having different habitat preferences (Murray 1981, Kumstatova et al. 2004). Alternatively, species could have similar habitat preferences and compete for the same habitat, while defending mutually exclusive territories (Garcia 1983, Alatalo et al. 1985, Bourski and Forstmeier 2000). Therefore, competing species can partition resources in several ways and at several scales in order to reduce competition and coexist. However, changing environments may alter habitat availability and shift species interactions, which can alter species coexistence (Davis et al. 1998).

Ptarmigan Ecology

Ptarmigan are the smallest members of the grouse family and there are three species that inhabit arctic and alpine regions of the Northern Hemisphere. Willow Ptarmigan (*Lagopus lagopus*) are the largest of the ptarmigan species (430-810 g; West et al. 1970, Robb et al. 1992) and mainly occupy shrub habitats (Moss 1972, Martin and Hannon 1987, Hannon et al. 1998) in North America, the United Kingdom, Scandanvia, Europe, Russia, and Northern Mongolia (Hannon et al. 1998). Rock Ptarmigan (*L. muta*; Figure 1-1) are the next largest species (445-640g; Cotter 1999) and occur in both arctic and alpine ecosystems of North America, Iceland, northern Scotland, Scandanvia, Russia, western Mongolia with isolated populations in the Alps, Pyrenees and central Japan (Montgomerie and Holder 2008). White-tailed Ptarmigan (*L. leucura*; Figure 1-1) are the smallest of the ptarmigan species (325-490g; Braun et al. 1993) and inhabit alpine habitats of western Canada, Alaska, Washington and Montana States with isolated and introduced populations in Oregon, Colorado, California and New Mexico and Utah (Braun et al. 1993).

Ptarmigan migrate between summer breeding grounds and wintering ranges. The wintering ranges consist primarily of shrubby habitat and, because ptarmigan species utilize similar winter habitats, there is potential for interspecific competition in regions of overlap. Weeden (1967, 1969) showed that different winter diets likely reduce both competition and territory overlap between the three species of ptarmigan in Alaska. The major part of the Willow Ptarmigan diet consisted of *Salix spp.* shrubs, while the diet of Rock and White-tailed Ptarmigan consisted mainly of *Betula spp.* and *Alnus spp.*, respectively. This differentiation in diet is reflected in their bill morphologies: Willow Ptarmigan have broad, deep bills for the larger *Salix* leaves and buds, while Rock Ptarmigan have narrow bills for the smaller *Betula* catkins and buds (Weeden 1967, 1969).

Although there is frequent range overlap between Willow and Rock Ptarmigan, the two species tend to occupy different habitats during the breeding season. Willow Ptarmigan use shrub habitats (Hannon et al. 1998), while Rock Ptarmigan use dry, rocky arctic and alpine tundra with mixed vegetation (Montgomerie and Holder 2008). Rock and White-tailed Ptarmigan occupy similar habitats where they occur separately, and it is unclear whether they exhibit territory overlap in areas of sympatry. During the breeding season, Wilson and Martin (2008) showed that Rock and White-tailed Ptarmigan had species-specific habitat preferences, which were maintained even in close proximity by defense of territories. However, during brood rearing females with chicks are mobile and do not defend territories. Furthermore, diets of Rock and White-tailed Ptarmigan broods are very similar, composing mainly of dwarf willow shrubs and forb species (Choate 1963, Weeden 1967, 1969, May and Braun 1972, Frederick and Gutierrez 1992, Pedersen et al. 1998, Allen and Clarke 2005, Clarke and Johnson 2005, Favaron et al. 2006, Montgomerie and Holder 2008). As a result, there is an opportunity to examine whether there is overlap in the foraging areas for the two species or whether they use different habitats in non-overlapping foraging areas. It is also possible to examine whether their niches retract compared to parts of their geographic range where they occur separately.

Ptarmigan are well studied species, particularly in the United Kingdom, Scandinavia and North America where they are important game birds (Pelletier and Krebs 1997, Hannon et al. 1998, Pedersen et al. 2004, Hornell-Willebrand et al. 2006, Evans et al. 2007). Despite proven survey techniques, including pointer dogs (Jenkins et al. 1963, Mougeot et al. 2003a, b, Evans et al. 2007), counts of calling males (Watson and O'Hare 1979, Pedersen et al. 2007), playbacks of territorial males (Evans et al. 2007) and pellet counts (Nystrom et al. 2005, Evans et al. 2007), there are few studies that examine the factors that affect spatial variation of abundance within the geographic range (but see Nopp-Mayr and Zohman 2008). Large-scale surveys may be difficult for Rock and White-tailed Ptarmigan due to their low densities (Pelletier and Krebs 1997), but the use of chick distress call playbacks may improve survey techniques by locating brood hens (Braun et al. 1973). The additional information of reproductive success would provide information on reproductive success, which is needed to assess habitat quality as well as identify source and sink populations (Pulliam 1988, Pulliam and Danielson 1991).

Climate Change in Arctic and Alpine Environments

Patterns of global climate change are well documented and there is growing concern of these effects in arctic and alpine ecosystems (Chapin and

Korner 1994, Krajick 2004, Post et al. 2009). Increased temperatures and shifts in precipitation regimes are thought to be causing early sea ice melt and melting permafrost, which are major concerns for arctic communities and wildlife, such as polar bears (Schuur et al. 2009, Cherry et al. 2009, Durner et al. 2009). In the alpine, the effects of changing climate are already having immediate effects on reproductive success and population growth of alpine species (Helle and Kojola 2008, Morrison and Hik 2007, Novoa et al. 2008).

Environmental change can alter habitat availability and change species distributions as observed in range expansions of migrating birds for example (Walther et al. 2002, Parmesan and Yohe 2003). Treeline and shrubline encroachment is causing the ‘greening’ of arctic (Chapin et al., 2005, Tape et al. 2006) and alpine (Walther et al. 2002, Pauli et al. 2007) ecosystems, which is reducing the amount of available alpine tundra (Sturm et al. 2001, Danby and Hik 2007a, 2007b, Sanz-Elorza et al. 2007). Furthermore, there is evidence of changing compositions within alpine plant communities (Grabherr et al. 1994, Klanderud and Totland 2005, Klein et al. 2007). A reduction in suitable habitat due to shifts in vegetation could result in large changes in the distribution and abundance of obligate alpine animals (Martin 2001).

A reduction of alpine habitat will likely affect the distribution and abundance Rock and White-tailed Ptarmigan and interactions between the two species may increase as tundra habitat decreases and resources become limited. To determine how these two species may cope with a shift in habitat availability, I examined the habitat selection of both species at the population and patch levels during brood rearing. Furthermore, I examined the level of niche differentiation between the two species at these different scales.

Study Area

The study area was located in the Kluane Lake Region, southwest Yukon (Figure 1-2; 61^{o} 130N, 138^{o} 160W). This region is composed of several mountain ranges, including the Kluane and Ruby Ranges. The main study site (study site 4) used to examine interspecific competition and habitat selection was located in a sub-arctic alpine meadow in the Ruby Range. This is roughly a 9 km^2 alpine valley composed of closed low shrub, open low shrub, wet tundra, dry tundra and rock habitats. The same site was used by Wilson and Martin (2008) to study nest site selection of sympatric Willow, Rock and White-tailed Ptarmigan. I conducted surveys of Rock and White-tailed Ptarmigan at the main site as well as adjacent valleys in the Ruby (Figure 1-3, Figure 1-4, Figure 1-5) and Kluane Ranges (Figure 1-6, Figure 1-7, Figure 1-8).

Given the mountainous nature of the Kluane Lake region, Rock and White-tailed Ptarmigan breed in alpine valleys and rarely leave these valleys until they flock in late summer. As a result, there are numerous distinct groups of breeding individuals. This segregates the entire population into discrete units, which is ideal for studying spatial variation of abundance within a portion of the geographic range of these species. Furthermore, there are several distinct mountain ranges in the region, each with their separate geologic and geomorphic histories, and it is possible to examine the differences in ptarmigan abundance as well as differences in abiotic and biotic characteristics between the various mountain ranges.

Research Goals

The first goal of this study was to determine whether Rock and White-tailed Ptarmigan maintained differences in habitat use during brood rearing by examining habitat selection at two different scales as presented in Chapter 2. I predicted that the two species would maintain differences in habitat selection in order to limit competition as shown in winter habitat selection (Weeden 1967, 1969) and nest site selection (Wilson and Martin 2008). I also wanted to examine at what scale the difference in habitat selection took place for both species. I expected differences in habitat selection to occur at the larger foraging area scale in order to limit competition and enable the species to coexist. However, given the similar diets of the two species where they occur separately, I predicted that patches within foraging areas would contain similar food items for both species.

The second goal of the study was to examine spatial variation in abundance within a portion of the geographic range of Rock and White-tailed Ptarmigan using pellet counts and a new survey technique that employs chick distress calls (Chapter 3). I also examined various abiotic and biotic factors that may explain differences in species abundance between the Kluane and Ruby Ranges. I predicted that there would be a difference in abundance of ptarmigan between the two mountain ranges due to differences in climate, topography, habitat and geologic/geomorphic variables.

Figure 1-1: Rock Ptarmigan (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucurus*) brood hens in summer plumage (from left to right).

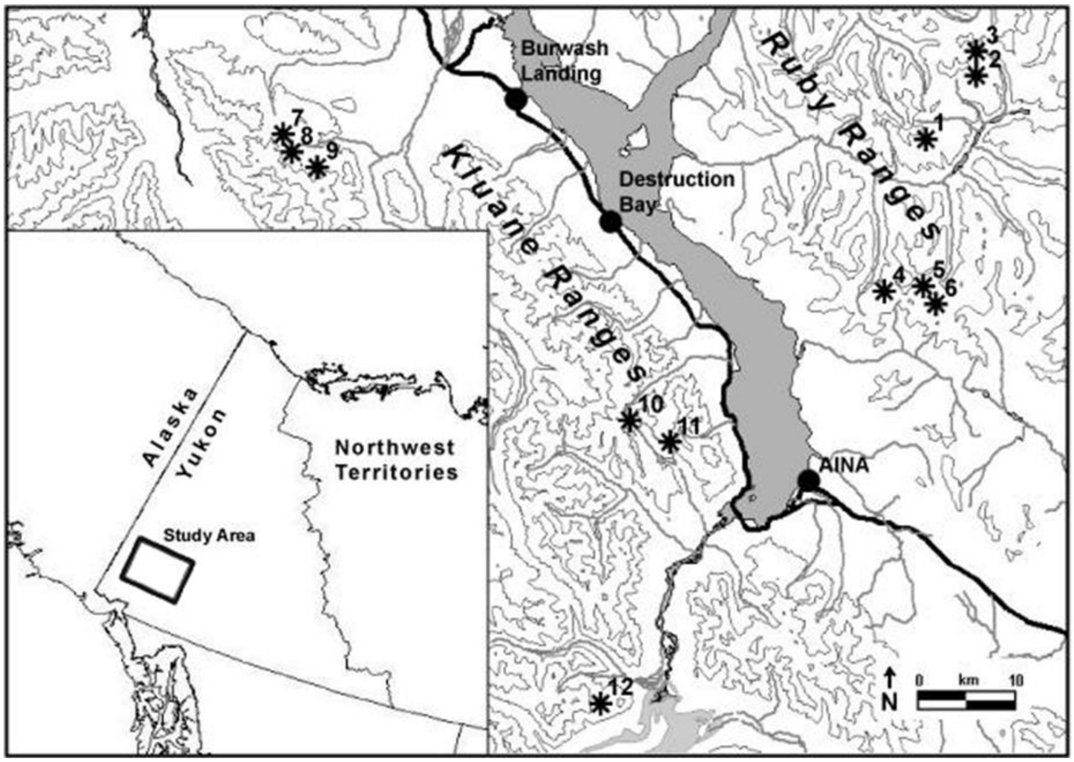

Figure 1-2: Location of study sites in the Kluane Lake region, Yukon Territory, Canada. Study site 4 was used to study niche partitioning and finer scale habitat selection in Chapter 2. Research for Chapter 3 was based out of the Kluane Lake Research Station, Arctic Institute of North America (AINA).

Figure 1-3: Sample images of habitat in study sites 1-3 (counterclockwise from top) in the Ruby Range, southwest Yukon Territory.

Figure 1-4: Sample image of habitat in study site 4 in the Ruby Range, southwest Yukon Territory. This was the main study site for Chapter 2 (Photo: S. Morrison).

Figure 1-5: Sample images of habitat in study sites 5 (top) and 6 (bottom) in the Ruby Range, southwest Yukon Territory.

Figure 1-6: Sample images of habitat in study sites 7 (Left) and 8 (Right) in the Kluane Range, southwest Yukon Territory.

Figure 1-7: Sample images of habitat in study sites 9 (top) and 10 (bottom) in the Kluane Range, southwest Yukon Territory.

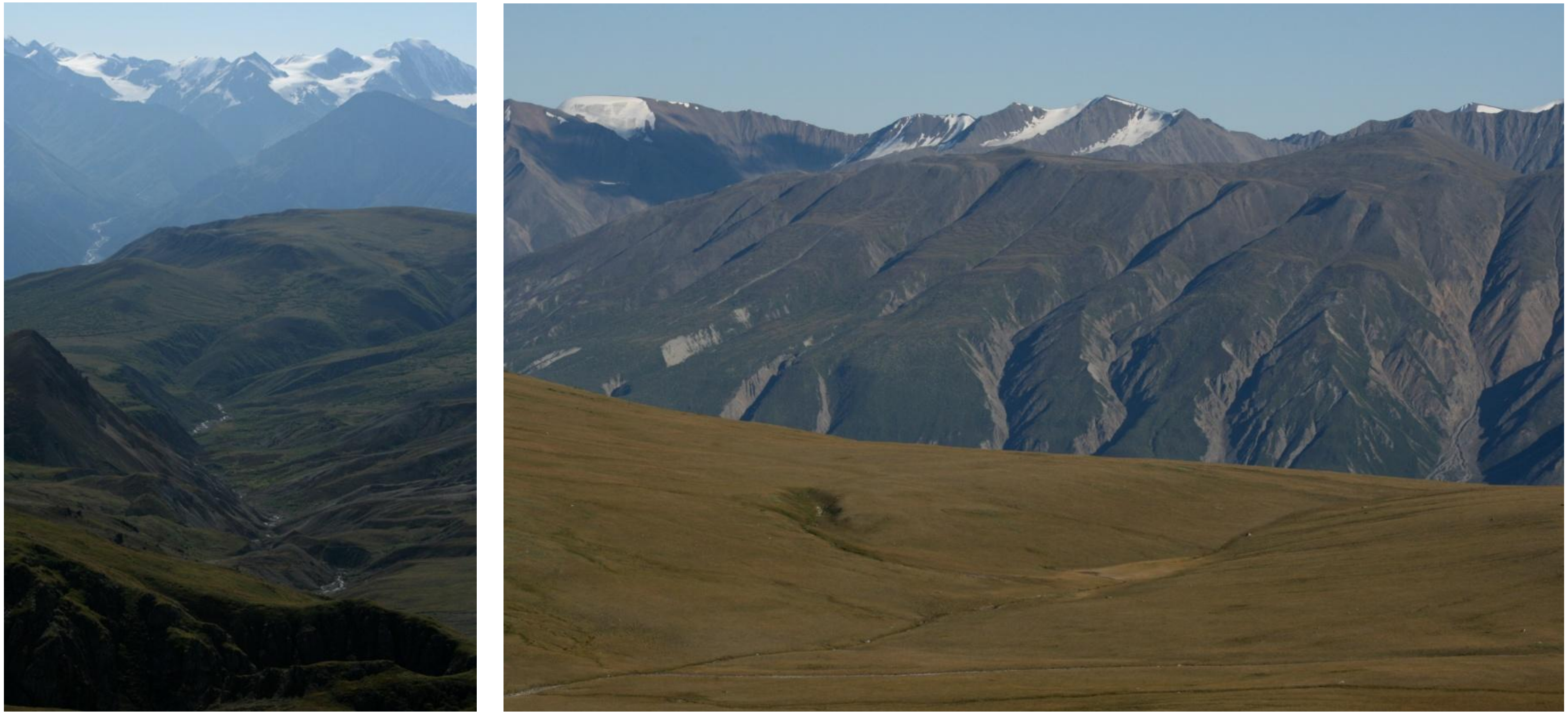

Figure 1-8: Sample images of habitat in study sites 11 (Left) and 12 (Right) in the Kluane Range, southwest Yukon Territory.

