INFLUENCE OF ENVIRONMENTAL VARIATION ON HABITAT
SELECTION, LIFE HISTORY STRATEGIES AND POPULATION DYNAMICS
OF SYMPATRIC PTARMIGAN IN THE SOUTHERN YUKON TERRITORY

by

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ABSTRACT

Climatic variation is an important driver of avian life history and population dynamics. Climate change models predict increased variability for many regions and to predict the effects on species, we need to examine how their life history characteristics influence their response to climate. I studied how environmental conditions influenced the ecology of white-tailed (*Lagopus leucura*) and rock ptarmigan (*L. mutus*) in tundra habitats of the southern Yukon Territory. Although sympatric in the study area, breeding territories were generally segregated, with white-tailed ptarmigan selecting steep, rocky slopes at higher elevations and rock ptarmigan preferring lower elevation sedge meadows. For both species, cold spring temperatures delayed the onset of breeding, resulting in smaller clutch sizes and fewer hatched young per female. However, delayed breeding led to a stronger reduction in these rates for rock ptarmigan, suggesting a lower resilience to extend reproductive effort in colder years. White-tailed ptarmigan were also more likely to re-nest following failure and had higher daily nest survival, both of which contributed to greater annual productivity compared to rock ptarmigan.

Annual adult survival showed the opposite pattern to productivity as rock ptarmigan survival was about 24% higher than white-tailed ptarmigan. This finding suggested a reproduction-survival trade-off exists for the two species, which may be driven by differing susceptibility to environmental factors in the region. Life history theory predicts that if the likelihood of future breeding opportunities is low, individuals should increase current reproductive effort, which may explain why white-tailed ptarmigan have longer breeding seasons and higher reproductive effort under unfavourable climatic conditions. Population models showed that growth rates (λ) were approximately stable for rock ptarmigan (λ=1.01), but declining for white-tailed ptarmigan (λ=0.96). Simulations showed that warmer spring temperatures over the next few decades would elevate λ by ~0.05 for both species, but the extent of increase in λ may be reduced with more variable spring conditions. Population growth will also depend on how changing winter conditions influence survival for each species. Model simulations suggest that if juvenile and adult survival are positively correlated, rock ptarmigan would be more resilient to severe years that simultaneously depress reproduction and survival.
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DEDICATION

This thesis is dedicated to my parents, Mary and Bruce Wilson, who first inspired my love for nature and provided never-ending support throughout my education.
This thesis is written in manuscript-based format with chapters 2 through 5 representing independent chapters that have or will be submitted in a similar format. For all chapters, I took the lead in developing the research program, performing the research, data analysis and manuscript preparation. However, each chapter greatly benefitted from many discussions with my supervisor Kathy Martin, who is a co-author on all of them. Many other individuals also contributed very helpful suggestions to earlier drafts of these manuscripts including (in alphabetical order): Peter Arcese, Stan Boutin, Christian Hagen, Susan Hannon, Greg Henry, Peter Marshall, Shawn Morrison, Brett Sandercock, Carl Walters and Amy Wilson. Chapter 2, on habitat selection, is in press for the Journal of Ornithology. The remaining chapters are either in review or have yet to be submitted.
CHAPTER 1 – GENERAL INTRODUCTION AND THESIS OVERVIEW

Understanding the ecological processes that influence the distribution and dynamics of animal populations requires knowledge of species habitat preferences, life history strategies and what factors affect demography and population dynamics (Krebs 1994, Royama 1992, Sæther and Bakke 2000, Jones 2001). Knowledge on these processes can then be used in applied cases such as harvest management, insect control and protection of endangered species (Royama 1992, Noon and McKelvey 1996, Beissinger et al. 2006). More recently, studies have focused on the potential impacts of climate change on animal populations (Wang et al. 2002, Ludwig et al. 2006, Saltz et al. 2006). Over the past century, global temperatures rose by about 0.6ºC and a further 2-4 degree rise is expected by the end of this century (IPCC 2007). A more substantial increase of 5-7 degrees is expected for some areas such as the Arctic (Hassol 2004). Wildlife within these ecosystems face risks related to the direct effects of climate on behavior and demography, and indirect effects related to change in other aspects of the ecosystem with which they interact (Sala et al. 2000, McCarty 2001).

The habitat requirements of a species are one of the most pivotal aspects affecting their distribution and on a smaller scale, habitat selection has important implications for individual fitness and demography (Cody 1985, Jones 2001). Early models of habitat selection typically correlated habitat characteristics with species abundance (MacArthur and Pianka 1966) and these were followed by models that introduced density effects via the ideal-free and ideal-despotic distribution models (Fretwell and Lucas 1970). Many earlier approaches focused on how selection is influenced by fine scale habitat characteristics, but we now recognize that habitat selection occurs in a hierarchical fashion with initial settlement based on landscape-level features and further refinement dependent on micro-habitat, competition, food abundance and predation pressure (Garcia 1983, Wiens et al. 1987, Jones 2001, Fontaine and Martin 2006). Shifts in plant species distribution are expected as warmer temperatures allow some species to occupy areas that were previously too extreme, while others are excluded because the climate is no longer suitable or because of competition from newly colonizing species (Walther 2003, Walker et al. 2006). If we are to predict how species might be affected by environmental change, we need to understand how they select habitat and the relationship between key habitat variables and demography.
Climate is an important mechanism that can directly influence behavior, fecundity and survival of individuals (reviewed in Newton 1998). Among the reproductive rates, spring temperature is particularly influential in determining annual timing of breeding of north temperate birds and earlier breeding often leads to enhanced reproductive success (Lindberg et al. 1997, Wilson and Arcese 2003, Martin and Wiebe 2004). There is now considerable evidence for an advance in breeding date of many bird species due to rising spring temperatures (Crick et al. 1997, Brown et al. 1999, Parmesan and Yohe 2004). Weather can also affect reproduction through impacts on nest survival and this may be a combination of direct losses related to extreme temperatures or precipitation and indirect effects of weather on predator or prey behavior (Morrison and Bolger 2002, Rodríguez and Bustamente 2003, Collister and Wilson 2007). Juvenile and adult survival are also dependent on climatic conditions outside the breeding season, although the mechanism often depends on the species biology. Some species are particularly influenced by heavy snowfall, which limits access to resources (Greenwood and Baillie 1991, Moynahan et al. 2006), while others are more strongly affected by weather conditions that influence food abundance (Yalden and Pearce-Higgins 1997, Seamans et al. 2002).

Climate is only one aspect of the environment that affects populations and studies must consider the role of other factors. For ground-nesting birds, predators are typically the dominant cause of nest failure (Ricklefs 1969) and thus any study on how reproductive output is affected by climate should simultaneously consider what determines nest predation rates (e.g. Wilson and Arcese 2006). This extends equally to the non-breeding period when climate and predators act on juvenile and adult survival (Valkama et al. 2005). Climatic effects might also interact with or be over-ridden by other processes such as density dependence, age structure or competition (Sætre et al. 1999, Wilson and Arcese 2003, Sæther et al. 2004, Wilson et al. 2007).

Understanding how life history strategies affect population dynamics is also critical for predicting how populations might respond to a changing environment. Species often vary along a life history continuum. At one end are long-lived species with high survival, delayed maturity and low reproductive effort (often labelled as ‘slow’ species), while at the other end are ‘fast’ species with low survival, rapid maturity and high reproductive effort (Stearns 1983, Roff 1992). Species at the slow end tend to be more strongly influenced by fluctuations in adult survival, while fast species are relatively more responsive to variation in the reproductive rates and
juvenile survival (Heppell et al. 2000, Sæther and Bakke 2000, Oli and Dobson 2003). These characteristics also influence the potential growth rates of populations and the degree to which they fluctuate, both of which can affect population persistence (May 1974, Lande 1993, Boyce et al. 2006).

**Thesis objectives**

In this thesis, I examine patterns of habitat selection and the influence of environmental variation on life history strategies, reproduction and population growth rates of sympatric rock and white-tailed ptarmigan in alpine tundra of the southern Yukon Territory, Canada. There has been very little study on the factors influencing vertebrate populations in northern alpine environments, and yet species in these regions inhabit some of the most rapidly changing ecosystems on the planet. Predicting how they might be influenced by climate change requires study on these factors. A unique feature of my thesis is that I can examine all of these aspects for two congeneric species exposed to the same environmental conditions year-round. This provides a much stronger comparative test of how the environment affects habitat selection, life histories and demography of ptarmigan generally. Although my primary focus was to understand the mechanisms affecting these processes, I attempt to integrate these findings with predictions about climate change within the region (e.g. Hassol 2004, Plummer et al. 2006) to suggest potential impacts on these populations.

**Terminology**

Throughout this thesis, I will use the terms weather, climate and environmental conditions. Weather refers to the meteorological conditions (e.g. temperature, precipitation) of an area at a particular point in time. Weather variability refers to the change in these conditions over a given period of time. Climate refers to the weather conditions of an area averaged over a longer period (e.g. years or decades). ‘Environmental conditions’ often has different meanings in different studies. In this thesis, I refer to environmental conditions as the sum of all features representing the environment of a location and this includes climate, degree of seasonality, elevational effects, predator and competitor communities.

**Study area**

The study was conducted in Pika Creek Valley of the Ruby Range Mountains, southwest Yukon Territory (61°13’N, 138°16’W) from 2004 through 2007 (Figure 1.1). The Ruby Ranges
flank the northern edge of the Kluane region at the western end of the boreal forest biome. Local weather patterns are influenced by westerly air flows over the St. Elias Range from the Pacific Ocean and Arctic air from the North (Webber 1974, Krebs and Boonstra 2001). Mean daily temperatures at the site during the breeding period (mid-May to end-July) averaged 8.0°C (sd=1.3, n=4) over the four year study. Site specific winter temperatures were not available, but long-term estimates from the Environment Canada weather station at Burwash Landing (50 km southwest of the study area) indicate average mid-winter (December-February) temperatures of -19°C (sd=3.73, n=35). Burwash Landing is lower in elevation (800m) than Pika Creek (~1650m) and these temperatures may be slightly warmer than those experienced by individuals at the study site. The Kluane region is classified as semi-arid and precipitation is typically less than 30 cm per year, most of which falls as rain during the summer months (Krebs and Boonstra 2001). The study was conducted over 10 km² of alpine and subalpine habitat at 1400-2200 m elevation (Figure 1.2). Chapter 2 provides additional detail on habitat within the study area.

**Study species**

White-tailed (Lagopus leucura), rock (L. muta) and willow ptarmigan (L. lagopus) are upland birds in the family Phasianidae (subfamily Tetraoninae). White-tailed ptarmigan are the smallest of the three (~300-450 g, Braun et al. 1993), followed by rock ptarmigan (400-600 g, Holder and Montgomerie 2008) and willow ptarmigan (500-675 g, Hannon et al. 1998). Males average slightly larger than females in all three species. White-tailed ptarmigan are restricted to western North America from New Mexico through Alaska where they inhabit alpine tundra (Figure 1.3, Frederick and Gutierrez 1992, Braun et al. 1993). Rock and willow ptarmigan have circumpolar distributions; the former typically breeds in sparse alpine and arctic tundra (Holder and Montgomerie 2008), while the latter selects shrubby subalpine and subarctic tundra (Schieck and Hannon 1993, Hannon et al. 1998). Ptarmigan are considered to be resident year-round, although high-arctic rock ptarmigan populations are migratory and individuals can move up to 1000 km in winter (Holder and Montgomerie 2008). In some locations, willow ptarmigan also make migratory movements of up to a few hundred kilometers (Weeden and Ellison 1968, Gruys 1993). All three species frequently move to lower elevations in winter (Weeden 1969, Braun et al. 1993).

All ptarmigan are monogamous, but polygyny is relatively frequent with two or more females on the territory of a single male (Hannon and Martin 1996). Males arrive on the breeding
grounds in mid-late April and establish territories, after which females join them in late April to early May. Females only produce one brood per year, which remain with her until late August to late September. Male willow ptarmigan remain with the female throughout incubation and brood-rearing, while male white-tailed and rock ptarmigan stay on the territory until mid to late incubation after which they leave and join flocks of other males. Individuals of all three species join other individuals to form flocks through fall and winter, and in areas of sympathy these flocks may contain multiple species (Weeden 1969, Braun et al. 1993, Hannon et al. 1998, Holder and Montgomerie 2008).