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Chapter 2: Niche differentiation and habitat selection of sympatric Rock (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucura*) during brood rearing in southwest Yukon

INTRODUCTION

There is compelling evidence for diverse ecological effects of rapid climate change in high latitude and high elevation ecosystems. The 'greening' of the arctic (Chapin et al., 2005, Tape et al. 2006) and alpine (Walther et al. 2002, Pauli et al. 2007) regions is thought to be the result of increased mean annual temperatures and changes in precipitation regimes, and these changing patterns of primary productivity can have an immediate effect on population dynamics of resident animals (Sandercock et al. 2005, Helle and Kojola 2008, Morrison and Hik 2007, Novoa et al. 2008). Over the longer-term, shifts in vegetation could result in a reduction in suitable habitat of obligate alpine animals and thus change their distribution and abundance (Martin 2001). Treeline and shrubline encroachment will reduce the amount of available alpine tundra (Sturm et al. 2001, Danby and Hik 2007a, 2007b, Sanz-Elorza et al. 2007) and change the composition of alpine plant communities (Grabherr et al. 1994, Klanderud and Totland 2005, Klein et al. 2007). In order to understand how ecological changes may affect future population dynamics, it is necessary to identify the ecological processes and resources that determine species' distribution.

Several taxa have shown range shifts and phonological change as a result of climate change (Hughes 2000, Parmesan and Yohe 2003). Coexisting species may react differently to changing environments (von dem Bussche et al. 2008) and these range shifts could alter interspecific competition; the competition between different species for limited resources (Davis et al. 1998, Anderson et al. 2009). The degree of interspecific competition can change with resource availability, the amount of overlap of fundamental niches and the competitive abilities of the competing species (Colwell and Fuentes 1975, Munday et al. 2001). The 'Competitive Exclusion Principle' states that competing species can coexist as a result of niche differentiation or partitioning (Begon et al. 1996). Although niche partitioning can arise through other processes (e.g. Strong 1982), the Competitive Exclusion Principle is widely accepted. There are several ways in which species can differentiate their realized niche and coexist. In the absence of territorial behaviour, where species use the same habitat but defend mutually exclusive territories (Garcia 1983, Alatalo et al. 1985, Bourski and Fortsmeier 2000), species can coexist by using different habitats in non-overlapping areas (Murray 1981, Kumstatova et al. 2004) or by using different resources within overlapping areas (Haila and Hanski 1987, Kumstatova et al. 2004). Therefore, species can partition resources at several spatial scales, and changes to habitat at one scale may affect different species differently. To assess potential interspecific interactions in future environment scenarios, it will be necessary to identify the habitat attributes that are important to several species at multiple scales (Davis et al. 1998, Anderson et al. 2002).

Multi-scale habitat selection studies have been widely adopted (Orians and Wittenberger 1991, Boyce et al. 2003, Ciarniello et al. 2007) and are useful tools in identifying important habitat for wildlife management (e.g. Johnson et al. 2004, Bellis et al. 2008). Recently developed remote sensing techniques are powerful tools for investigating spatial patterns of wildlife and its habitat (Boyce and McDonald 1999, Boyce et al. 2002, Gottschalk et al. 2005, Elith et al. 2006). Researchers are able to use a wide variety of published maps or create their own using readily available remotely sensed data and ground-truthed data, which improves model accuracy by focusing on features important to the study organism (Homer et al. 1993, Turner et al. 2003, Bellis et al. 2008).

We examined brood habitat selection of Rock (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucura*) where they coexist with Willow Ptarmigan (*L. lagopus*) in southwest Yukon Territory, Canada. Ptarmigan produce precocial young that hatch mid-summer and forage with their non-territorial mother or parents (Willow Ptarmigan) until late summer when juveniles and adults form large flocks for the winter. Willow Ptarmigan are the largest of the three species and select tall shrub habitats of subalpine and arctic tundra within their circumpolar distribution (Schieck and Hannon 1993, Hannon et al. 1998). Rock Ptarmigan also have a circumpolar distribution, and select dry, rocky arctic and alpine tundra (Montgomerie and Holder 2008). White-tailed Ptarmigan are only found in the alpine regions of western North America, from New Mexico to Alaska (Braun et al. 1993). While an expanding shrubline (e.g. Sturm et al. 2001, Tape et al. 2006) may benefit Willow Ptarmigan in this region, Rock and White-tailed Ptarmigan may be negatively affected as their preferred habitat decreases in availability. Furthermore, interactions between Rock and White-tailed Ptarmigan may increase as tundra habitat and resources become more limited.

There is evidence of niche partitioning and character displacement in sympatric populations of ptarmigan. Weeden (1967, 1969) showed that the three ptarmigan species coexist in the same wintering grounds in central Alaska by selecting different diets, which is reflected in their different bill morphologies. At our study site, Wilson and Martin (2008) found Rock and White-tailed Ptarmigan had species-specific breeding habitat preferences, which were maintained in close proximity by defending territories. However, brood hens are mobile and do not defend territories during brood rearing. Furthermore, diet and habitat selection of Rock and White-tailed Ptarmigan broods are very similar at sites where they occur separately (Choate 1963, Weeden 1967, 1969, May and Braun 1972, Frederick and Gutierrez 1992, Pederson et al. 1998, Allen and Clarke 2005, Clarke and Johnson 2005, Favaron et al. 2006, Montgomerie and Holder 2008). As a result, there is an opportunity to examine the scale at which niche differentiation occurs between Rock and White-tailed Ptarmigan during brood rearing.

Our overall objective was to identify brood-rearing habitats important for Rock and White-tailed Ptarmigan and to determine the scale at which the two species showed niche partitioning. First, we created a ptarmigan-specific landcover classification scheme for the region with an emphasis on alpine plant communities. Secondly, we used this classification scheme to develop population-level occurrence models for brood-rearing Rock and White-tailed Ptarmigan. We defined a population as an alpine valley, since there is limited movement of broods between valleys, and we examined habitat characteristics of foraging areas within a population for each species. We applied these models to our study site and we used an independent data set collected in different years to validate their predictive capacity. Thirdly, we used paired habitat plots to identify important characteristics of used patches within foraging areas for each species. Finally, we discuss how shifts in vegetation communities as well as temperature and moisture regimes may affect each species as it relates to each habitat scale.

METHODS

Study Area

This study was conducted in the Ruby Ranges, Kluane Lake region, Yukon Territory (61^{o} 130N, 138 ^{o} 160W) from 2004 through 2007. The study was closely coordinated with a nest site selection study conducted by Wilson and Martin (2008). The region is located in the rain shadow of the St. Elias Mountain Range (Figure 2-1). The study site was an alpine valley of roughly 9 km^2, with mixed ground cover consisting primarily of sub-alpine and alpine vegetation and bare rock (Wilson and Martin 2008). In general, habitat could be segregated by elevation into three classes; upper sub-alpine (1400-1550 m), transition between upper sub-alpine and high alpine (1500-1750 m), and high alpine (1750-2200 m). The upper sub-alpine consisted of large patches of tall and low shrubs (*Salix pulchra, Salix glauca, Betula glandulosa*) with areas of low vegetation types (e.g. graminoids). The transition between upper sub-alpine and high alpine consisted of graminoids (Carex spp., sedge) interspersed with small patches of open low shrubs (*S. pulchra, S. glauca, B. glandulosa*), dwarf shrubs (*Salix reticulata, Salix arctica, Salix polaris, Dryas octopetala*), and rock outcrops. The high alpine was dominated by exposed rock, with patches of dwarf shrubs (mainly *D. octopetala*) and lichen species. Forbs were present throughout the study area and productivity and abundance varied by elevation. Forb species are listed in Appendix I.

Field Methods

Field work was conducted from early May to mid-August. Birds were captured during courtship (May to early June) using noose poles (Zwickel and Bendell 1967) and ground nets. Individuals received a numbered metal band as well as a combination of plastic colour bands on both legs. Females were fixed with a 4 or 7 g radio transmitter (Holohil Inc.) to locate and monitor nests and broods. Nests were monitored every 2-5 days until failure or hatch and we followed the survival of the subsequent broods for 3-6 weeks post-hatch. Detailed methods are described in Wilson and Martin (2008).

We used relocations of collared brood hens from 2006 to model brood occurrence at the population scale. Broods were relocated every 3-5 days until failure or chicks were older than 45 days. Locations were recorded with a handheld GPS unit once broods were at least 25 m from the initial point of visual contact. Location uncertainty was less than 8 m. We assumed minimal temporal autocorrelation between points, given the amount of time between locations (3-5 days), and we treated each relocation as an independent sample. An independent set of relocations of Rock (n= 38) and White-tailed Ptarmigan (n= 29) collected in 2004, 2005, 2007 were used as a validation data set.

Data for patch scale analysis were collected during the brood-rearing season from 2004-2007. Collared females were relocated 1-3 times/season with at least a week between relocations of the same brood hen. Upon relocation, we marked used sites with a rock cairn or piece of flagging tape, and an available habitat plot was measured 50 m from the used plot at a random compass bearing chosen by spinning a compass several times and walking 50 m at the specified angle. We measured distance by walking 50 m from the coordinates recorded on a GPS unit.

Foraging Area Level

GIS predictor variables

We developed a collection of biologically relevant variables in a Geographic Information System (GIS) to model brood occurrence at the population level at our study site for Rock and White-tailed Ptarmigan. These variables related to either the topography or the habitat characteristics of the study site. The topographic variables were derived from a 30 m Digital Elevation Model (DEM) and included elevation, slope angle, terrain ruggedness and soil moisture. White-tailed Ptarmigan tend to nest at higher elevations and on steeper slope angles compared to Rock Ptarmigan in the study area (Wilson and Martin 2008), so we included these variables in our analysis. Similarly, we incorporated the terrain ruggedness index (TRI) in our analysis since White-tailed Ptarmigan broods tend to occur in steep terrain, such as rock falls and moraines (Choate 1963). TRI was developed by Riley et al. (1999) and is the measure of the sum change in elevation between a pixel and its eight neighbouring grid pixels. Greater values of TRI imply more rugged terrain. In Alaska, Rock Ptarmigan broods use areas of intermediate moisture (Weeden 1959); we used the compound topographic index (CTI) as a steady state wetness index. CTI is derived from a DEM and it is a function of the slope and the upstream contributing area per unit width to the flow direction (Evans 2002). CTI is also correlated with soil moisture and soil nutrients (Gessler et al. 1995). We used a quadratic term for CTI in our analysis, since broods utilised areas of moderate moisture.

We created a landcover classification scheme with a specific focus on the alpine areas of the Ruby Range. The classification was created using a combination of the National Topographic Database (NTDB) and the normalized difference vegetation index (NDVI: Tucker and Sellers 1986) calculated from Landsat Thematic Mapper. Landcover classes from the NTDB maps were used to classify forest, water and permanent ice/snow, while NDVI was used to classify alpine plant communities. NDVI was calculated as the difference between the red and near-infrared bands divided by the sum of the same two bands (Tucker and Sellers 1986) using a Landsat Thematic Mapper image from 9 August 2003 at a 30 m x 30 m resolution. The model was conducted using ERDAS Imagine 9.1 (Leica Geosystems Geospatial Imaging, LLC) in which NDVI values were scaled between 0 and 1. The scaled values were then multiplied by 255 to convert into 8-bit data. The resulting scaled NDVI values were used in the landcover classification scheme.

We used 124 ground-truthed vegetation plots (25 m radius) to group NDVI values into categories based on coarse-level vegetation communities derived from the “Alaska Vegetation Classification Guide” by Viereck et al. (1992). We used third order classification, percent rock and percent shrub to create six vegetation classes; ‘rock’ = rock cover that is equal or greater than 50%, ‘Dry’ tundra = *D. octopetala* and lichen dominant (third order; if the sub-dominant species was lichen we also included this as dry tundra), ‘Wet’ tundra = graminoid dominant (third order), ‘open low shrub’ = open canopy (<25%) shrub (<1 m in height) dominant (third order), ‘closed low shrub’ = closed canopy (>25%) shrub (<1 m in height) and ‘tall’ shrub = shrub (>1 m in height) dominant (third order). The criteria for the designation of ‘dry’ and ‘wet’ tundra were independently derived by Koh et al. (unpublished data). Unfortunately there was not a distinct range of scaled NDVI values for wet tundra habitat, so some cover classes were merged to improve accuracy. Overall, the map correctly classified 77% of the 124 vegetation plots and the resulting landcover classification scheme had 9 classes with an emphasis on the alpine (Table 2-1). We used all alpine landcover classes as predictor variables for our models, since Rock and White-tailed Ptarmigan occur exclusively in the alpine (Braun et al. 1993, Montgomerie and Holder 2008). For more details on the landcover classification scheme see Appendix II.

The average area covered in a 10-hour period by White-tailed Ptarmigan broods is about 1.2 ha (Schmidt 1988). We considered this area to be similar for Rock Ptarmigan and we termed it their ‘foraging area’. To match this 1.2 ha area, we used a moving window with a 60 m radius when calculating the mean and proportion of the topographic and habitat characteristics of the foraging area. All spatial analyses were conducted in ArcGIS 9.3 (ESRI 2008).

Model Development

We followed the Hosmer and Lemeshow (2000) approach to model selection for modeling brood occurrence at the population level. We conducted univariate analyses for each predictor variable using a Wald z statistic $P<0.25$ cut-off for inclusion in the multivariate model (Hosmer and Lemeshow 2000). We examined correlation coefficients among variables and if two variables were correlated ($|r| > 0.60$), we kept the variable with the smaller P-value. We also retained variables that were biologically relevant in the literature (Hosmer and Lemeshow 2000). A reduced model was created by excluding variables that had $P>0.05$. We tested for confounding effects in the dropped variables and included biologically plausible interactions between the remaining covariates (Hosmer and Lemeshow 2000). Variables were tested for linearity in the logit and changes were made if necessary before presenting the final model. All analyses were conducted using the R 2.9.0 (R Development Core Team 2009).

Statistical Analysis

We used resource selection functions (RSFs; Manly et al. 2002) to 1) examine selection of foraging areas within the study site for Rock and White-tailed Ptarmigan separately (intraspecific) and 2) directly compare habitat selection between the two species by examining the range of overlap for the two species (interspecific). We used a design II approach (Manly et al. 2002), where marked individuals were employed to identify used resources and resource availability was assessed at the population level. RSFs are proportional to a logistic discriminant function, which examines the distribution of used and available resource units (Aldridge and Boyce 2007). Habitats are ranked with respect to the probability of use, but not proportional to the actual probability of use (Keating and Cherry 2004). For the intraspecific analysis, relocations were the used sites (1), while 500 randomly generated points within the study area were the available sites (0). For the interspecific comparison, we designated the White-tailed Ptarmigan used sites as “1” and the Rock Ptarmigan used sites as “0”. Random points were generated using Hawths-Tools in ArcGIS 9.3 (ESRI 2008).

Model Assessment and Validation

Goodness of fit of the intraspecific and interspecific models was assessed using the Le Cessie-van Houwelingen normal test statistic in the Design library for R (Le Cessie and van Houwelingen 1991, Hosmer et al. 1997). We used the selection coefficients from our intraspecific models to create our RSF equations and spatially apply the models to the study area. The predicted RSF values were used to generate a relative index of occurrence scores, and pixels were ranked into five quantile bins. We used five bins instead of ten in order to avoid bins lacking any validation points (given our limited independent data set; see Aldridge et al. 2007). Our validation data set came from an independent set of relocations in the study site from 2004-2005 and 2007 (Rock Ptarmigan: n=38; White-tailed Ptarmigan: n=29). Spearman rank correlation was used to test for correlation between the frequency (area-adjusted) of validation points and increasing bin rank (Boyce et al. 2002). A strong RSF should produce a strong positive correlation with the frequency of validation points increasing with increasing bin rank values.

Patch Level

Predictor Variables

At the patch level, predictor variables focused on structural cover and potential food items within a 5-m radius plot at the used and available sites. North American Rock Ptarmigan use low shrubs as a source of cover and food (Weeden 1959, Holder and Montgomerie 2008), while European populations utilize rock habitats for cover (Favaron et al. 2006, Zohman and Moss 2008). White-tailed Ptarmigan also use rock habitats, while also following retreating snow lines (Weeden 1959, Choate 1963). As a result, we used a Range Finder (Bushnell Co.) to measure the distance (up to 100 m) to shrubs <1m in height, >1 m in height, rock (continuous cover >1 m^2), and snow/water (standing water and intermittent streams). Food items for broods of both species include dwarf willow shrubs and a variety of forb species, particularly *Polygonum* species (Choate 1963, Weeden 1967, Weeden 1969, May and Braun 1972, Frederick and Gutierrez 1992, Pederson et al. 1998, Allen and Clarke 2005, Clarke and Johnson 2005, Favaron et al. 2006, Holder and Montgomerie 2008, Zohman and Woss 2008). Dwarf shrubs, such as *Dryas octopetala* and *Cassiope spp.* are also eaten along with graminoid seed heads and insects (Weeden 1967, Weeden 1969, May and Braun 1972, Clarke and Johnson 2005, Holder and Montgomerie 2008). We measured the overhead percent cover of potential food items as well as the structural components within each 5-m radius plot: water, rock, bare ground, moss, heather, lichens, graminoids (sedges, grasses and rushes), woody shrubs (>15 cm in height), dwarf shrubs (<15 cm in height) and forbs within each 5-m radius plot.

Ground cover below woody shrubs was not included, since cover was measured from overhead (Wilson and Martin 2008). Lichens, heather, woody shrubs, dwarf shrubs and forbs were identified to genus or species. Graminoids and mosses were only identified to functional groups in part because diet studies of ptarmigan have generally not distinguished between species within these functional groups (e.g. Frederick and Gutierrez 1992).

Model Development

We used Akaike Information Criterion (AIC) to find the most parsimonious model from a set of candidate models and to identify variables that influence occurrence at the patch level (Burnham and Anderson 2002). Given the limited sample size, AIC was used instead of the Hosmer-Lemeshow (2000) approach; this limits the number of variables in a model and avoids over-fitting the models (Burnham and Anderson 2002). AIC differences (ΔAIC) and Akaike weights (w_i) were used to determine the relative likelihood of each model being the best of the set of candidate models. Models with Akaike weights closer to 1 are considered better models and models with AIC differences <2 are considered comparable (Burnham and Anderson 2002). We used AIC_c for the patch level analysis, because $n/k < 40$ (Burnham and Anderson 2002). Correlation of predictor variables was examined using Pearson’s correlation coefficient (r). Variables with correlations $\geq$0.6 were not included in the same models.

Statistical Analysis

We used paired-logistic regression models to identify patch selection within foraging areas of brood hens. In paired-logistic regression, the response variable is a vector of 1's and the independent variable is the covariate difference between the case (used) and control (available) (Compton et al. 2002). Therefore, positive values indicate selection for a particular covariate, whereas negative values indicate selection against (Wilson and Martin 2008). There are no intercepts in the models.

We also reported the odds ratio for each variable in the top model. The odds ratio indicates the relative risk or the ratio of probability of an event occurring given two outcomes of a categorical variable or a meaningful change in a continuous variable (Hosmer and Lemeshow 2000). For continuous variables, the odds ratio is calculated as $exp(c\beta_i)$, where β_i is the coefficient estimate and c represents a meaningful change in the variable (Hosmer and Lemeshow 2000). In paired logistic regression, the explanatory variables are the differences between case vs. control observations, so these values must be interpreted as differences in habitat rather than absolute measures of habitat (Compton et al. 2002).

RESULTS

We used 55 relocations of 10 individual Rock Ptarmigan broods (5.50 ± 0.94 locations/brood; mean ± s.e.) and 46 relocations of 9 individual White-tailed Ptarmigan broods (5.11 ± 0.77 locations/brood; mean ± s.e.) in 2006 to examine brood site selection at the population level. 45 of the 55 Rock ptarmigan relocations and 24 of the 46 White-tailed Ptarmigan relocations were used to examine the habitat use in the area of overlap in elevation for the two species. We used 44 used-available site pairs for 26 Rock Ptarmigan broods and 33 used-available site pairs for 17 White-tailed Ptarmigan broods from 2004-2007 to examine brood site selection at the patch level.

Foraging Area Level

The brood occurrence model using the stepwise modeling approach (Hosmer and Lemeshow 2000) for Rock Ptarmigan contained four parameters (Table 2-2). Rock Ptarmigan broods showed strong preference for wet tundra-open low shrub habitat (β_{wet_low}= 2.381) and closed low shrub habitat ($\beta_{cl\_low\_cat}$= 0.62). We changed closed low shrub habitat to a categorical variable (present/absent) due to a lack of linearity in the logit (Hosmer and Lemeshow 2000). Rock Ptarmigan broods also selected areas of intermediate moisture (CTI) (quadratic relationship; β_{CTI}= 3.901 + β^2_{CTI}= -0.250; Table 2-2).

The model did fit our data well (Z= 0.0181, P=0.986) and we applied this model to the study area and ranked the RSF scores into five quantile bins (Figure 2-2). We intersected the validation sample (years 2004-2005, 2007, n=38 brood observations) with the ranked bins (1 being the lowest rank), and examined the area-adjusted frequency for each ranked bin. The model explained the validation points well using Spearman rank correlation (r_S= 0.962, P<0.01; Figure 2-4) and 58% of the validation points fell in the top two bin ranks.

Our results using the Hosmer and Lemeshow (2000) stepwise approach for White-tailed Ptarmigan also contained four paramaters (Table 2-2). White-tailed Ptarmigan broods showed a preference for high elevations (β_{elev} = 0.0022) and intermediate slope angles (β_{slope}= 0.429 + β^2_{slope}= -0.010). In contrast to Rock

Ptarmigan broods, White-tailed Ptarmigan broods showed a strong avoidance towards wet tundra-open low shrub habitat ($\beta_{wet\_low\_cat}$= -0.626). Although wet tundra-open low shrub habitat did not initially pass into the reduced model, we retained the variable due to its confounding effect on elevation (Hosmer and Lemeshow 2000). Furthermore, we changed wet tundra-open low shrub habitat into a categorical variable (present/absent) due to a lack of linearity in the logit (Hosmer and Lemeshow 2000).

Similar to Rock Ptarmigan, the model described the data well (Z=0.865, P=0.387) and we applied this model to the study area with the RSF values ranked into five quantile bins (Figure 2-3). 55% of the validation sample (years: 2004-2005, 2007, n=29; Figure 2-4) fell into the top two ranked bins. The model described the validation sample well, but it was not quite statistically significant (r_S= 0.866, P= 0.058; Figure 2-4).

We examined the variables that affect habitat use in the region of overlap in elevation for Rock and White-tailed Ptarmigan. White-tailed Ptarmigan used a wider range of elevation than Rock Ptarmigan, so the area of overlap should have been between 1600 m and 1875 m (Table 2-3). However, there were no observations of White-tailed Ptarmigan between 1600 m and 1700 m. We used 1675 m as the lower end of the overlap, because it represented half of the observations of Rock Ptarmigan between 1600-1700 m, while accounting for the fact that White-tailed Ptarmigan use areas at lower elevations as well.

White-tailed Ptarmigan broods generally occurred at higher elevations, with greater rock and dry-wet tundra cover, while Rock Ptarmigan broods used a greater proportion of wet tundra-open low shrub habitat (Table 2-3). However, our final model contained two variables using the Hosmer and Lemeshow (2000) stepwise approach (Table 2-2) and the model had poor fit (Z=2.02, P= 0.04). In the region of overlap, White-tailed Ptarmigan broods generally occurred in areas of greater ruggedness (TRI) (β_{tri}= 0.126), but tended to avoid wet tundra-open low shrub habitat (β_{wet_low} = -2.851) compared to Rock Ptarmigan broods.

Patch Level

We used 13 candidate models, including a null model, to examine patch site selection of Rock Ptarmigan brood hens. Nine models of our analysis were comparable (ΔAIC <2) and all models contained rock (combined w_i = 1.00). The top four models contained distance to shrub (<1 m) (combined w_i = 0.64), while a majority of the models contained total dwarf willow (combined w_i = 0.66; Table 2-4). The top model consisted of these three variables and, despite the marginal difference in the top nine models, we considered it our best model. We were confident in this decision given the combined weights of total forb and *Polygonum spp.* were low (0.39 and 0.29, respectively). Model averaged coefficient estimates and odds ratios suggest that Rock Ptarmigan broods select for patches with greater rock cover (β_{rock}= 0.067, odds ratio: 1.40 (5%, 0.98, 1.98)) that are close to low shrubs ($\beta_{dis<1}$= -0.015, odds ratio: 0.93 (5 m, 0.85, 1.01)), but contain less dwarf willow ($\beta_{dwsaltot}$= -0.049, odds ratio: 0.86 (5%, 0.59, 1.02); Table 2-5). We consider these values to indicate selection for and against the different variables even though the 95% confidence intervals of the odds ratio do marginally overlap 1.0.

We also used 13 candidate models, including a null model, to examine patch site selection for White-tailed Ptarmigan. The top two models were comparable and both contained cover features with rock cover (combined w_i = 1.00) and distance to water/snow (combined w_i = 0.92) as significant contributing variables to patch site selection (Table 2-4). The top model performed the best, contained fewer variables and included total forb cover (combined w_i = 0.80). The model averaged coefficient and the odds ratio show that White-tailed Ptarmigan brood hens selected patches closer to water/snow ($\beta_{dis\_snow/water}$= -0.031, odds ratio: 0.85 (5 m, 0.74, 0.99)) with increased rock (β_{rock}= 0.066, odds ratio: 1.39 (5%, 1.07, 1.80)) and total forb cover ($\beta_{forbtot}$= 0.154, odds ratio: 2.16 (5%, 1.01, 2.52); Table 2-5).

DISCUSSION

Foraging Area Level

Niche partitioning was evident at the population level as Rock and White-tailed Ptarmigan selected different foraging area characteristics overall and within a region of overlap. Intraspecific analysis showed that Rock Ptarmigan selected foraging areas with intermediate moisture (CTI), a greater proportion of wet tundra-open low shrub habitat and some closed low shrub habitat. The model validated an independent data set well, confirming its predictive capacity. Weeden (1959) observed Rock Ptarmigan broods foraging in ‘low shrub’ zones near the headwaters of small streams. Although Rock Ptarmigan generally don’t feed on the leaves or buds of the shrubs during the summer, low shrubs provide cover from predators. Low shrubs are used less frequently by Willow Ptarmigan, which prefer tall shrub habitats (Weeden 1959, Weeden 1969). Wet tundra habitat likely acts as a food source, while the patchy distribution of shrubs acts as cover. Areas of intermediate moisture contain insects, which are an important food item for developing Galliformes chicks (Spidso 1980, Savory 1989, Hannon and Martin 2006, Wegge and Kastdalen 2008), and a source of mesic vegetation (Frederick and Gutierrez 1992). Weeden (1969) found that insects were poorly represented in the diet of Rock Ptarmigan and their chicks, so these areas of intermediate moisture may be more productive and important for obtaining vegetative food sources.

White-tailed Ptarmigan tended to select foraging areas at high elevations with intermediate slope angles, while avoiding wet tundra-open low shrub habitat. Although the predictive capacity of the intraspecific model was strong, the validation of the independent data set was not quite statistically significant. However, we are confident that this model is representative of brood occurrence for White-tailed Ptarmigan given its performance with an independent data set of limited sample size. White-tailed Ptarmigan only inhabit alpine ecosystems and tend to use areas of delayed snow melt, which are typically found at higher elevations during brood-rearing (Choate 1963, May and Braun 1972, Schmidt 1988). White-tailed Ptarmigan also tend to use rocky habitat, such as rock falls, boulder fields and wasting glaciers (Weeden 1959, Choate 1963, Schmidt 1988).

These physical features are more unstable and poorly vegetated with moderate to steep slopes compared to surrounding alpine meadows. These two elements explain their predominant occurrence at high elevations with intermediate slope angles. Unlike during winter, White-tailed Ptarmigan are not usually associated with shrubs in the summer, which explains their avoidance of wet tundra-open low shrub habitat. There was also a moderate negative correlation (r= -0.514) between wet tundra-open low shrub habitat and rock habitat. Although rock habitat was not significant in our model selection, it is possible that this was masked by the avoidance of wet tundra-open low shrub habitat.

Overall, White-tailed Ptarmigan used a wider range of elevations than Rock Ptarmigan, but the range of overlap fell between 1675-1875 m. Two significant parameters explained the segregation between Rock and White-tailed Ptarmigan in the range of overlap between the two species. Although the interspecific model did not perform well in the Goodness of fit test, we were comfortable with our final model given its similarity with the intraspecific models. White-tailed Ptarmigan broods used foraging areas with greater ruggedness, but less wet tundra-open low shrub habitat compared to Rock Ptarmigan broods. The segregation based on wet tundra-open low shrub habitat corresponds to the intraspecific models for each species. Weeden (1959) observed similar preferences with his populations of ptarmigan in Alaska. Rock Ptarmigan were found in the ‘low shrub’ zone which is characterized by shrubs of 1-3 feet in height. Terrain ruggedness (TRI) was highly correlated with slope (r= 0.99) and is a measure of the sum change in elevation between a pixel and its eight neighbouring grid pixels (Riley et al. 1999). ‘Peaks’ and ‘pits’ have high TRI values, while gradual undulating slopes have low values (Riley et al. 1999). The biological reasoning behind this difference is unclear, but it likely pertains to the tendency for White-tailed Ptarmigan to use intermediate steep and less stable slopes.

Patch Level

The resource selection of Rock and White-tailed Ptarmigan brood hens also differed at the patch level, but there were some similarities. Both species selected patches with a greater rock cover compared to what was available within the foraging area. Rock within foraging patches may provide cover from predators and help with thermoregulation (Weeden 1959, Frederick and Gutierrez 1992). Populations of Rock Ptarmigan in the Arctic and the Alps are typically associated with rock cover (Favaron et al. 2006, Holder and Montgomerie 2008, Zohman and Woss 2008). Low shrubs provide similar cover for Rock Ptarmigan, but only to a certain extent. Greater shrub cover changes the understory plant community (Anthelme et al. 2007), which decreases potential food items for ptarmigan (Weeden 1959). As a result, Rock Ptarmigan broods may use foraging areas of relatively open habitat, while using patches that are close to low shrubs for cover.

Curiously, Rock Ptarmigan broods used patches with less dwarf willow than available in the foraging area, despite the fact that dwarf willows are an important food item during brood rearing (Weeden 1969, Pederson et al. 1998, Holder and Montgomerie 2008). Furthermore, they did not tend to select patches that had greater amounts of forbs, particularly *Polygonum spp.*, which are a major part of their diet in the summer (Weeden 1969, Favaron et al. 2006, Pederson et al. 1998, Holder and Montgomerie 2008). These items may be equally abundant across their foraging areas, or perhaps proximity to cover is a more important variable when considering patches. However, the odds ratio for distance to low shrub was fairly weak (0.93) and the 95% confidence interval overlapped with 1.0, suggesting that they were not selecting for areas closer to shrub relative to what was available.

White-tailed Ptarmigan brood hens were selecting areas with greater rock and forb cover within foraging areas. Rock patches provide excellent cover from predators and heat, provided they are stable enough to produce low lying vegetation for food (Choate 1963, Frederick and Gutierrez 1992). The flowers, leaves and seeds of forbs, such as several *Saxifraga spp.*, *Artemesia spp.*, *Ranuncula spp.* and *Polygonum spp.*, found in these rocky habitats are food sources for ptarmigan during the summer months (Choate 1963, Weeden 1967, May and Braun 1972, Schmidt 1988, Frederick and Gutierrez 1992). Surprisingly, dwarf willows were not important in patch selection, despite the fact they are an important food item at other locations (Choate 1963, Weeden 1967, Frederick and Gutierrez 1992, Clarke and Allen 2005). However, dwarf willows are particularly common throughout the study area, so there may be no need to seek out patches with greater dwarf shrub cover. White-tailed Ptarmigan were typically observed close to patches of snow/water. This has been well documented in other populations of White-tailed Ptarmigan in North America, where broods have been observed following the migration of snow line to access newly exposed vegetation (Choate 1963, Weeden 1967, Frederick and Gutierrez 1992).