**General field methods**

A general description of the field methods used throughout this study are provided below with field methods specific to the questions of a particular chapter given there. Field work was conducted from early May through July of 2004-2007. Prior to breeding, individuals of both sexes were caught using ground nets or noose poles, and were color-marked with an aluminum band on one leg and a numbered plastic color band on the other. Females were fit with a 4 or 7 g radio-transmitter (Holohil Inc., Carp, Ontario) to facilitate nest finding. For all individuals, I measured wing length, tail length and mass, and aged them as second-year (SY, 10-11 months) or after-second year (ASY) based on the pigmentation on the primaries and primary coverts following Weeden and Watson (1967) and Braun et al. (1993). For white-tailed and rock ptarmigan, SY birds (prior to their second full body molt) had dark pigmentation on the outer two primaries (P9, P10) and primary coverts, but no pigmentation on P4-P8, the middle primaries. ASY birds had either no pigmentation on any primaries, or the greatest pigmentation on P4-P8. For both rock and white-tailed ptarmigan, ASY males rarely had pigmentation on the middle primaries (rock ptarmigan – 12%, white-tailed ptarmigan – 8%). Among 21 ASY white-tailed ptarmigan females, 5 (23%) had some pigmentation on P4-P8 while the remainder had no primary coloring. In contrast, 35 of 46 (76%) ASY rock ptarmigan females had pigmentation on P4-P8, which was always greater than that on P9 or P10. For rock ptarmigan, this difference between the sexes was similar to that observed in Alaska and Scotland (Weeden and Watson 1967).

During the laying period, females were located every 2 to 4 days until the nest was found, after which it was checked every 2 to 4 days to determine clutch size. An Ibutton temperature logger (Maxim Integrated Products, Dallas, TX) was placed in the side of the nest, which
allowed me to precisely determine the time of failure or hatch. I estimated the date of first egg by observing nests during the laying stage, back-dating from date of hatch or floating a single egg if the nest was found after incubation had begun (Westerkov 1950). I assumed that incubation began with the laying of the penultimate egg, which is typical for most ptarmigan (Wiebe and Martin 1995, Holder and Montgomerie 2008). For most nests, I measured the length and width of 1-3 eggs. During incubation, nests were checked visually every 3-5 days to determine if they were still active. Females were not disturbed on the nest unless we needed to change the Ibutton (every 10-12 days). Nests were monitored more frequently near the expected hatch date to determine the number of chicks hatched and when they left the nest. In 2004 and 2005, we caught the chicks soon after hatch to determine their weight and wing length. Broods were re-located every 3 to 7 days to count the number of chicks and in some cases to capture chicks for additional measurements. If a nest failed, the female was re-located every few days to determine if she re-nested. At the start of the next breeding season, we conducted extensive surveys of the immediate study area and adjacent regions to search for returning adults for estimates of annual survival.

**Chapter descriptions**

My thesis is organized around four empirical chapters discussing habitat selection, the determinants of reproductive success, comparative life history strategies and population dynamics, each written as a stand-alone manuscript. In chapter 1, I introduce the overall objectives of the thesis along with background information on the issues that will be addressed in the data chapters. I also include information on the study area and species, as well as general field methods.

In chapter 2, I examine breeding habitat selection for sympatric rock, white-tailed and willow ptarmigan. I address three main questions: 1) how do the three species segregate in their selection of breeding habitat within a common environment, 2) do habitat selection patterns shift in relation to spring environmental conditions, and 3) within species, how much and what type of cover do females select for nest-sites. I found clear evidence for breeding habitat segregation among the three species, but little tendency for habitat selection patterns to shift depending on spring conditions. This raised the question of whether different habitat preferences of each species influenced their reproductive success and how spring conditions might affect timing of breeding.
In Chapter 3, I examine the factors affecting reproductive success of rock and white-tailed ptarmigan. I first examine how year, time of season, nest age, habitat and temperature affect nest survival with a particular emphasis on whether the habitat differences observed in Chapter 2 lead to differential nest success of rock and white-tailed ptarmigan. I also consider how timing of breeding is affected by spring temperature, which is known to be particularly influential in tundra environments where breeding seasons are short (Lindberg et al. 1997, Martin and Wiebe 2004). I then consider how timing of breeding affects clutch size and the number of young produced, and whether the two species show similar patterns in these relationships. I found no strong effects of habitat type on nest survival but temperature was influential with greater nest survival and earlier breeding under warmer conditions. This analysis also showed that clutch size and the number of hatched young declines more quickly over time for rock ptarmigan than white-tailed ptarmigan, and was one indication of how these two closely related species might have differing life history strategies in the same environment.

Chapter 4 examines how environmental conditions shape life history evolution in ptarmigan. For this analysis, I compare life history and demography of rock and white-tailed ptarmigan in the Yukon with another white-tailed ptarmigan population in Colorado, studied from 1987-1996. This comparison allowed me to focus on two main questions. First, to what extent do life history strategies converge in a common environment? To test this, I compared which reproductive traits and overall life history strategies of white-tailed ptarmigan were more similar to a congeneric species in the same environment than to their own species in a different environment. Second, for those traits that differed between Yukon rock and white-tailed ptarmigan, I examined the potential ecological mechanisms behind those differences. I found two key results: 1) characteristics of the first nesting attempt (clutch size, egg mass and incubation length) tended to be more similar among the two species in the same environment than among white-tailed ptarmigan across environments, 2) even in the same location, white-tailed ptarmigan maintained greater reproductive effort across the breeding period than rock ptarmigan; they did so via larger clutches late in the season and a greater probability of renesting following failure. The latter finding appears to represent a trade-off as rock ptarmigan have higher adult survival, which theory suggests should lead to a reduction in reproductive effort (Stearns 1983, Roff 1992). These life history differences raised the question of whether the two species differ in the influence of demographic rates on population growth.
In Chapter 5, I utilize the findings on life history strategies in chapter 4 and ask how the different strategies of rock (‘slow’ life history) and white-tailed ptarmigan (‘fast’ life history) affect population growth and response to climate change. Using matrix models, I first examined demographic and stochastic growth rates of the two species in the Yukon based on a projection matrix that was parameterized with data collected over the four year study. I then examined how the different life history strategies influence sensitivity and elasticity of each population to fluctuations in the demographic rates and tested predictions on how a change in breeding season climate might influence populations of the two species. A key result was that white-tailed ptarmigan were more sensitive to changes in the reproductive rates, while rock ptarmigan were more sensitive to changes in adult survival. Both species were strongly influenced by fluctuations in juvenile survival. In chapter 6, I summarize the main findings of each chapter, and discuss the implications of these results for our understanding of life history evolution, population ecology, and potential effects of climate change. I also emphasize areas where further study is needed.
Figure 1.1: Location of the study site within the Ruby Range Mountains of the Kluane Lake region, Yukon Territory, Canada (original map produced by Ryan Danby, modified by Scott Wilson).
Figure 1.2: North-facing view of the Ruby Range study area. The photo was taken in early July from the south end of the Pika Creek valley (photo by Scott Wilson).
Figure 1.3: Distribution of rock, white-tailed and willow ptarmigan in North America including areas of overlap, which primarily occurs in the Yukon, southwest Alaska and northwest British Columbia. There were no known areas where rock and white-tailed ptarmigan overlapped in the absence of willow ptarmigan. The study site is noted with a white circle. Ranges in Greenland and Siberia were not included. To generate the figure, I used breeding distribution maps from Ridgley et al. (2005) and incorporated them into ArcGIS 9.0 (ESRI, Redlands, California).
References