Niche Partitioning

Despite increased mobility and lack of territoriality during brood rearing, Rock and White-tailed Ptarmigan differed in their selection of foraging areas and patches. These results support the findings of resource partitioning between Willow, Rock and White-tailed Ptarmigan during other times of the year. Weeden (1967, 1969) found that the three species segregated in their winter diets in central Alaska, despite occupying the same winter range. Despite territorial behaviour, Wilson and Martin (2008) found that the three species had species-specific nesting habitat preferences, which allowed for coexistence during the breeding season. Furthermore, these results support findings in other congeneric species. Kumstatova et al. (2004) found that tree pipits (*Anthus trivialis*) and meadow pipits (*A. pratensis*) co-occurred in transition zones where they showed niche differentiation by selecting different vegetation heights and densities. Rolando and Palestrini (1989) found that Great Reed Warblers (*Acrocephalus arundinaceous*) defended territories against Marsh Warblers (*A. palustris*) even though they had different habitat preferences. Although brood rearing could be a period of increased competition between Rock and White-tailed Ptarmigan, the two species differed in their selection of foraging areas and patches; consistent with other times of year and other congeneric species.

Another way to examine interspecific competition is to examine the shift in the realized niche in the presence of other species. If competing species have large niche overlaps with similar competitive abilities, there is expected to be niche contraction for both species in areas of sympatry (Colwell and Fuentes 1975). However, if one species is dominant over the other, the subordinate species should display greater niche contraction (Colwell and Fuentes 1975, Munday et al. 2001). In the Alps, Rock Ptarmigan prefer rocky habitats with sporadic patches of vegetation, while neither selecting for nor avoiding alpine grasslands, meadows and dwarf shrub habitats (Favaron et al. 2006). However, in our study, Rock Ptarmigan were mainly restricted to areas of wet tundra-open low shrub habitats. Conversely, White-tailed Ptarmigan used similar habitats as described at other locations (Choate 1963, Weeden 1967, Frederick and Gutierrez 1992, Braun et al. 1993, Clarke and Allen 2005). Therefore, White-tailed Ptarmigan may be dominant over Rock Ptarmigan, based on the Competitive Exclusion Principle, and they are indirectly outcompeting Rock Ptarmigan for resources through exploitation competition. However, caution must be used as studies differ in habitat classification, and habitat structure varies at different geographic locations (Wilson and Martin 2008). A removal experiment would better address interspecific competition between the two species (Garcia 1983), but this was not feasible at our site.

Potential Consequences of Climate Change

Climate change models predict that arctic and alpine ecosystems will see changes in mean annual temperatures and precipitation (Parmesan and Yohe

2003). ACIA (2004) predicts greater winter precipitation and elevated winter temperatures in southwest Yukon. Greater precipitation might benefit some species, but frequent warming periods may decrease the snow pack and create icy conditions on the snow surface. These layers of ice may decrease access to food during the cold winter months for some species, such as caribou (Tews et al. 2007) and ptarmigan. Furthermore, a smaller snow pack may benefit some species by increasing the growing season, but it may also reduce water availability and decrease opportunities for thermoregulation during the summer months.

We can assess the impact of these changes on Rock and White-tailed Ptarmigan by examining their habitat use at the foraging area and patch levels. At the foraging level, Rock Ptarmigan may benefit from a rising shrubline as their foraging areas generally consist of wet tundra-open low shrub and closed low shrub habitats. Furthermore, at the patch level, Rock Ptarmigan broods forage in close proximity to low shrubs, which act as a potential source of cover. However, a rising shrubline would also expand areas of tall shrub, which are used by Willow Ptarmigan. This could potentially increase interactions between these two species (Weeden 1959) and have negative consequences for Rock Ptarmigan, since Willow Ptarmigan are the largest ptarmigan species and tend to be socially dominant over Rock Ptarmigan in regions of sympatry (Moss 1972). Furthermore, over time, suitable habitat would decrease further due to a fixed ridgeline and increasing pressure of expanding tall shrub habitat from below. So although initially it may be considered positive, a rising shrubline due to climate change could have a negative effect on Rock Ptarmigan brood-rearing habitat at, both, the population and patch levels.

White-tailed Ptarmigan may also be affected by climate change through increasing shrub habitats and decreasing snow packs. White-tailed Ptarmigan mainly selected foraging areas based on topographic features (elevation and slope), which will not be altered with changing climate. However, White-tailed Ptarmigan avoided wet tundra-open low shrub habitat at this scale. This would suggest that a rising shrubline and increased shrub habitat would decrease the amount of suitable habitat for White-tailed Ptarmigan. White-tailed Ptarmigan are typically associated with rocky habitat (Weeden 1959, Choate 1963, Frederick and Gutierrez 1992), which can occur at a variety of elevations as a result of geomorphic features, such as rock slides and boulder fields. In our study, White-tailed Ptarmigan tended to forage at higher elevations, but they did utilize a wide range of elevations and it is possible they were using these rocky habitats at lower elevations. Although it is likely that increased shrub habitat would decrease the amount of suitable habitat for White-tailed Ptarmigan, they may be able to use the refuges of rock habitat within the matrix of shrub for brood-rearing.

At the patch level, climate change could have a different impact on White-tailed Ptarmigan broods. Although it is difficult to predict how fluctuating winter temperatures and precipitation would affect snow pack, it is generally accepted that snow pack would decrease in seasonal persistence, resulting in a longer growing season and decreased moisture availability. We found that White-tailed Ptarmigan broods chose patches close to snow and water. Although White-tailed

Ptarmigan have a broad diet in the summer (Weeden 1967), they typically feed on fresh and low lying plant species that are continually exposed by retreating snow patches (Choate 1963, Schmidt 1988, Frederick 1992). A decreased snow pack could decrease the number and size of snow patches, which could affect the ability of White-tailed Ptarmigan broods to thermoregulate and locate suitable food types, such as forbs.

In summary, although Rock and White-tailed Ptarmigan share some similarities in habitat use at the patch level, they do show niche partitioning at both habitat scales. Observed consequences of climate change may have an effect on both species of ptarmigan through shifts in vegetation communities and changes in moisture availability. We identified at what scale these changes may have an impact, which will be important for predicting the status and distribution these populations in the future.

Table 2-1: The cover classes and the method in which they were derived for the Ruby Range landcover classification scheme. NDVI values were scaled between 0 and 1, and multiplied by 255 to convert into 8-bit data. Scaled NDVI values were derived from a Landsat Thematic Mapper image (9 August, 2003). The National Topographic Database map (NTDB) was provided by the Natural Resources of Canada.

Value	Cover Class	Description
0	Unclassified	Unclassified pixels. Likely shadow or rock
1	Rock	Derived from scaled NDVI values (100-153)
2	Dry-wet tundra	Derived from scaled NDVI values (154-175)
3	Wet tundra-open low shrub	Derived from scaled NDVI values (176-187)
4	Closed low shrub	Derived from scaled NDVI values (188-195)
5	Tall shrub	Derived from scaled NDVI values (>195)
7	Forest	Derived from the NTDB maps (1:50 000)
8	Ice/permanent snow	Derived from the NTDB maps (1:50 000)
9	Water	Derived from NTDB maps (1:50 000)

Table 2-2: Estimated coefficients (β_i), standard errors (SE) and P-values (P) of the final brood occurrence models for Rock (n=55) and White-tailed (n=46) Ptarmigan in southwest Yukon for 2006.

Rock Ptarmigan

Variable	β_i	**SE**	**P**
CTI	3.901	1.812	0.0313
CTI^2	-0.250	0.124	0.0438
cl_low_cat	0.620	0.321	0.0534
wet_low	2.381	0.466	<0.001

White-tailed Ptarmigan

Variable	β_i	**SE**	**P**
Elevation	0.002	0.001	0.119
Slope	0.429	0.195	0.028
$Slope^2$	-0.010	0.005	0.063
wet_low_cat	-0.626	0.345	0.071

Overlap

Variable	β_i	**SE**	**P**
TRI	0.126	0.057	0.026
wet_low	-2.851	0.882	0.001

‘CTI’ (Compound Topographic Index) is an index of moisture, ‘cl_low_cat’ is the categorical variable for closed low shrub habitat, ‘wet_low’ is the proportion of wet tundra-open low shrub habitat, ‘elev’ is elevation (m), ‘slope’ is the slope angle (degrees), ‘wet_low_cat’ is the categorical variable for wet tundra-open low shrub habitat. Proportions were calculated by using the proportion of pixels that were classified as the respective habitats within a 60m radius.

Table 2-3: The brood site characteristics for Rock and White-tailed Ptarmigan at the population level in southwest Yukon for 2006.

Variable	**Rock Ptarmigan (n=55)**			**White-tailed Ptarmigan (n=46)**		
	Mean	**SD**	**Range**	**Mean**	**SD**	**Range**
Elevation (m)	1724	60	1600-1869	1842	120	1454-2015
Slope (degrees)	17	5	4-30	18	5	9-25
TRI (ruggedness index)	22.1	7.1	5-43	25.5	6.6	13-41
CTI (moisture index)	7.1	0.9	4-10	6.2	1.0	4-9
Rock (%)	6	16	0-69	24	36	0-100
Dry-wet tundra (%)	22	28	0-100	55	34	0-100
Wet tundra-open low shrub (%)	65	34	0-100	20	27	0-100
Closed low shrub (%)	8	15	0-85	1	6	0-38
Tall shrub (%)	N/A	N/A	N/A	N/A	N/A	N/A

Table 2-4: Model selection of brood occurrence at the patch level for Rock and White-tailed Ptarmigan using paired-logistic regression. Only the top models (ΔAIC_c<4) and the null models are presented for each species. We present models that were within $2AIC_c$ of the top model for Rock Ptarmigan, because 11 of the 13 candidate models were within $4AIC_c$.

Rock Ptarmigan

Model	**k**	**Loglik**	**AIC_c**	**ΔAIC_c**	**w_i**
rock + dist_shrb(<1 m) + dwsaltot	3	-23.03	52.65	0	0.15
rock + dist_shrb(<1 m) + dwsaltot + forbtot	4	-21.93	52.86	0.21	0.14
rock + dist_shrb(<1 m) + forbtot	3	-23.31	53.21	0.56	0.12
rock + dist_shrb(<1 m) + dwsaltot + polyg	4	-22.18	53.36	0.71	0.11
rock + dwsaltot + forbtot	3	-23.58	53.75	1.10	0.09
rock + dwsaltot + polyg	3	-23.60	53.79	1.14	0.09
rock + dwsaltot	2	-24.78	53.85	1.20	0.08
rock + dist_shrb(<1 m) + polyg	3	-23.87	54.33	1.68	0.07
rock + dist_shrb(<1 m)	2	-25.14	54.57	1.92	0.06
Null	0	-30.50	61.00	8.35	0.00

White-tailed Ptarmigan

Model	**k**	**Loglik**	**AIC_c**	**ΔAIC_c**	**w_i**
rock + dist_snow/water + forbtot	3	-11.07	28.73	0	0.49
rock + dist_snow/water + dwsaltot + forbtot	4	-10.58	30.16	1.43	0.24
rock + dist_snow/water	2	-14.09	32.47	3.74	0.08
Null	0	-22.87	45.74	17.01	0.00

k is the number of parameters, Loglik is the log-liklihood, AIC is the Akaike Information Criterion, ΔAIC is the scaled AIC value with respect to top model, w_i is the Akaike weights. 'rock'= % rock cover, 'dist_shrb(<1 m)'= distance (m) to shrub (<1 m height), 'forbtot'= % total forb cover, 'dwsaltot'=% total dwarf willows, 'dist_snow/water'= distance (m) to water/snow, 'dwsaltot'=% total dwarf willows, 'polyg'= % Polygonum spp. cover.

Table 2-5: The model averaged coefficients (β_i), standard errors (SE) and odds ratios for the top brood site selection models for Rock and White-tailed Ptarmigan at the patch level. The values in parentheses for the odds ratio represent a meaningful change in the variable.

Rock Ptarmigan

Variable	β_i	SE	Odds ratio	95% CI of Odds ratio
rock	0.067	0.036	1.40 (5%)	0.98 to 1.98
dist_shrub (<1 m)	-0.015	0.009	0.93 (5 m)	0.85 to 1.01
dwsaltot	-0.049	0.029	0.86 (5%)	0.59 to 1.02

White-tailed Ptarmigan

Variable	β_i	SE	Odds ratio	95% CI of Odds ratio
rock	0.065	0.027	1.39 (5%)	1.07 to 1.80
dist_snow/water	-0.031	0.015	0.85 (5 m)	0.74 to 0.99
forbtot	0.154	0.078	2.16 (5%)	1.01 to 2.52

‘rock’= % rock cover, ‘dist_shrub(<1 m)’= distance (m) to shrub (<1 m height), ‘forbtot’= % total forb cover, ‘dwsaltot’=% total dwarf willows, ‘dist_snow/water’= distance (m) to water/snow.

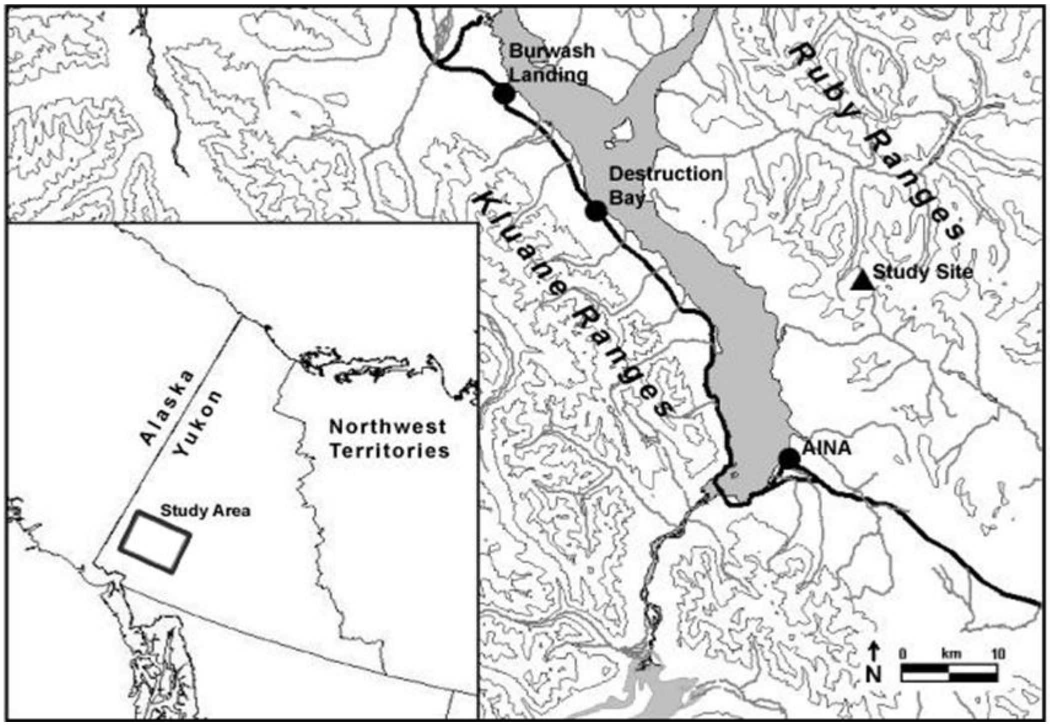

Figure 2-1: The location of the study site in the Ruby Ranges, Yukon Territory.