CHAPTER 2 – BREEDING HABITAT SELECTION OF SYMPATRIC WHITE-TAILED, ROCK AND WILLOW PTARMIGAN

Introduction

Selection of avian breeding habitat occurs in a hierarchical fashion (Wiens et al. 1987). At landscape levels, settlement may be largely determined by the availability and configuration of suitable habitat features, while at finer scales, selection of a territory may be further influenced by other ecological factors (Cody and Walter 1976, Fontaine and Martin 2006). Interspecific competition among related species (e.g. congeners) can be a particularly important factor affecting breeding habitat selection especially when related species have similar habitat preferences (Alatalo et al. 1985, Bourski and Forstmeier 2000, Kumštátová et al. 2004). Patterns of habitat selection might also vary over temporal or spatial scales (Wiens et al. 1987), such as when yearly fluctuations in environmental conditions (e.g. timing of snowmelt) affect the amount of available habitat at the onset of breeding (e.g. Martin and Wiebe 2004, Madsen et al. 2007). Within territories, breeding females must also select a nest-site within territories and individuals often select locations that offer protection from predators and climatic factors (Martin 1992, Etterson et al. 2007). Identifying how individuals select habitat at different scales has implications for predicting the effects of vegetation change on populations.

I examined breeding habitat selection of white-tailed (Lagopus leucura), rock (L. muta) and willow ptarmigan (L. lagopus) at a site where all three co-exist in the southern Yukon Territory, Canada. Previous studies have examined habitat selection where these species exist individually, but there are almost no detailed studies on how all three segregate in a common environment (but see Weeden 1959). The three species overlap from northern British Columbia through south-central Alaska where competition may limit the range of habitat used by each (e.g. Garcia 1983, Kumstatova et al. 2004). Willow ptarmigan are socially dominant over rock ptarmigan in areas of sympatry (Moss 1972), but the latter avoid dense shrubs during breeding, which may lower competition. Rock and white-tailed ptarmigan select habitats with similar structure, providing the potential for increased competition for breeding territories where they co-exist.

1 A version of this chapter has been accepted for publication.
I first compared how topographic and vegetation features differed among nest-sites of each species as an indication of territory level habitat differences across the study area. Interspecific habitat selection is more likely related to initial settlement and competition among males, but as I show, the habitat around nests within territories is a reliable measure of differences between species. To better understand what might lead to interspecific patterns, I also conducted a restricted analysis between white-tailed and rock ptarmigan across a narrow elevational zone where they are present in equal abundance. My second objective tested the hypothesis that individuals adjust habitat preferences when the availability of habitat varies among years. During the study, the Kluane area of the southwest Yukon territory experienced the warmest spring in nearly four decades in 2005 and a colder than normal spring in 2006. These temperature differences had marked effects on timing of spring snowmelt between years and provided a unique natural experiment to test whether individuals shift to different habitat or delay breeding when there is heavy snow cover early in the season. My final objective examined how females select nest sites with respect to cover and vegetation within territories. When compared against environmental conditions, intraspecific comparisons of nest and random sites can provide insight into why females select particular sites (Wiebe and Martin 1998).

Methods

Study area habitat

The upper subalpine zone at approximately 1400-1500 m contained large patches of tall shrubs (> 15 cm, primarily tealeaf willow (Salix pulchra), grayleaf willow (S. glauca) and scrub birch (Betula glandulosa)) interspersed with lower vegetation (e.g. sedges (Carex spp.)) and small wetlands. The zone from 1500 m to 1750 m was a transition from subalpine to high alpine and consisted of meadows of sedges, grasses and rushes, mixed with smaller patches of tall shrubs, rock outcrops and dwarf shrubs (<15 cm). Higher elevation habitats above 1750m have few tall shrubs and are dominated by rocky areas mixed with low vegetation, mostly dwarf shrubs and lichens. Common dwarf shrubs at the study site included white mountain avens (Dryas octopetala), net-leaved willow (Salix reticulata), polar willow (S. polaris) and arctic willow (S. arctica). These dwarf shrubs were typically less than 3 cm in height with most of their woody base underground. Smaller patches of four-angled mountain heather (Cassiope tetragona) and moss were interspersed throughout the site. Over the three years, densities of rock and white-
tailed ptarmigan respectively ranged from about 4-5 and 2-3 pairs/km². Willow ptarmigan were only located on approximately 10-15% of the study area at about 3 pairs/km².

**Habitat sampling**

Nest habitat was measured on a 10 m diameter plot around each nest. Ptarmigan leave the nest immediately after hatch and nest habitat was measured within 7 days of hatch for successful nests or the expected date of hatch for failed nests. For each nest, I also measured habitat at a random site within the territory. The random site was selected by standing at the center of the nest plot and spinning a compass to determine a distance and direction from the nest plot. For the random site, I made a depression similar to the shallow scrape females construct for their nest prior to measurement.

I first measured topographic features including elevation (m), slope aspect (from 0° to 360°) and angle of the slope (degrees). I also measured distance to shrubs <1 m in height, >1 m in height, rock (continuous cover >1 m²) and standing water. To measure overhead and lateral cover, I placed a cloth the size of an incubating female in the nest scrape. Overhead cover was estimated as the percent of the cloth obstructed when looking down on the nest from 1 m, and lateral cover as the average percent of the cloth concealed when looking at the nest from each of the four cardinal directions at a height of 0.3 m above the ground and 1 m from the nest. I chose lateral cover as an index rather than vegetation height because in tundra, lateral cover often includes rock and natural undulations. For all sites containing shrubs within 1 m of the plot center, I measured stem density as the number of stems less than or greater than 2.5 cm in diameter at a height of 10 cm. For plots with tall shrubs, I measured 5-10 individuals to estimate mean shrub height.

Percent cover within the plot was visually estimated for water, rock, bare ground, moss, heather, lichens (not included if on rock), sedges, grasses, rushes, tall shrubs (minimum height ≥ 15 cm), dwarf shrubs (maximum height < 15 cm) and forbs. For this analysis, I pooled grasses (Poaceae), sedges (Cyperaceae) and rushes (Juncaceae) as ‘graminoids’. Sedges were the most common graminoid with several species of the *Carex* genus present at the site. Percent cover refers to the top vegetation layer and where tall shrubs were present, the composition of the ground layer under the shrubs would not be included. I identified lichen, heather, dwarf shrubs, tall shrubs and forbs to genus or species where possible. It was difficult to identify graminoids
and mosses to genus or species across the entire plot and therefore I only identified them to functional groups.