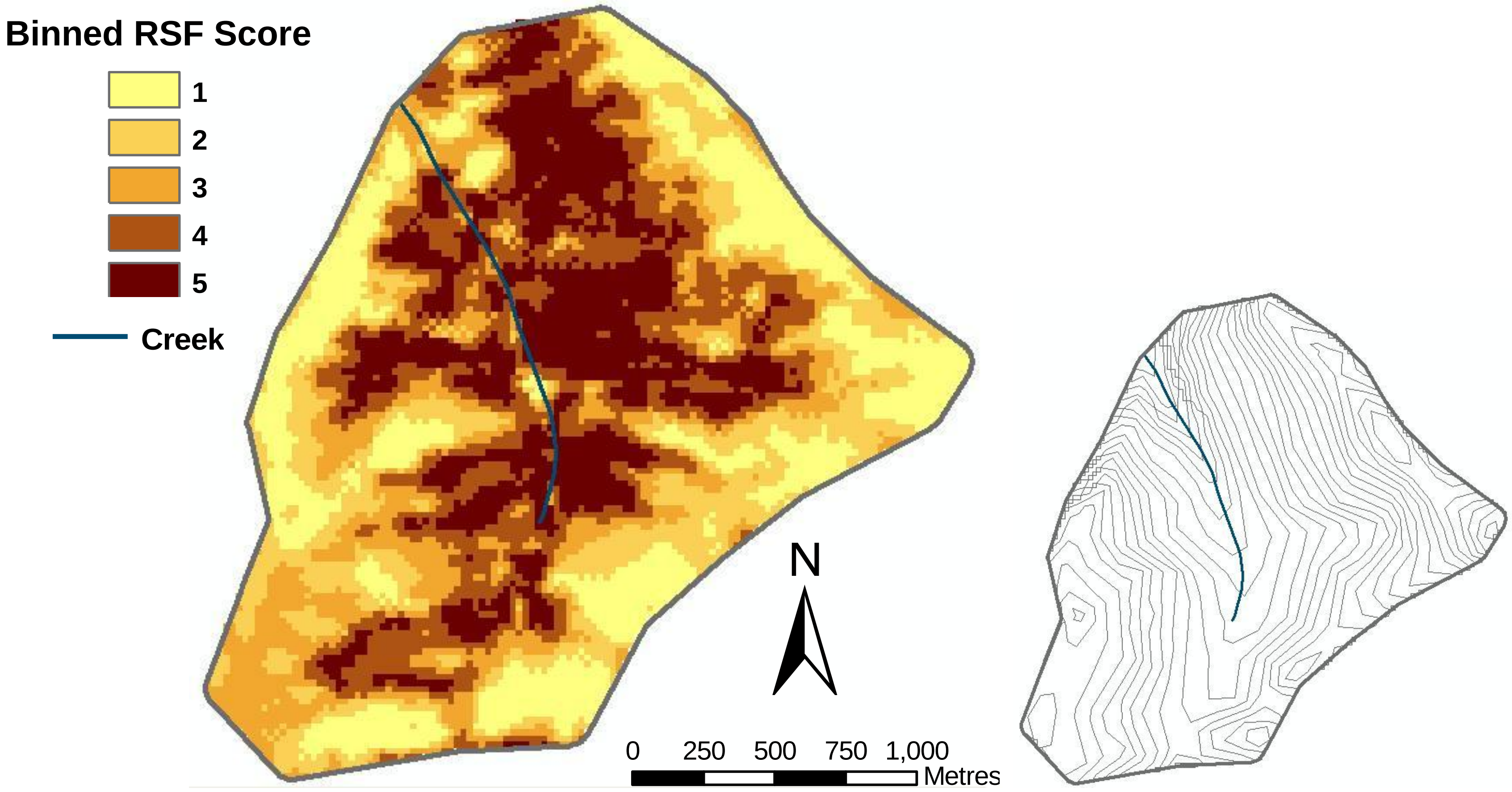

Figure 2-2: The relative index of Rock Ptarmigan brood occurrence at the study area in southwest Yukon using logistic regression occurrence models. Darker regions indicate areas Rock Ptarmigan brood hens are likely to use during brood rearing. The contour map shows the elevation change at 25 m intervals from [low] to [high] m at the study area with a 100 m buffer. Solid line is the creek at the valley bottom.

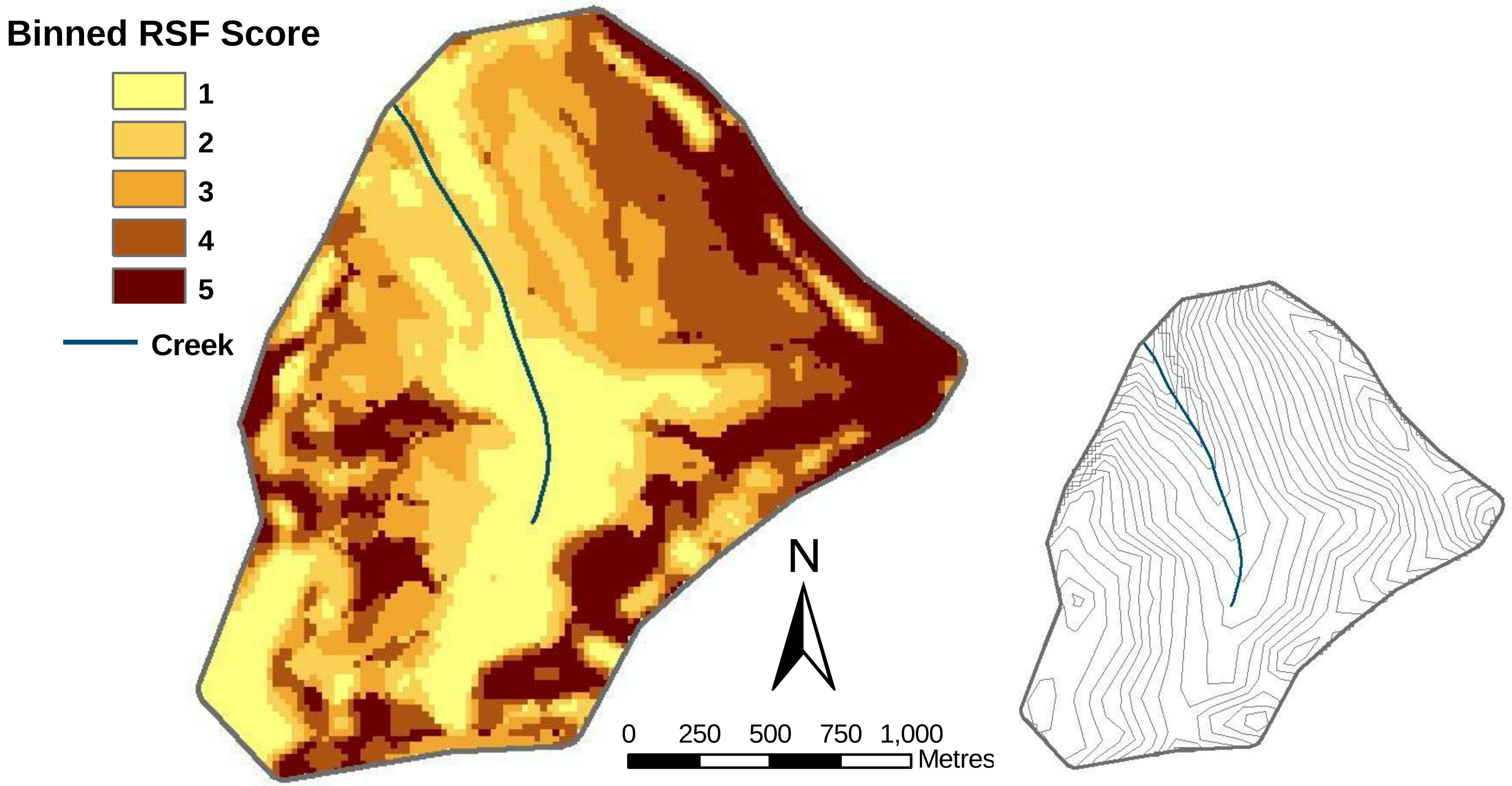

Figure 2-3: The relative index of White-tailed Ptarmigan brood occurrence at the study site using logistic regression occurrence models. Darker regions indicate areas that White-tailed Ptarmigan are likely to use during brood rearing. The contour map shows the elevation change at 25 m intervals from [low] to [high] m at the study area with a 100 m buffer. Solid line is the creek at the valley bottom.

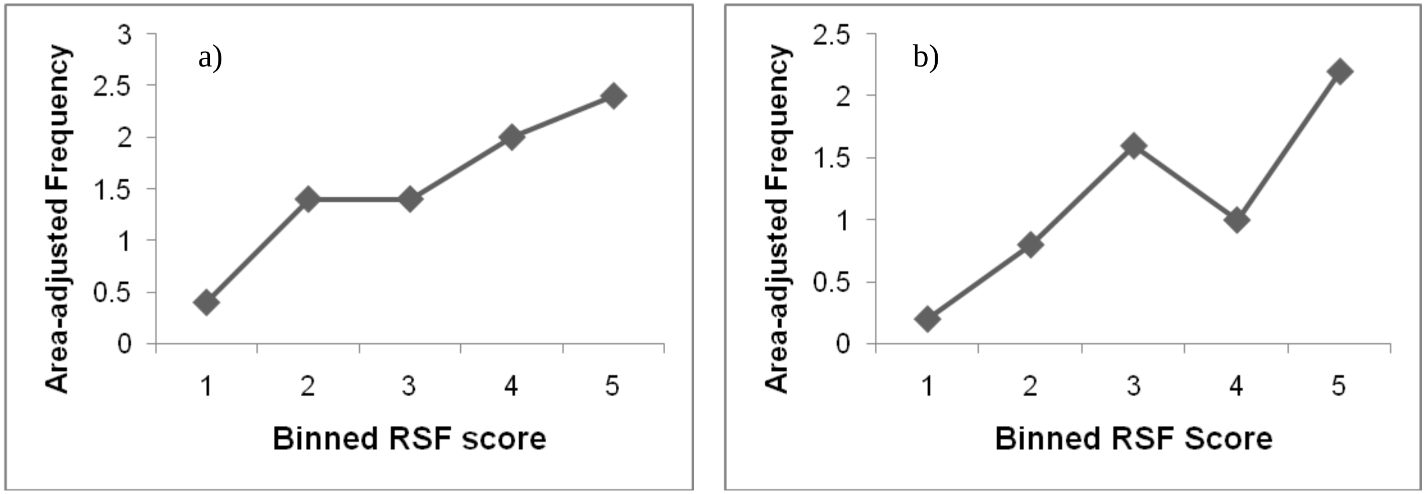

Figure 2-4: The area-adjusted frequency of the validation sample for each binned RSF score for a) Rock Ptarmigan and b) White-tailed Ptarmigan. RSF values were created from the brood occurrence models for each species and the RSF scores were binned by quantiles. The validation sample was collected from collared brood hens in 2004-2005 and 2007.

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Chapter 3: A survey of spatial variation in abundance of Rock (*Lagopus muta*) and White-tailed Ptarmigan (*L. leucura*) in southwest Yukon

INTRODUCTION

A fundamental goal in ecology is to understand the biological and environmental factors that limit the distribution and abundance of an organism (Andrewartha and Birch 1954, Ritchie et al. 2008). The geographic range of a species is the limit of a species' distribution and it is typically depicted by a range map derived from the literature and other sources of data. However, species distribution and abundance is rarely uniform across the entire geographic range (Brown et al. 1995, Brown et al. 1996). Relatively little attention has been given to the patterns and processes of spatial variation in abundance within a species, which can be explained by broad-scale biotic (food availability, competitors, vegetation structure, habitat fragmentation) and abiotic (geomorphology, climate) variables (Brown et al. 1996, Carrascal and Seoane 2009). Increased availability of databases with geographic, geologic, climatic and soil information over large areas combined with advances in technology, such as Geographic Information Systems (GIS), have encouraged further research (Brown et al. 1996). Identifying these factors within the geographic range is important for addressing the effects of large-scale environmental change on species distributions (Peterson et al. 2001, Hughes 2003, Rondinini et al. 2005, Ritchie et al. 2008), and may provide information to guide conservation in large-scale geographic contexts (Carrascal and Seoane 2009).

Measuring abundance of a species over a large geographic area requires a large investment in time and effort and typically involves large-scale surveys, such as those conducted by the North American Breeding Bird survey. Alternatively, studies can focus on a portion of the geographic range to examine specific factors and offer greater insight into the patterns and processes that affect spatial variation in abundance (Brown et al. 1996). There are several techniques to quantify species abundance and estimate population density, including census and survey sampling of populations (Cochrane 1977). Although a census is more precise, it may be impractical over larger areas (Pelletier and Krebs 1997). Line transect sampling, when combined with a detectability function, is a reliable and accepted method to estimate population density (Rosenstock et al. 2002, Buckland 2006, Marques et al. 2007). While it is recommended that at least 60 individuals are needed in order to get a reliable population estimate to compare between populations (Buckland et al. 1993), this may not be a possible for rare or low density species. In these cases, pellet counts might be more effective as an index of relative abundance; this technique has been employed in several systems to estimate abundance of birds and mammals (Bennett et al. 1940, Forys and Humphrey 1997, McCurdy 1997, Vernes 1999, Nystrom et al. 2005, Evans et al. 2007). Although pellet counts do not yield exact numbers of animals, detailed information, such as the sex and age of individuals, it can provide an index of relative abundance (Evans et al. 2007).

Several methods have been used to estimate population density of ptarmigan, including pointer dogs (Jenkins et al. 1963, Mougeot et al. 2003a, b, Evans et al. 2007), counts of calling males (Watson and O'Hare 1979, Pedersen et al. 2006, Nopp-Mayr and Zohmann 2008), playbacks of calls from territorial males (Evans et al. 2007) and pellet counts (Nystrom et al. 2005, Evans et al. 2007). Pelletier and Krebs (1997) used line transect sampling for surveying Willow Ptarmigan in southwest Yukon, but concluded that the technique would not be suitable for lower density Rock and White-tailed Ptarmigan or during the summer months when birds are less conspicuous. White-tailed Ptarmigan brood hens are quite receptive to chick distress calls (Braun et al. 1973), and the use of playbacks in a systematic survey may be a useful tool for surveying ptarmigan in the summer season. Additionally, this technique would yield data on reproductive output of different breeding populations over a portion of the geographic range, which could be used to identify source and sink populations (Pulliam 1988, Pulliam and Danielson 1991).

Three species of ptarmigan inhabit North America (Willow Ptarmigan (*Lagpopus Lagopus*), Rock Ptarmigan (*L. muta*), and White-tailed Ptarmigan (*L. leucura*). These species overlap in some areas within their respective geographic ranges. The Kluane Lake region, Yukon Territory, Canada is an area where the ranges overlap, and is currently experiencing rapid ecological change due to winter warming (ACIA 2004). As a result, the region is seeing large-scale environmental change through expanding tree and shrub lines (Sturm et al. 2001, Tape et al. 2006, Danby and Hik 2007a, b). These changes could have variable effects on Willow Ptarmigan, who occupy shrub habitats, and Rock and White-tailed Ptarmigan, who occupy alpine tundra during the breeding season in this region (Wilson and Martin 2008). Given that environmental change could affect distribution and abundance of ptarmigan, it is important to identify variables that affect abundance in this portion of their geographic range. We focus our study on Rock and White-tailed Ptarmigan living in alpine tundra habitat as these populations are likely to be most severely reduced as a consequence of an expanding tree and shrub line.

In this study, we examined two survey techniques to determine spatial variation in abundance in two mountain ranges of the Kluane Lake region. We expected a strong correlation between the two techniques and a significant difference in relative abundance between the Kluane and Ruby mountain ranges. We also examined various climate, habitat, topographic and geologic/geomorphic variables that may explain any difference in abundance between the two mountain ranges using several GIS databases and thematic maps.

METHODS

Study Area

This study was conducted in two major mountain ranges in the Kluane Lake Region, Yukon Territory (61^{o} 130N, 138^{o} 160W), the Kluane and the Ruby Ranges (Figure 3-1). The Ruby and the Kluane Ranges are separated by the Shakwak Trench, a major valley created by the Denali Fault, and they have different origins and characteristics. The Ruby Range is an 80 million year old mountain belt composed of metamorphic and igneous rock, and is characterized by small, rounded mountains (Israel 2004). The Kluane Range is composed of sedimentary and volcanic rock from the Wrangellia terrane, which collided with the North American Plate. The Kluane Range is characterized by taller, rugged mountains (Israel 2004).

The alpine habitat was similar for both mountain ranges and can be segregated into several major classes; closed low shrub, open low shrub, wet tundra, dry tundra, and rock. Closed low shrub habitat consisted of areas with low shrubs (*Salix pulchra, S. glauca, Betula glandulosa*) comprising greater than 25% of the overhead cover, while open low shrub habitat consisted of small patches of low shrubs with areas of short vegetation types (eg. graminoid species, dwarf shrubs). Wet tundra was dominated by graminoid species interspersed with dwarf shrubs (*Salix reticulata, S. arctica, S. polaris, Dryas octopetala*) and small rock patches, while dry tundra was dominated by *D. octopetala* and lichen species. Rock habitat was found along ridges, cliffs, and within the matrix of the other habitat classes as rockfalls, boulder fields and moraines. Forbs were present throughout the habitat types with productivity and abundance varying by elevation.

Field Methods

Field work was conducted during the brood-rearing period from July 1 through August 11, 2008. We used alpine valleys as our study unit, as breeding pairs rarely travel outside of these valleys during the breeding season (personal observation). Ridgelines thus provide a clear boundary between study units. Valleys were mainly accessed on foot, but a helicopter was used to reach Valleys 1 to 3. A camp was set up in the actual valley to be surveyed or in an adjacent valley. Surveys were conducted from 8:00 to 18:00 during days with minimal to no rain and when winds did not exceed Beaufort Wind Force Scale number 4 (20-28 km/h). We used topographic maps to divide valleys into eight sections for survey. The total length of the ridge within a valley was divided into eight equal lengths, while the length of the valley bottom was divided into four equal lengths. Lines were drawn from the points on the ridge to the points on the valley bottom to yield eight, numbered sections of the valley (Figure 3-2). We randomly selected four numbers (1 through 8) with each number representing a section of the valley to be surveyed. If one of the slope aspects of the valley was not selected, we drew another number to ensure all aspects of the valley were represented.

Transects started by following a bearing that generally followed the contours of the slope. Any change of bearing needed to maintain the selected route was recorded, as well as the distance between changes of bearing. Transects never bisected steep (>50^{o}) slopes. In order to properly represent the different habitat types (open low shrub, wet tundra, dry tundra and rock), we set 3 km targets for each habitat type for a total of 12 km of transect for each valley. We performed playbacks of chick distress calls at 100 m intervals along and at the end of each transect to locate brood hens of any species. Upon location of any individual or brood, we took a waypoint from the location of detection using a handheld GPS unit (Garmin Ltd.) with location uncertainty of 8 m or less. We then recorded the actual location of the bird or brood and calculated the straight line distance between detection and location.

Groups of droppings were recorded along each transect as an indirect measure of relative abundance. Although droppings can be indistinguishable between ptarmigan species (Nystrom et al. 2005), we were comfortable distinguishing droppings of Willow Ptarmigan from Rock and White-tailed Ptarmigan. Willow Ptarmigan droppings appear to be larger with greater amounts of undigested plant material compared to Rock and White-tailed Ptarmigan (personal observation). Additionally, our surveys were restricted to areas outside of typical tall shrub/Willow Ptarmigan habitat. A group of droppings was only considered if there were at least 5 droppings in a group, with at least 0.5 m between each group (Nystrom et al. 2005). GPS locations were not recorded for each pile, but the total number of groups was recorded for each transect. We used the dropping density (droppings/km) as our estimate of abundance for each valley by dividing the total number of groups of droppings by the distance surveyed.

Climate, Topographic, Habitat and Geologic/Geomorphic Variables

We used climate, habitat and topographic variables to characterize each valley, and examined similarities and dissimilarities between mountain ranges. We delineated each valley with a 100 m buffer and used GIS datasets to obtain the habitat and topographic variables. We excluded water, forest and permanent ice landcovers from our analysis using the National Topographic Data Base (NTDB) maps, as ptarmigan do not use these habitats. Climate variables were derived from modeled precipitation and temperature data created by Jarosch et al. (unpublished data) at a 30 m resolution. Koh et al. (unpublished data) used the precipitation and temperature data to create layers of the average summed precipitation and average degree days above 0 ºC between April 5 and August 22 from 1986 to 2007. This annual interval was considered the growing season in the alpine at our study region. The average summed precipitation was an indicator of moisture availability, which can affect survival of ptarmigan in summer months (Novoa et al. 2008). Positive degree days are an index of heat accumulation. Positive degree days were calculated as the integral of degrees above 0 ºC times the number of days taken over the sampling interval (Gruber et al. 2009). This index is not only an important indicator of productivity of plants, but also for relative timing of snowmelt which can delay reproduction and reduce reproductive success of breeding ptarmigan (Martin and Wiebe 2004, Novoa et al. 2008). Unfortunately, summed precipitation and degree day data were not available for all of the surveyed valleys, so we compared the means between mountain ranges for the remaining valleys (Ruby Range: n=4, Kluane Range; n=5).

There was no alpine habitat dataset covering the Kluane Range, so we examined the possibility of extrapolating the Ruby Range landcover classification scheme (see Appendix II) to the Kluane Range. We used 30 ground-truthed landcover plots conducted in 2007 to assess the accuracy of the extrapolated model. Only 50% of the 30 ground-truthed plots for the Kluane Range were correctly classified using the Ruby Range Landcover Classification. As a result, we did not compare the habitat composition between the two mountain ranges. Instead, we used the Normalized Difference Vegetation Index (NDVI: Tucker and Sellers 1986) calculated from Landsat Thematic Mapper (August 9, 2003) as an index of productivity (mean and variability). NDVI values were scaled between 0 and 1, and multiplied by 255 to obtain 8-bit data. These scaled NDVI values generate a greater range of values, while maintaining the same principles of the index. Low values indicate poor primary productivity, while large values indicate greater primary productivity. Topographic variables were derived from the Digital Elevation Model (DEM) and consisted of the mean and variability (standard deviation) in elevation and slope for each valley.

We used geologic and geomorphic maps to further characterize the valleys from the Ruby and the Kluane Ranges. We examined the composition of rock classes for each valley using the Yukon bedrock geology layer (Gordey and Makepeace 1999). Only major rock classes (metamorphic, plutonic, volcanic, sedimentary, and unconsolidated material) were used to characterize valleys. The geomorphology of each valley was constructed using thematic maps for the region (Rampton 1974, Rampton 1978a, Rampton 1978b). All calculations and derivations were conducted in ArcGIS 9.3 (ESRI 2008).

Statistical Analysis

We examined the correlation between the droppings density (droppings/km of transect) and the number of adults/broods encountered per km of transect in each valley. Data were tested for normality using the Shapiro-Wilk normality test, and a Pearson’s or Spearman’s rank correlation was used for parametric and non-parametric data. We used an alpha level of 0.10, given our limited sample size (n=12). We compared the mean brood density, mean bird density and mean dropping density for each valley between mountain ranges using a Student's t test (assuming equal or unequal variances) or a Wilcoxon's rank test. Additionally, we tested for a significant difference in mean valley area (km^2) between the two mountain ranges, as this could account for any discrepancies in mean abundance.

Climate, habitat and topographic variables were also examined for significant differences between mountain ranges with sequential Bonferroni correction (α/n) using Student's t-tests (assuming equal or unequal variances) or a Wilcoxon's rank test. All comparisons of habitat variables were tested for normality and equality of variances using the Shapiro-Wilk test and the Fisher's F test, respectively. We provided descriptive comparisons between mountain ranges of the composition of rock classes and the geomorphology of each valley.

RESULTS

There was a weak, significant correlation between dropping density and the number of adults encountered per km of transect (Spearman rank correlation: r= 0.516 df= 10, P= 0.086; Figure 3-3). However, the number of adults and broods encountered along transects was low (0-1 adults/km, and 0-0.45 broods/km), so it was deemed that the observations of birds along transects were not useful in the analysis between mountain ranges (see Nystrom et al. 2005). Comparisons between mountain ranges were restricted to the use of pellet counts. There was a greater mean dropping density in the Ruby Range compared to the Kluane Range (t= 2.451, df= 10, P= 0.0342; Figure 3-4a). Meanwhile, there was no significant difference in the mean valley area between the two mountain ranges (t= 0.558, df= 10, P> 0.5; Figure 3-4b).

Table 3-1 shows the characteristics of the Ruby and Kluane Ranges based on the valley means of the various climatic, topographic and habitat variables. Only the mean positive degree days (0ºC) and the mean standard deviation of scaled NDVI showed a significant difference between mountain range using sequential Bonferroni correction (t= 5.16, df= 7, P= 0.0045, t= 3.96, df= 10, P= 0.0027, respectively).

The rock class composition of each of the valleys surveyed also differed by mountain range (Table 3-2). The valleys in the Ruby Range were composed mainly of metamorphic and plutonic rock classes with some unconsolidated material, while the valleys in the Kluane Range were dominated by sedimentary and volcanic rock classes with some plutonic and unconsolidated material. The geomorphology was similar for both mountain ranges, which was composed of mainly blanketed colluvium with gentle to moderate slopes (Table 3-2). However, valleys 4-6 of the Ruby Range were composed mainly of boulders, which have clasts that are greater than 30 cm in diameter. Data were not available for valleys 1-3, but adjacent areas also contained a large proportion of boulder.

DISCUSSION

Our results suggest that our survey technique using playbacks of chick distress calls during the brood-rearing period is not suitable for estimating population density of ptarmigan. We encountered few adults and broods during our surveys and these numbers were not useful in our comparison of abundance between mountain ranges (see Nystrom et al. 2005). Pelletier and Krebs (1997) observed that ptarmigan were inconspicuous during the summer months and that surveys during this time would not be suitable. Nevertheless, we thought the use of playbacks would help locate birds given that White-tailed Ptarmigan brood hens are responsive to foreign chick distress calls (Braun et al. 1973). During our surveys, we noted that Rock Ptarmigan brood hens were much less responsive to the playbacks than were White-tailed Ptarmgian brood hens, which may account for our limited success in locating Rock Ptarmigan broods. Non-breeding individuals were difficult to locate and were unresponsive to the playback, which supports the statement by Pelletier and Krebs (1997). Additionally, our results may have been confounded by low densities of ptarmigan in the entire region after a significant decline in the regional population during the previous year (S. Wilson personal communication).

Despite the lack of success, there are merits to our survey technique and greater effort may improve accuracy. We spent only one day surveying each site, while covering roughly 12 km of transect in a mean area of 9.21 km^2. Greater effort or a complete census using a greater number of observers would likely increase the number of birds encountered and increase the reliability of the technique. The use of pointer dogs has proven successful in other ptarmigan surveys and it could improve detectability of birds during the summer as well (Jenkins et al. 1963, Mougeot et al. 2003a, b, Evans et al. 2007). Other survey techniques take place during the spring, when displaying cocks are more conspicuous; and they obtain better estimates of population density (Evans et al. 2007). However, summer surveys also produce information on reproductive output of a population. Comparisons of reproductive output between several sites could possibly identify source or sink populations (Pulliam 1988, Pulliam and Danielson 1991). Furthermore, many alpine study areas may be difficult to access during the spring due to inaccessibility of roads, snow depth and inclement weather. Travel in the alpine is much easier in the summer, increasing access to a greater number of sites. As a result, the summer may be more suitable for questions at the geographic range scale (or portion of thereof) of a species.

Although understanding the biological and environmental factors that limit species distribution and abundance is a fundamental goal of ecology, there are few studies that examine spatial variation of species abundance (Brown et al. 1995). We examined spatial variation in ptarmigan abundance using pellet counts as the index of relative abundance for each site given the lack of success with our proposed survey method. We considered pellet counts to be a reliable estimate of population density given the weak and significant correlation between bird density and dropping density ($\alpha = 0.10$), as well as its use to estimate abundance of ptarmigan in other studies (Nystrom et al. 2005, Evans et al. 2007). There was a significant difference in mean dropping density with no significant difference in mean area between the Ruby and Kluane Ranges. As a consequence there appears to be spatial variation in abundance of Rock and White-tailed Ptarmigan within this portion of their geographic range. This is surprising given the close proximity of these two mountain ranges, but it could be explained by broad-scale variation of climate, habitat, topography, and physical geography between the two ranges (Brown et al. 1996, Carrascal and Seoane 2009).

We examined the climate, habitat, topographic, and geological/geomorphic characteristics between the two mountain ranges using a suite of variables derived from GIS and thematic maps. The valleys in the Kluane Range had significantly fewer positive degree days above 0 °C than the Ruby Range, which could help explain the lower pellet counts. The length of the breeding season decreases with increasing elevation, and weather conditions are more unpredictable in alpine regions (Martin 2001). Delayed snowmelt is also common, which can delay reproduction (Martin and Wiebe 2004) and decrease reproductive success in ptarmigan (Novoa et al. 2008). Therefore, recruitment of Rock and White-tailed Ptarmigan could be reduced in the Kluane Range and, subsequently, population density would be lower, consistent with the pellet count data. We also examined the difference in summed precipitation over the breeding season between the two ranges, since rainfall after hatching may have a negative effect on chick survival (Novoa et al. 2008). However, there was no significant difference in precipitation between the two ranges and we did not segregate summed precipitation into pre- or post-hatch.

Using scaled NDVI values as our measure of productivity, we found the mean standard deviation of scaled NDVI was significantly different between the Kluane and the Ruby Ranges using sequential Bonferroni correction. Mean elevation also appeared to differ between the two ranges, but this was not statistically significant. The difference in variation of scaled NDVI could indicate a wider distribution of habitat types. Although incorporating topographic variables (Dirnbock et al. 2003) and a greater number of spectral bands (Sivanpillai et al. 2009) can improve landcover classification, NDVI can be used to classify landcover (see Appendix II, Stow et al. 2008). Alpine valleys in the Kluane Range could have a greater proportion of rocky habitats and tall shrub habitats, while maintaining a mean productivity value that is similar to the Ruby Range. This wider distribution of habitats may not be suitable for Rock and White-tailed Ptarmigan, since Willow Ptarmigan use tall shrub habitats, while Rock and White-tailed Ptarmigan do not (see Chapter 2, Weeden 1959, 1969, Choate 1963, Hannon et al. 1998, Montgomerie and Holder 2008). Therefore, the amount of suitable habitat for Rock and White-tailed Ptarmigan may be reduced in the Kluane Range; decreasing their relative abundances.

Rock and White-tailed Ptarmigan use rock habitat in the brood-rearing period as it provides cover from predators and helps with thermoregulation (Choate 1963, Weeden 1967, Schmidt 1988, Frederick and Gutierrez 1992, Favron et al. 2006, Zohman and Woss 2008). Both species may benefit from increased rock habitat in the Kluane Range, however, the geology and geomorphology of this rock habitat may be important to the biology of the birds. Israel (2004) described the different geologic histories of the two mountain ranges, which has resulted in different geomorphologies between the Ruby and Kluane Ranges. Both mountain ranges are generally covered with a thick layer (>1 m) of colluvium, but the Kluane Ranges also have areas of thin veneer. The texture of the colluvium also differs between mountain ranges. The colluvium of the Ruby Ranges is composed primarily of boulders (clast size >30 cm), whereas the colluvium of the Kluane Ranges is composed of smaller material. The variation in texture of the colluvium may be of some significance. Finer texture colluvium, such as those found in glacial moraines can be avoided in summer months (Favron et al. 2006) and may not provide suitable cover for ptarmigan (Weeden 1959, Choate 1963). This may help explain the decreased relative abundance in the Kluane Range. Colluvium texture is likely not the only factor, but rather one in a suite of factors, that explains the difference in relative abundance between the two mountain ranges.

In summary, although we concluded that conducting surveys using playbacks of chick distress calls may not be suitable for estimating population densities of ptarmigan, this technique could likely be improved with increased effort. Furthermore, our method provides information on reproductive output for a population and could be used to examine source and sink dynamics within the geographic range of a species. We did find a significant difference in relative abundance between the Ruby and Kluane Ranges using pellet counts, which shows spatial variation in abundance within a portion of the geographic range of the two species. We identified factors that may contribute to the spatial variation in abundance by providing descriptive accounts of the climate, habitat, topographic and geologic/geomorphic variables of the different mountain ranges. Other studies have found broad-scale abiotic and biotic factors to influence distribution and abundance. Russel et al. (2005) found that physical features of streams, such as streambed substrate and physical landforms, influence distribution and abundance of the Cascade torrent salamander (*Rhyacotriton cascadae*). Nopp-Mayr and Zohmann (2008) found lower densities of calling Rock Ptarmigan cocks in the eastern Austrian Alps, which could be attributed to the lack of suitable, heterogeneous habitat, compared to the rest of the Austrian Alps. Continued studies would help identify factors that influence ptarmigan distribution and abundance within their geographic range, which is important for addressing the effects of large-scale environmental change, such as climate change (Peterson et al. 2001, Hughes 2003, Rondinini et al. 2005, Ritchie et al. 2008).