**Temperature and snowmelt**

To evaluate the influence of spring conditions on habitat selection in 2005 and 2006, I obtained daily temperature data for April and May from the Environment Canada weather station located at Burwash Landing (http://climate.weatheroffice.ec.gc.ca/climateData). April and May represents the pre-breeding period when individuals return to territories and initiate breeding, and is when daily temperature will have the greatest influence on rate of snowmelt. I took photographs of the study area every five days, which were used to estimate the approximate date at which 50% snow cover remained.

**Statistical analyses**

I used standard logistic regression under a model-selection framework to compare breeding habitat of white-tailed and rock ptarmigan (Hosmer and Lemeshow 2000, Burnham and Anderson 2002). Given the smaller sample size, I only examined habitat selection of willow ptarmigan using descriptive statistics. For all species, I used the initial attempt for a female in a particular year to avoid the confounding effects of seasonal change in vegetation on nest site selection. Because nest-site selection is restricted to areas within the territory, I only used multiple attempts for females between years if they switched territories. This was the case for six rock ptarmigan and three white-tailed ptarmigan. Separate analyses without these multiple attempts produced the same results and therefore, I used the larger data set for interpretation. For interspecific comparisons, I modeled white-tailed ptarmigan nests as a “success” (1) and rock ptarmigan as a “failure” (0). Positive and negative coefficients for a variable indicate association with white-tailed or rock ptarmigan breeding sites respectively. I also used logistic regression to compare whether habitat selection of each species differed between a warm year with early snowmelt and a cold year with late snowmelt. Densities of each species were similar between those two years (rock ptarmigan: ~ 4.5 pairs/km², white-tailed ptarmigan: ~ 2.5 pairs/km²).

An assumption of standard logistic regression is that any habitat within the study area is available, but this is not the case in territorial species where nest sites are limited to locations within the territory (Jones 2001). Thus, for intra-specific comparisons of nest versus random sites, I used paired logistic regression (Compton et al. 2002). With this method, the response variable is a vector of 1’s and is regressed on a matrix of predictor variables measured as the case
(nest) – the control (random site). An intercept term is excluded from the model. A positive coefficient in this case suggests a particular variable tends to be associated with the nest site.

For analyses I also report the odds ratio (OR) for a variable, which gives the odds of an event occurring in one group relative to the odds in the other group. For continuous predictor variables the odds ratio is estimated as $OR = \exp(c\beta_i)$ where $c$ represents a meaningful change in the predictor variable and $\beta$ describes the relation between the predictor and the response variable (Hosmer and Lemeshow 2000). Global models were tested for goodness of fit using a modified version of the Hosmer-Lemeshow GOF test (Hosmer et al. 1997). All tests were performed using the R statistical language and environment (R Development Core Team, 2006).

**Selection of candidate models**

My aim was to identify models that separate key topographic and habitat features. I first added elevation, slope and aspect representing potential landscape-level effects on habitat selection. To the top models containing these three topographic features, I added the six cover variables: graminoids, rock, dwarf shrubs, tall shrubs, heather and lichens. An intercept only model was also included in standard logistic regression analyses, which if supported would indicate none of the variables were influential in predicting habitat selection. For each analysis, I examined correlation coefficients among variables across plots and if $r$ was $> 0.60$, I only included one member of the pair in a particular model. The variable that led to greater support individually was then used for subsequent models. I did not include forbs, shrub height, stem density or overhead cover in the models because either their abundance varied seasonally (e.g. forbs) or the majority of plots had zero entries.

For nest-random site analyses, I used the results of interspecific comparisons to construct candidate models believed to represent the range of available cover types on the territories of each species, as well as lateral cover. I intended to include overhead cover but most comparisons had a value of 0 (i.e. no overhead cover for the nest or the random plot) and it was difficult to fit models containing this variable. Akaike’s information criterion for small samples (AICc, Burnham and Anderson 2002) was used for model selection, and I used the $\Delta$AICc and Akaike weights ($w_i$) to infer support for different models. Because there was no evidence of lack of fit or overdispersion, I chose AICc rather than Quasi AICc, which is recommended if overdispersion is an issue (Burnham and Anderson 2002). Parameter estimates were determined using model averaging.
Results

Interspecific nest-site selection

For regression analyses, I compared 23 candidate regression models using 43 white-tailed ptarmigan nests from 39 females and 58 rock ptarmigan nests from 52 females (Table 2.2a). All top models contained elevation (combined $w_i = 1$), slope (combined $w_i = 1$), and percent cover of graminoids (combined $w_i = 0.86$). The addition of lichens also improved model support but to a lesser extent (combined $w_i = 0.79$). Coefficients and odds ratios indicated that white-tailed ptarmigan breeding sites tended to be at higher elevations, on steeper slopes and located amidst greater lichen cover, whereas rock ptarmigan preferred to breed at lower elevations and in areas of higher graminoid cover (Table 2.3, Figure 2.1a,b). Rock cover was also higher on white-tailed ptarmigan than rock ptarmigan territories (Table 2.1), but because of negative correlations between graminoid and rock ($r = -0.541$), there was less support for models that included both. Rock ptarmigan territories tended to have greater tall shrub cover than white-tailed ptarmigan (but less than willow ptarmigan, see below). Both rock and white-tailed ptarmigan more often selected sites on the northeastern slopes of the valley, which have a southwestern aspect, although there was variability (white-tailed ptarmigan $\bar{x} = 168^\circ$, angular deviation $= 100.7^\circ$; rock ptarmigan $\bar{x} = 199^\circ$, angular deviation $= 85.8^\circ$). Willow ptarmigan were most common in subalpine habitat at lower elevations and on flatter slopes than white-tailed or rock ptarmigan (Table 2.1). Ground cover on willow ptarmigan territories was dominated by tall shrubs mixed with open patches of graminoids, dwarf shrubs, heather and small wetlands. Shrub cover on these territories contained taller Salix spp. with an open understory, and dense patches of low Betula glandulosa (scrub birch).

Some habitat variables were correlated with elevation, and to test if preferences for slope and ground cover were consistent across elevations, I conducted a second analysis using white-tailed and rock ptarmigan nests located within the 1725 m – 1825 m elevational zone where the two species frequently overlapped in distribution (Table 2.2b). Within this 100 m zone there were 22 white-tailed ptarmigan and 20 rock ptarmigan nests with a mean elevation of 1778 m for the former and 1759 m for the latter. I compared 11 models and found that slope, rock and graminoids were the best predictors of differences within this range. Addition of graminoid and rock together did not enhance model support, suggesting these two variables explain similar
variation \((r=-0.56\) for rock and graminoids in this analysis). On average, white-tailed ptarmigan within this zone nested on steeper slopes \((\beta_{\text{slope}} = 0.15 \pm 0.06 \text{ (SE)})\) and with greater rock \((\beta_{\text{rock}} = 0.041 \pm 0.02)\) and lower graminoid cover \((\beta_{\text{gramin}} = -0.085 \pm 0.05)\) compared to rock ptarmigan. There was no evidence that cover of tall shrubs, dwarf shrubs, lichens or heather differed among the two within this zone. Overall, these patterns suggest that white-tailed ptarmigan consistently select steeper slopes and the two maintain ground cover preferences even within the same elevational zone.

**Influence of spring conditions on breeding habitat selection**

Spring temperatures varied considerably between 2005 and 2006. Mean April-May temperatures were 4.9°C in 2005 and were the warmest of any year from 1970-2006 (average = 1.99°C). In contrast, mean April-May temperatures were colder than average at 1.7°C in 2006 \((z\text{-score deviate 2005: 1.72, 2006: -0.15})\). These conditions in turn influenced timing of snowmelt. In 2005, I estimated 49% snow cover on 2 May (the first field day), and 50% snow cover on 26 May in 2006. The mean date of first egg for 2005 and 2006 respectively was 19 May and 8 June for white-tailed ptarmigan, and 21 May and 3 June for rock ptarmigan.

For white-tailed ptarmigan, I compared 15 models with 17 nests in 2005 and 21 in 2006, and found that the intercept only model had the greatest support (Table 2.4a). For rock ptarmigan, I compared 16 models with 20 nests in 2005 and 25 in 2006. The top model included dwarf shrubs with a tendency for higher dwarf shrub cover around nest sites in the later year \((\text{estimate with SE: } 0.034 \pm 0.025)\). However, the intercept only model had equal weight and the improvement in log likelihood with dwarf shrubs was slight. Overall, these results suggest there was little tendency for breeding habitat of either species to shift in response to annual variation in climatic conditions. Angular deviation in aspect was lower in 2006 for both species \((\text{white-tailed ptarmigan: 104.8 (2005) vs 93.4 (2006); rock ptarmigan: 94.3 (2005) vs 82.5 (2006)})\), suggesting a weak tendency for nests to be less evenly distributed throughout the study site in cold years.

**Intraspecific nest-site selection**

To examine white-tailed ptarmigan nest-site selection within territories, I used 35 nest-random site-pairs and 12 candidate models. Females selected areas with higher lateral cover, on average 30% greater than random-sites (Table 2.4b, 2.5). The estimate for lateral cover was \(0.082 \pm 0.029\) and the odds ratio with \(c=5\%\) was 1.51 \((95\% \text{ CI: 1.23 to 1.80})\). The inclusion of other habitat variables led to little improvement in model support. For rock ptarmigan, I used 53
nest-random site pairs and compared 14 models. As with white-tailed ptarmigan, only lateral cover appeared to differ between nest and random sites, with nest-sites having on average 24% greater lateral cover than random-sites (Table 2.4b, 2.5). The estimate for lateral cover was 0.076 ± 0.020 SE and the associated odds ratio with c=5% was 1.46 (95% CI: 1.26 to 1.66). Willow ptarmigan nest-sites had on average 50% greater lateral cover than random sites. They also selected sites with higher stem density, but a lower shrub height (Table 2.5), which was largely due to a preference for nesting in dense scrub birch (Betula glandulosa), rather than taller and more open willows (Salix spp.).

Discussion

Interspecific nest-site selection

Selection of habitat at the territory level is likely the result of initial settlement and competition among males who establish territories in late April before the arrival of females. Although my plots were centered around nest sites, random selection of a site within the territory allowed me to infer territory-level habitat features based on those plots (but see below for willow ptarmigan). Based on modeling and descriptive statistics, habitat segregation was most evident by elevation, slope and ground cover. White-tailed ptarmigan typically bred on steeper slopes in high alpine habitat with a mixed cover of rock and low vegetation (e.g. lichen, dwarf shrubs). Rock ptarmigan territories were more often in lower alpine meadows at intermediate elevations, with a ground cover of graminoids interspersed with rock, tall shrubs and heather. Willow ptarmigan bred in upper subalpine habitat at the lowest elevations where the ground cover was dominated by tall shrubs. Willow ptarmigan tended to nest in dense scrub birch, potentially biasing territory level inference. In general, willow ptarmigan territories had an equal mix of scrub birch, taller and more open willows, and open meadows.

At elevations of approximately 1725-1825 m, white-tailed and rock ptarmigan overlapped with equal abundance. Yet, patterns of selection by slope and ground cover in this zone were similar to those found over the entire study site suggesting that rock and white-tailed ptarmigan maintain their habitat preferences even when nesting in close proximity. Species-specific preferences for different micro-habitats would allow overlap in areas where both features are present. In Italy, where great reed (Acrocephalus arundinaceous) and marsh warblers (A. palustris) are sympatric, the former defends territories against the latter but the two have
different habitat preferences that reduce competition (Rolando and Palestrini 1989). Sympatric coexistence via habitat segregation was also observed between tree (Anthus trivialis) and meadow pipits (A. pratensis) in the Czech Republic (Kumštátová et al. 2004).

Segregation between rock and white-tailed ptarmigan might be enhanced by interspecific territoriality as observed previously for other sympatric avian congeners (Cody and Walter 1976, Garcia 1983, Rolando and Palestrini 1989). Because my study was observational, I am uncertain on the extent to which either species would expand their niche width in the absence of the other.