Table 3-1: Means and standard deviations of climate, habitat and topographic variables for sites in Ruby and Kluane Ranges. P values are shown for comparison of variable means between mountain ranges.

	Mountain Range (mean +/- SD)		
Variable	**Ruby Range**	**Kluane Range**	**P**
Climate Variables			
Summed Precipitation (cm)$^{\Psi,c}$	222.09 +/- 16.43	253.73 +/- 41.92	>0.25
Degree Days (0°C)$^{\Psi,b}$	313.15 +/- 4.37	230.46 +/- 34.48	<0.005*
Habitat Variables			
NDVI^{a}	157.86 +/- 6.80	153.26 +/- 14.52	>0.25
SD NDVI^{a}	19.12 +/- 2.64	26.29 +/- 6.76	<0.005*
Topographic Variables			
Elevation (m)^{b}	1796.73 +/- 18.32	1854.14 +/- 67.78	0.057
SD Elevation (m)^{a}	150.97 +/- 21.13	171.46 +/- 37.69	0.043
Slope (deg.)^{a}	17.50 +/- 2.66	18.61 +/- 4.13	>0.25
SD Slope (deg.)^{a}	7.96 +/- 1.26	8.24 +/- 1.47	>0.10

$^{\Psi}$ data were not available for all sites (Ruby Range: n=4 and Kluane Range: n=5)

^{a} represents a parametric variable that was analyzed using a Student's t-test assuming equal variances.

^{b} represents a parametric variable that was analyzed using a Student's t-test assuming unequal variances.

^{c} represents a non-parametric variable that was analyzed using a Wilcoxon rank-sum test.

* represents a significant difference between mountain ranges using sequential Bonferroni correction.

Table 3-2: Rock class composition and geomorphology of each valley in the Ruby and Kluane Ranges. Rock class data was derived from Gordey and Makepeace 1999. Geomorphology data was derived from thematic maps by Rampton (1974), Rampton (1978a) and Rampton (1978b).

Site	Mountain Range	Rock Class	Geomorphology
1	Ruby Range	Plutonic with some metamorphic	N/A
2	Ruby Range	Plutonic	N/A
3	Ruby Range	Plutonic with some unconsolidated material	N/A
4[a]	Ruby Range	Metamorphic with some unconsolidated material	Blanketed[1] colluvium with gentle[ψ] to moderate[§] slope; bouldery* texture
5[a]	Ruby Range	Metamorphic with some unconsolidated material	Blanketed[1] colluvium with moderate[§] slope; bedrock cliff; bouldery* texture
6[a]	Ruby Range	Metamorphic	Blanketed[1] colluvium with gentle[ψ] to moderate[§] slope; bouldery* texture
7[b]	Kluane Range	Sedimentary and Volcanic	Blanketed[1] colluvium with gentle[ψ] to moderate[§] slope; alluvial fan
8[b]	Kluane Range	Sedimentary, Volcanic and Plutonic	Blanketed[1] and veneer[2] colluvium with moderate[§] slope; blanketed moraine
9[b]	Kluane Range	Sedimentary, Volcanic and Plutonic	Blanketed[1] with some veneer[2] colluvium with gentle[ψ] to moderate[§] slope, blanketed moraine
10[a]	Kluane Range	Sedimentary and Volcanic	Blanketed[1] with some veneer[2] colluvium with moderate[§] slope; bedrock cliff; alluvial fan
11[a]	Kluane Range	Sedimentary and Volcanic	Blanketed[1] with some veneer[2] colluvium with moderate[§] to steep[¥] slope; alluvial fan
12[c]	Kluane Range	Sedimenary and unconsolidated material	Blanketed[1] colluvium; ground moraine

[a] geomorphology data taken from Rampton 1978a
[b] geomorphology data taken from Rampton 1978b
[c] geomorphology data taken from Rampton 1974
[1] blanketed refers to continuous cover that is equal to or greater than 1 m thick
[2] veneer refers to thin broken cover that is less than 1 m thick
[ψ] gentle slope (5°-15°)
[§] moderate slope (15°-35°)
[¥] steep slope (>35°)
* bouldery texture refers to clast size >30 cm in diameter

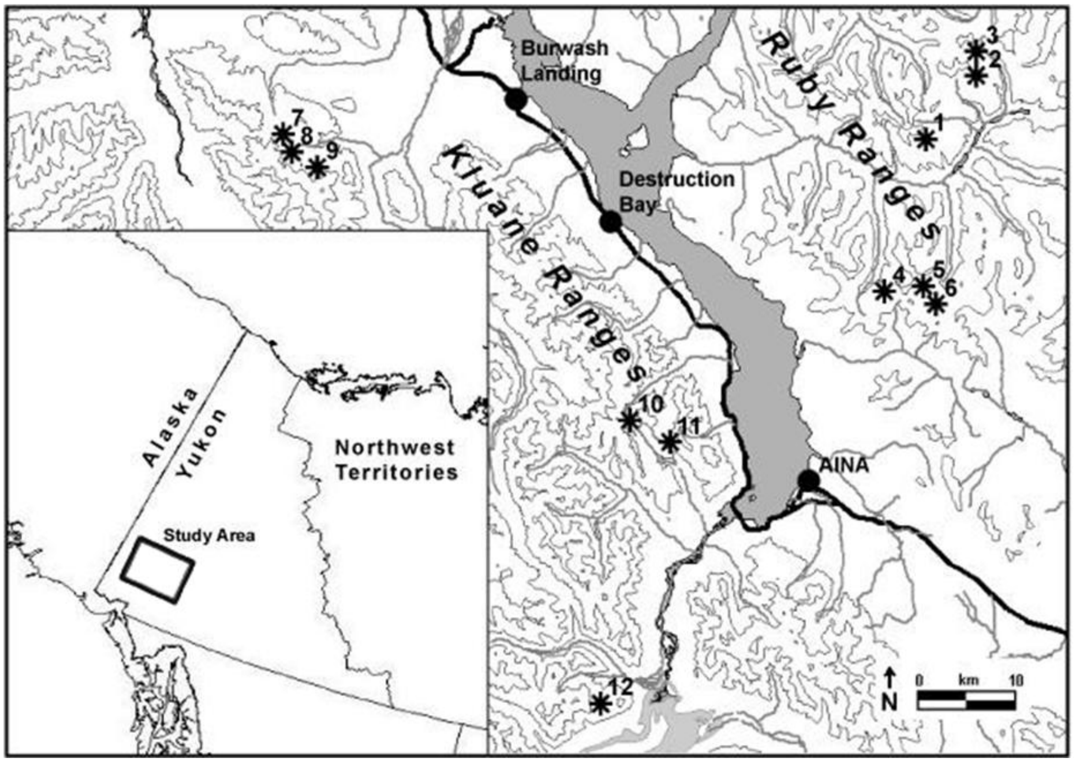

Figure 3-1: Location of study sites in the Kluane Lake region, Yukon Territory, Canada. Research was based out of the Kluane Lake Research Station, Arctic Institute of North America (AINA).

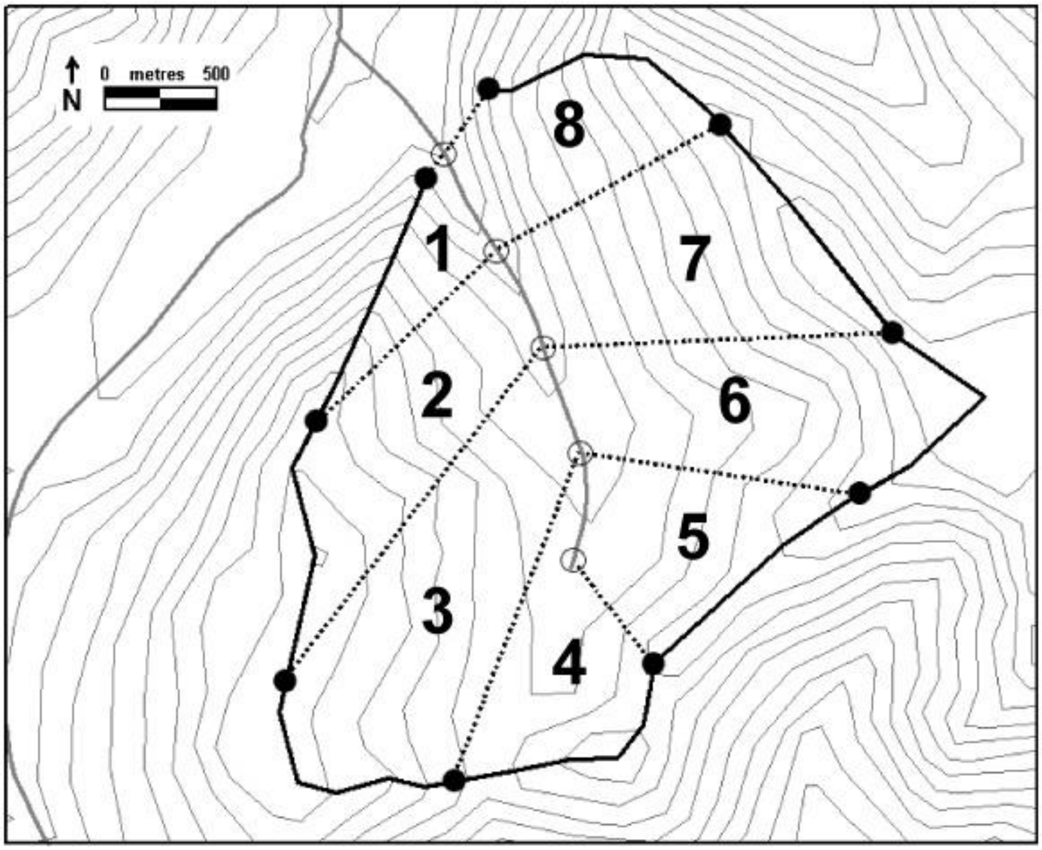

Figure 3-2: A diagram depicting how valleys were segregated prior to surveying. The total length of the ridge within the valley was measured and divided into eight equal lengths. The length of the valley bottom was also measured and divided into four equal lengths. Lines were drawn from points along the ridge to the points in the valley bottom to divide the valley into eight sections. Numbers were drawn by random for surveying. The valley drains to the northwest.

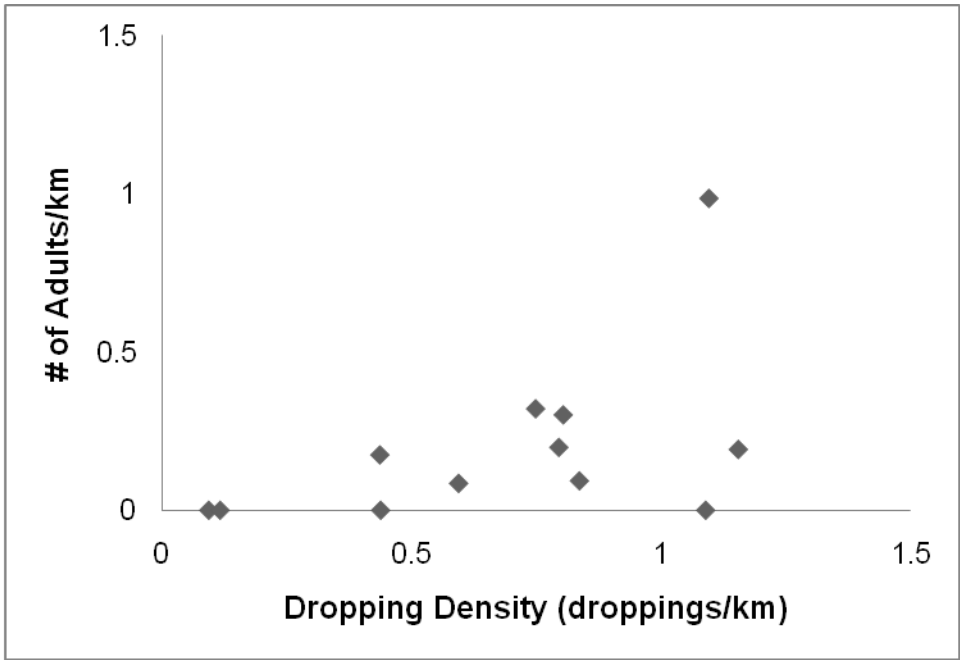

Figure 3-3: The correlation between dropping density (droppings/km) and bird density (birds/km). There was a weak and significant correlation between dropping density and bird density at α = 0.10 (Spearman Rank Correlation: rho= 0.516, df= 10, P= 0.086).

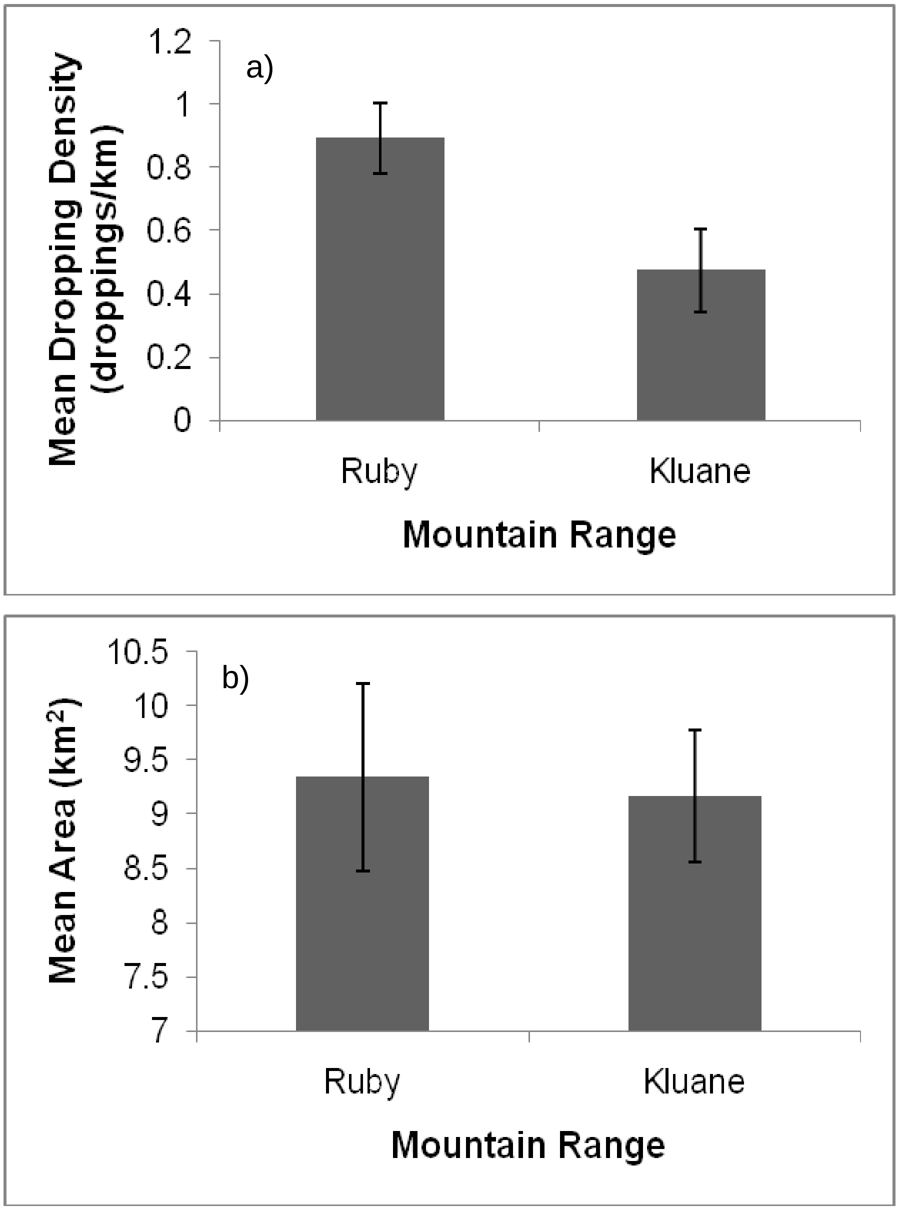

Figure 3-4: The a) mean dropping density (droppings/km), and b) mean valley area (km^2) for the Ruby and Kluane Ranges. Error bars represent the standard error of the mean. There is a significant difference in mean dropping density between mountain range (t= 2.451, df=10, P= 0.0346), but no significant difference in mean area (t= 0.428, df= 10, P> 0.5).