Males of the two species were aggressive to one another during the pre-breeding period with frequent chases following territory intrusion. Because rock ptarmigan males are highly mobile during pre-breeding (due to their flight displays), it was more common for white-tailed ptarmigan males to chase intruding rock ptarmigan but I also observed the reverse in several cases. Ptarmigan males remain near females during pre-breeding and these chases may also have been related to mate guarding. These interactions combined with the potential to use similar habitats (see Table 2.1) suggest that interspecific competition likely contributes to a more restricted niche width for each. In Colorado, white-tailed ptarmigan are the only species present and appear to have a greater niche width, nesting from treeline to the upper limits of vegetative cover (Braun et al. 1993, Wiebe and Martin 1998, see also Frederick and Gutierrez 1992). In the European Alps where rock ptarmigan are the only grouse present, Favaron et al. (2006) showed that territories were equally common in high altitude grassland, dwarfshrub vegetation and debris/early pioneer vegetation. This range of habitat appears to be greater than at my site but caution is required as studies differ in habitat classification and habitat structure varies among geographic locations. Weeden (1967, 1969) studied all three ptarmigan species in Alaska and showed that different bill morphologies and winter diets likely reduce competition outside the breeding period. However, summer diets are much more varied and it is not clear that breeding habitat segregation would be influenced by food abundance, particularly for white-tailed and rock ptarmigan. My observations suggest that these two species select similar foods in summer, although dependent on availability within territories (unpublished data). Overall, it would appear that ptarmigan habitat selection in this region is shaped by species-specific habitat preferences and interspecific territoriality but further study would be useful. Removal experiments might allow for an examination of how one species expands its niche width in the absence of another, although this might be logistically difficult with continuous populations and constant
replacement of individuals. An alternative would be to use density as a covariate and examine how niche width changes with natural fluctuations in the abundance of a competitor.

**Does annual variability in spring climate influence breeding habitat selection?**

Understanding whether birds shift among habitats in response to environmental change is particularly important given that spring conditions in many areas are expected to become more variable with climate change (IPCC 2007). I examined whether individuals adjusted their habitat selection between a warm and a cold year with more than a three week difference in timing of snowmelt. If birds shift among habitats during late years, we might expect a movement to lower elevations or a greater concentration in snow-free areas. Although I found a slight tendency for territories to be more concentrated on warmer, south-facing slopes during the cold year, there was no adjustment by elevation or ground cover. In contrast, individuals delayed breeding until habitat was available (see Chapter 3). Other studies on grouse have observed greater concentration in snow-free areas during years of late snowmelt (Weeden 1959, Martin and Wiebe 2004), but in general, delayed breeding rather than a shift in habitat appears to be a more common response for ground-nesting tundra birds (Hannon et al. 1992, Clarke and Johnson 1992, Hendricks 2003, Madsen et al. 2007). A delay may also be necessary because snow cover reduces available forage, which may increase the amount of time females need to build energetic reserves prior to breeding (Clarke and Johnson 1992, Martin and Wiebe 2004).

**Intraspecific nest-site selection**

Within territories, females must select nest-sites that offer protection from predators and weather. Weather extremes can be severe in open environments, which may affect hatching success or chick survival (Webb 1987), and can increase thermoregulatory costs of incubating females (Wiebe and Martin 1997). Individuals can compensate by selecting nest-sites with a favorable orientation (With and Webb 1993, Nelson and Martin 1999) and this has been found to influence hatching success (Burton 2006). In my study it was not possible to measure nest orientation because the scrapes ptarmigan use do not face an obvious direction. However, using video cameras, I observed that females often switch directions during incubation (S. Wilson, unpublished data), which may allow them to compensate for changes in wind direction and the angle of solar radiation throughout the day. The tendency for females to nest on warmer west or south facing slopes would also offer thermoregulatory benefits.
Nest-site cover is another means to increase protection from unfavorable weather and I found that all three species selected sites with higher lateral cover than expected at random. This finding is similar to that of other ground nesting birds (Davis 2005), including grouse and ptarmigan (Schieck and Hannon 1993, Campbell et al. 2002, Holloran et al. 2005). Greater nest-site cover may also reduce exposure to predators by lowering visibility of the female or reducing dispersion of her scent (Wiebe and Martin 1998). Higher lateral cover had a slight positive influence on daily nest survival (Chapter 3). Some studies have also suggested that the benefits of nest cover may represent a tradeoff between nest and adult survival with intermediate levels representing an optimal scenario that provides some nest protection while allowing females to avoid detection and ambush by predators (Götmark et al. 1995, Wiebe and Martin 1998).

While lateral cover was important, white-tailed and rock ptarmigan showed no tendency to select particular features (i.e. different ground cover types) for a nest-site within territories. Although sample sizes were small, willow ptarmigan appeared more likely to nest in patches of low scrub birch rather than taller willows, likely because willow has a more open understory and nests would be more exposed to mammalian predators. At Chilkat Pass, British Columbia, approximately 200 km south of my study area, willow ptarmigan selected areas with higher lateral cover but showed no tendency for specific vegetation types (Schieck and Hannon 1993). Within the alpine zone, there may be less variation in how different ground cover types within a territory influence nest success, perhaps explaining why white-tailed and rock ptarmigan did not select particular features other than higher lateral cover.

**Potential implications of climate change on availability of ptarmigan habitat**

Climate warming is expected to have dramatic effects on availability and distribution of arctic and alpine tundra (Hassol 2004) and these impacts will almost certainly influence ptarmigan nesting habitat. Observational studies indicate a latitudinal and altitudinal advance of conifers and tall shrubs throughout the northern hemisphere (Tape et al. 2006, Danby and Hik 2007) and model projections suggest a 40% reduction of current tundra by the end of the century (Hassol 2004). Experimental studies report that warmer temperatures and nutrient addition lead to increased abundance and/or richness of graminoids, often at the expense of more specialized plant groups such as Dryas and lichens (Klanderud and Totland 2005, Walker et al. 2006). In certain environments, more complex interactions may arise. Shrub growth is greater in low arctic/mesic habitats than in high arctic/xeric habitats, likely because the latter has lower soil
nutrient availability and moisture, which limits growth (Svoboda and Henry 1987, Walker et al. 2006). The effects in alpine tundra are also influenced by elevation, slope and aspect which affect plant community composition and the response to changes in temperature or nutrients. As a consequence, the advance of tall shrubs and conifers into the alpine zone will likely be more rapid on warmer, south-facing slopes (Danby and Hik 2007).

Predicting how such changes will influence ptarmigan is complex, but some general patterns appear likely. In the short term, warmer spring temperatures may increase the availability of breeding sites for ptarmigan if earlier snowmelt opens up habitat on north-facing slopes. Over time frames long enough to affect an altitudinal advance of tall shrub cover, I predict that a) nesting habitat of willow ptarmigan will increase in extent and rise in elevation, b) rock ptarmigan breeding habitat will shift to the upper alpine zone and c) white-tailed ptarmigan may decline in abundance or, perhaps more often inhabit NE slopes where vegetation change may be slower. Overall, these changes have the potential to increase interspecific competition to the degree that rock and white-tailed ptarmigan are forced to share an alpine zone that is reduced in extent. If tall shrubs are more responsive to change in mesic than other habitats (Walker et al. 2006), we may also expect a more abrupt transition from shrub to non-shrub habitat to develop, at the cost of a reduction in the extent of low alpine meadows. Although speculative, these scenarios represent potential outcomes given current understanding of climate warming and change in tundra habitats.
Table 2.1. Nest-site characteristics of rock, white-tailed and willow ptarmigan in the Ruby Range Mountains of the Southern Yukon Territory, 2004-2006.