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Chapter 4: Conclusions

Introduction

Animals require adequate quantities of usable resources to sustain healthy populations (Manly et al. 2002), and understanding how an animal uses its environment is fundamental in ecology and wildlife management (Johnson 1980, Boyce et al. 2003). Habitat selection occurs at several temporal and spatial scales, which are linked to species-specific behaviours and life-history traits (Mayor et al. 2007). Therefore, identifying the proper relevant temporal and spatial scales is important when assessing habitat availability and identifying factors that influence habitat selection. Interspecific interactions can also affect habitat availability, particularly at fine scales, as species compete for similar resources or use alternate resources in the presence of other species (Cody and Walter 1976). In addition, climate change is causing range shifts in many species (Hughes 2003, Parmesan and Yohe 2003), which could increase interspecific interactions (Anderson et al. 2009). Species may react differently to changing environments, which can affect the availability of suitable habitat for other sympatric species (von dem Bussche et al. 2008). Therefore, environmental change may not only affect habitat availability directly, but indirectly, by altering interspecific interactions. Identifying important habitat features at various spatial scales of sympatric species, can help in assessing the impacts of future environmental change.

This study contributes to our understanding of interspecific competition and sympatry in related species and, specifically, examines habitat selection of ptarmigan at several spatial scales during brood-rearing. Habitat selection was examined for a sympatric population of Rock and White-tailed Ptarmigan at the foraging area and patch levels. Furthermore, pellet counts and a new survey technique was used to examine spatial variation in abundance of the two species in two mountain ranges. Selected abiotic and biotic factors were examined for each mountain range in an attempt to explain differences in relative abundance.

How Rock and White-tailed Ptarmigan use their environments

Interspecific competition can have a large influence on habitat selection at fine scales (Cody and Walter 1976), and habitat use can expand or retract in the presence or absence of other species (Alatalo et al. 1985). In cases where species are not territorial, species must partition resources in overlapping or non-overlapping areas (Murray 1981, Haila and Hanski 1987, Kumstatova et al. 2004). Two objectives of the study presented in Chapter 2 were to examine the habitat selection of Rock and White-tailed Ptarmigan at the foraging area and patch levels, and to explore at what scales the two species differed in their habitat use. I predicted that the two species would continue to use patches with similar food items, but differ in their habitat selection at the foraging area level. Results from habitat selection models were consistent with the hypotheses at the foraging area level, but not at the patch level. Rock and White-tailed Ptarmigan selected different habitats at the foraging area scale, including areas of overlap. However, at the patch level they differed in their selection of potential food items, while similarly selecting patches with greater rock cover, despite having similar diets based on previous studies (Choate 1963, Weeden 1967, 1969, May and Braun 1972, Frederick and Gutierrez 1992, Pedersen et al. 1998, Allen and Clarke 2005, Clarke and Johnson 2005, Favaron et al. 2006, Montgomerie and Holder 2008). These results suggest that, although there may be some similarities in habitat selection, sympatric populations of Rock and White-tailed Ptarmigan partition resources at the foraging area and patch level.

Interspecific differences of habitat selection between Rock and White-tailed Ptarmigan are a product of interspecific competition, which allows the two species to coexist. In regions where congeneric species live in sympatry, species can segregate by differences in habitat selection. I identified the habitat scales at which this occurs for sympatric Rock and White-tailed Ptarmigan. These findings support the findings of resource partitioning between Willow, Rock and White-tailed Ptarmigan during other times of the year. Weeden (1967, 1969) showed that the three species have different winter diets in central Alaska, which limits competition and territorial overlap despite occupation of the same winter range. Wilson and Martin (2008) found that Willow, Rock and White-tailed Ptarmigan had species-specific nesting habitat preferences, which allowed for coexistence. Furthermore, these results support the findings in other congeneric species, such as sympatric populations of the tree pipit (*Anthus trivialis*), meadow pipits (*A. pratensis*) (Kumstatova et al. 2004), and warbler communities in Italy (Rolando and Palestrini 1989).

This study examined habitat selection for a single sympatric population of Rock and White-tailed Ptarmigan. Similar studies have compared habitat selection of sympatric populations to local allopatric populations (Alatalo et al. 1985, Kumstatova et al. 2004) or populations with experimentally removed competitors (Garcia 1983). There were no local populations where each species occurred separately and removal experiments were not feasible at our sites. Instead, we compared our population to allopatric populations described in the literature. Allopatric populations of White-tailed Ptarmigan appeared to have similar habitat distributions, whereas the habitat distribution of Rock Ptarmigan appeared to retract, particularly when compared to populations from the Alps (Favaron et al. 2006, Zohman and Woss 2008). These findings suggest that White-tailed Ptarmigan may be the superior competitor based on the Competitive Exclusion Principle. However, this comparison only provides a rudimentary comparison, as habitat classification differs between studies and habitat structure can vary among geographic locations (Wilson and Martin 2008).

Variation in the Distribution and Abundance of Ptarmigan

A geographic range encompasses the entire distribution of a species and species use a variety of habitats within their geographic range (Pulliam 1988, Brown et al. 1996). Broad-scale biotic and abiotic factors are thought to influence selection within the geographic range of a species (Brown et al. 1996, Carrascal and Seoane 2009). Climate change is thought to be the cause of observed range shifts in several organisms (Hughes 2003, Parmesan and Yohe 2003), so identifying factors that influence distribution and abundance of species within their geographic range is important for addressing effects of large-scale environmental change (Petersen et al. 2001, Hughes 2003, Rondinini et al. 2005, Ritchie et al. 2008). In Chapter 3, I examined spatial variation of abundance and reproduction of Rock and White-tailed Ptarmigan within a portion of their geographic range. I surveyed ptarmigan populations in two mountain ranges using pellet counts and transect surveys using chick distress call playbacks during brood-rearing. Pellet counts provided a moderate to good estimate of population density when compared to the transect surveys. There was greater relative abundance of ptarmigan in the Ruby Range compared to the Kluane Range using pellet counts. Unfortunately, too few broods were found during the surveys to estimate reproduction among the different populations. However, greater effort with more observers would likely improve this survey technique.

Another objective of Chapter 3 was to identify differences in biotic and abiotic features between the Ruby and the Kluane Ranges. Although we could not test which of these factors influence relative abundance of Rock and White-tailed Ptarmigan, we discussed how these may affect relative abundance. We found that the Kluane Range had fewer degree days above 0 ºC, a greater mean standard deviation of scaled NDVI, and was overlain with fine textured colluvium. Fewer degree days (0ºC) may indicate delayed snowmelt, which can delay reproduction (Martin and Wiebe 2004) and reduce reproductive success of ptarmigan (Novoa et al. 2008). Increased standard deviation of scaled NDVI could be an indication of a wider distribution of habitat types, such as tall shrub and rock. A greater proportion of tall shrub would reduce the amount of suitable habitat available to

Rock and White-tailed Ptarmigan. Increased rock habitat would likely benefit Rock and White-tailed Ptarmigan, since rocks provide cover from predators and help in thermoregulation during the breeding season (Choate 1963, Weeden 1967, Schmidt 1988, Frederick and Gutierrez 1992, Favron et al. 2006, Zohman and Woss 2008). However, boulders typically need to be greater than 30 cm in diameter to be useful (Choate 1963). So, although the Kluane Range may have a greater proportion of rock cover, it may not provide adequate shelter for ptarmigan.

Relatively few studies have examined spatial variation in abundance of species within their geographic range (Brown et al. 1996). Identifying factors that influence relative abundance can provide information to guide conservation efforts and design management programs in large-scale geographic contexts (Carrascal and Seone 2009). Russel et al. (2005) found that physical features of stream habitats influence distribution and abundance of Cascade torrent salamanders (*Rhyacotriton cascadae*), which would be important for designing conservation management strategies in the Pacific Northwest. Nopp-Mayr and Zohmann (2008) found lower densities of calling cocks of Rock Ptarmigan in the eastern plateau of the Austrian Alps compared to sites in other parts of the range. Nopp-Mayr and Zohmann (2008) attribute this difference to restricted availability of suitable, heterogeneous habitats (Woss and Zohmann 2008) compared to the rest of the Austrian Alps. Studying spatial variation in abundance is useful in identifying areas of conservation and management concern, which is particularly important for drawing conclusions and management plans during times of rapid environmental change (Peterson et al. 2001, Hughes 2003, Rondinini et al. 2005, Ritchie et al. 2008).

This study would have been improved with increased effort and a larger sample size. A larger number of observers would have increased the ability to locate birds and improved density estimates at the different sites. Other survey techniques could be used to estimate population densities, but they would likely ineffective in a large-scale study given the limited access to a majority of these sites. A larger sample size would have allowed for stronger statistical analyses, allowing an improved understanding of the relationship between relative abundance and the broad-scale biotic and abiotic factors of the study sites. Furthermore, a more detailed landcover classification scheme may have provided a better understanding of the differences in habitat structure between the Kluane and Ruby Ranges.

Suggestions for Future Research

Given the potential threat of environmental change to alpine communities (Walther et al. 2002, Pauli et al. 2007), it is important to recognize the factors that influence distribution, abundance and reproduction of alpine animals. Habitat selection studies can identify these factors and address potential threats of changing weather patterns and shifts in vegetation communities (Sturm et al. 2001, Danby and Hik 2007a, 2007b, Grabherr et al. 1994, Klanderud and Totland 2005). Although ptarmigan are not critical to the survival of northern people, they are a managed game species, particularly in Scandanavia, the United Kingdom and other parts of Europe. Even in the Yukon, ptarmigan hunting is subject to bag limits and seasonal limitations (http://environmentyukon.gov.yk.ca/huntingtrapping/documents/hunting_regs_0910web.pdf). More generally, identifying factors that influence their distribution and abundance provides a basis from which to consider how other alpine animals might respond to environmental change, interspecific competition and other influences.

This study examined habitat selection and resource partitioning of Rock and White-tailed Ptarmigan at several different spatial scales, while introducing a new survey technique for estimating population density. Continued research into the diets of Rock and White-tailed Ptarmigan in sympatry and in allopatry would enhance our understanding of resource partitioning between these two species. This could be accomplished by identifying local populations where the two species occur in allopatry or, where logistically feasible, through removal experiments. Furthermore, predator-prey interactions could also be examined and whether these relationships may change with climate change. Surveys to measure relative abundance within a portion of the geographic range could be improved with a greater number of surveys and greater effort. However, there is a need to incorporate reproductive success in these surveys in order to identify source and sink populations.

In summary, this study has extended our knowledge of habitat selection and resource selection of Rock and White-tailed Ptarmigan at several spatial scales. The two species showed resource partitioning at both the foraging area and patch levels. Surveys for both species showed spatial variation in relative abundance between mountain ranges, which could be influenced by mean degree days above 0 ºC, distribution of habitat and local geology and geomorphology. The results presented in this thesis provide insight into species interactions and the relationship between species and their environmental at several spatial scales.

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Appendix I: List of forb species present at study site in the Ruby Ranges, Yukon Territory. Forbs not identified to species level are in bold.

Species
Aconitum delphinifolium
Anemone parviflora
Artemisia norvegica
Aster alpines
Campanula lasiocarpa
Cardamine purpurea
Castilleja hyperborean
Claytonia bostocki
Claytonia sarmentosa
Claytonia tuberose
Dodecatheon frigidum
Draba spp.
Epilobium latifolium
Erigeron pallens
Gentiana algida
Lloydia serotina
Minuartia macrocarpa
Oxyria digyna
Oxytropis spp.
Papaver macounii
Parrya nudicaulis
Pedicularis capitata
Pedicularis lanata
Petasites frigidus
Polemonium acutiflorum
Polygonum bistorta
Polygonum viviparum
Potentilla spp.
Pyrola grandiflora
Ranunculus sulphureus
Saussurea angustifolia viscid
Sax flagellaris
Saxifraga bronchialis
Saxifraga davurica
Saxifraga hieracifolia
Saxifraga nelsoniana porsildiana
Saxifraga oppositifolia
Saxifraga punctata
Saxifraga serpyllifolia
Saxifraga tricuspidata
Sedum rosea
Senecio atropurpureus frigidus
Silene acaulis acaulis
Valeriana captitata

Appendix II: The Ruby Range Landcover Classification Scheme

The Ruby Range landcover classification scheme was created as a means to examine habitat selection of Rock and White-tailed Ptarmigan at the foraging area level. The classification was created using the National Topographic Database Map (NTDB) and the normalized difference vegetation index (NDVI: Tucker and Sellers 1986) calculated using ERDAS from Landsat Thematic Mapper (taken 9 August 2003, 30 m pixels). NDVI values were scaled between 0 and 1, and then multiplied by 255 to convert into 8-bit data. The resulting scaled NDVI values were used in the landcover classification scheme. Landcover classes below treeline were created using the NTDB, while the alpine plant communities were classified using scaled NDVI values. Forest stand characteristics, water and permanent ice/snow were interpreted from aerial photos and stereoscopic imagery at a 1:50 000 scale for the NTDB. The forest inventory map focused on forest cover and it was used for delineating forest cover, while the NTDB was used to classify water and permanent ice/snow. All feature layers were converted to a 30 m pixel raster layer.

In 2007, we conducted vegetation surveys to ground-truth alpine communities for classification. In total, 124 plots were selected from areas with homogeneous vegetation within a 25 m radius as well as locations of encountered ptarmigan. Locations were recorded using a handheld GPS unit with an accuracy of 8 m or less. A site description for the 25 m plot was recorded based on the "Alaska Vegetation Classification Guide" by Viereck et al. (1992). The guide describes Alaskan and Yukon vegetation communities based on dominant and sub-dominant species and their structure at four orders. We recorded the vegetation community at the third and fourth order, and included a percent cover estimate for rock and shrub >1 m in height for the 25 m plot. The size of rock and the species of shrub was also noted. There were six major landcover classifications for the alpine at the third order; ‘rock’ = rock cover that is equal or greater than 50%, ‘Dry’ tundra = *D. octopetala* and lichen dominant (third order; if the sub-dominant species was lichen we also included this as dry tundra), ‘Wet’ tundra = graminoid dominant (third order), ‘open low shrub’ = open canopy (<25%) shrub (<1 m in height) dominant (third order), ‘closed low shrub’ = closed canopy (>25%) shrub (<1 m in height) and ‘tall’ shrub = shrub (>1 m in height) dominant (third order). The designations of ‘dry’ and ‘wet’ tundra were also independently derived by Koh et al. (unpublished data) using ordination.

We intersected the ground-truthed points with the scaled NDVI map and we determined the range of scaled NDVI values for each cover class. We used the natural break-points in the data to associate (place into ‘bins’) the scaled NDVI values within the different vegetation classes. Unfortunately there was no clear break for wet tundra habitat, so some cover classes were merged together: rock (100-153), dry-wet tundra (154-175), wet tundra-open low shrub (176-187), closed low shrub (188-195), and tall shrub (>195). The accuracy of the classification was examined by calculating the proportion of ground-truthed points that were correctly classified (Table A1). Overall, the map correctly classified 77% of the 124 vegetation plots. However, there was a noticeable lack of precision when classifying the rock cover class with mainly dry-wet tundra and wet tundra-open low shrub plots falling within the scaled NDVI range for rock cover. The lack of precision may be explained by the amount of rock cover within these misclassified plots, since the cutoff to be classified as rock was set at 50%.

Table A1: The proportion of correctly classified ground-truthed points based on the cover classification created from scaled normalized difference vegetation index (NDVI) values. Scaled NDVI values were binned into cover classes based on natural breaks in the data. NDVI was calculated from a Landsat Thematic Mapper image (9 August, 2003) in ArcGIS 9.3 (ESRI 2008).

Cover Class	**Scaled NDVI Range**	**Correct**	**Total**	**Proportion Correctly Classified**
Rock	100-153	27	41	0.66
Dry-wet tundra	154-175	43	54	0.80
Wet tundra-open low shrub	176-187	18	20	0.90
Closed low shrub	188-195	9	10	0.82
Tall shrub	>195	NA	NA	NA
Total		**97**	**126**	**0.77**

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