<table>
<thead>
<tr>
<th>Species</th>
<th>White-tailed ptarmigan (n=44)</th>
<th>Rock ptarmigan (n=58)</th>
<th>Willow ptarmigan (n=7)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>StDev</td>
<td>Range</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1826.9</td>
<td>106.0</td>
<td>1585-2052</td>
</tr>
<tr>
<td>Slope (deg)</td>
<td>29.8</td>
<td>11.4</td>
<td>10-63</td>
</tr>
<tr>
<td>Dist woody shrub (m)</td>
<td>72.8</td>
<td>88.0</td>
<td>0-300</td>
</tr>
<tr>
<td>% nests with shrubs within 1m</td>
<td>19%</td>
<td>34%</td>
<td></td>
</tr>
<tr>
<td>Mean # stems within 1m</td>
<td>15.1</td>
<td>11.7</td>
<td>1-34</td>
</tr>
<tr>
<td>Mean shrub height (m)</td>
<td>0.29</td>
<td>0.16</td>
<td>0.12-0.58</td>
</tr>
<tr>
<td>% rock</td>
<td>34.2</td>
<td>24.0</td>
<td>0-83</td>
</tr>
<tr>
<td>% graminoids</td>
<td>12.7</td>
<td>7.6</td>
<td>3-40</td>
</tr>
<tr>
<td>% tall shrubs</td>
<td>1.5</td>
<td>3.7</td>
<td>0-16</td>
</tr>
<tr>
<td>% dwarf shrubs</td>
<td>23.3</td>
<td>17.4</td>
<td>3-61</td>
</tr>
</tbody>
</table>
Table 2.1 (continued). Nest-site characteristics of rock, white-tailed and willow ptarmigan in the Ruby Range Mountains of the Southern Yukon Territory, 2004-2006.

<table>
<thead>
<tr>
<th>Variable</th>
<th>White-tailed ptarmigan (n=44)</th>
<th>Rock ptarmigan (n=58)</th>
<th>Willow ptarmigan (n=7)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>StDev</td>
<td>Range</td>
</tr>
<tr>
<td>% lichens</td>
<td>12.9</td>
<td>9.6</td>
<td>1-36</td>
</tr>
<tr>
<td>% heather</td>
<td>5.6</td>
<td>10.1</td>
<td>0-37</td>
</tr>
<tr>
<td>% forbs</td>
<td>4.1</td>
<td>2.4</td>
<td>1-12</td>
</tr>
</tbody>
</table>

* Only calculated for nests with shrub cover within 1 m
* Based on shrubs within 5 m of the nest (m)
* % cover for all types determined from a 5 m radius plot centered at the nest
Table 2.2. Model selection results for nest habitat comparisons of rock ptarmigan and white-tailed ptarmigan across a) the entire study site and b) the 1725-1825 m elevational range, in the southern Yukon Territory, 2004-2006. k is the number of parameters, Log_e(L) is the log-likelihood, AIC_c is Akaike’s Information Criterion for small samples, ΔAIC_c is the scaled AIC_c relative to the top model, w_i are the Akaike weights. For a) and b), we only show models with w_i > 0.05 but also include an intercept only (null) model as a control. Elev=elevation, Slope = slope angle, Gramin=% graminoid cover, Rock = % rock cover, Tshrub = % tall shrub cover, Lichen = % lichen cover, Heather = % heather (Cassiope tetragona) cover. See text for additional detail.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Log_e(L)</th>
<th>AIC_c</th>
<th>ΔAIC_c</th>
<th>w_i</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Entire study site</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elev+Slope+Gramin+Lichen</td>
<td>5</td>
<td>-33.89</td>
<td>78.39</td>
<td>0.00</td>
<td>0.31</td>
</tr>
<tr>
<td>Elev+Slope+Gramin+Heather+Lichen</td>
<td>6</td>
<td>-32.80</td>
<td>78.46</td>
<td>0.07</td>
<td>0.30</td>
</tr>
<tr>
<td>Elev+Slope+Gramin</td>
<td>4</td>
<td>-36.04</td>
<td>80.49</td>
<td>2.10</td>
<td>0.11</td>
</tr>
<tr>
<td>Elev+Slope+Rock+Lichen</td>
<td>5</td>
<td>-35.14</td>
<td>80.90</td>
<td>2.51</td>
<td>0.09</td>
</tr>
<tr>
<td>Elev+Slope+Gramin+Tshrub</td>
<td>5</td>
<td>-35.65</td>
<td>81.91</td>
<td>3.52</td>
<td>0.05</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-68.89</td>
<td>139.82</td>
<td>61.43</td>
<td>0.00</td>
</tr>
<tr>
<td><strong>b) 1725-1825 m elevational range</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Slope+Rock</td>
<td>3</td>
<td>-18.82</td>
<td>44.26</td>
<td>0.00</td>
<td>0.35</td>
</tr>
<tr>
<td>Slope+Gramin</td>
<td>3</td>
<td>-18.93</td>
<td>44.48</td>
<td>0.22</td>
<td>0.31</td>
</tr>
<tr>
<td>Slope+Gramin+Rock</td>
<td>4</td>
<td>-18.10</td>
<td>45.25</td>
<td>1.00</td>
<td>0.21</td>
</tr>
<tr>
<td>Slope</td>
<td>2</td>
<td>-21.41</td>
<td>47.12</td>
<td>2.87</td>
<td>0.08</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-29.70</td>
<td>61.50</td>
<td>17.24</td>
<td>0.00</td>
</tr>
</tbody>
</table>
Table 2.3. Model averaged parameter estimates and odds ratios (with 95% CI) from interspecific nest habitat comparisons (Table 2a) in the Yukon Territory, Canada, 2004-2006. For logistic regression, white-tailed ptarmigan nest sites were assigned a 1 and rock ptarmigan a 0.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Parameter ± SE</th>
<th>Odds Ratio (OR)</th>
<th>95% CI for OR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>0.011 ± 0.004</td>
<td>1.316 (25m)</td>
<td>1.120 to 1.512</td>
</tr>
<tr>
<td>Slope</td>
<td>0.162 ± 0.045</td>
<td>1.382 (2 deg)</td>
<td>1.205 to 1.559</td>
</tr>
<tr>
<td>Graminoids</td>
<td>-0.118 ± 0.035</td>
<td>0.702 (3%)</td>
<td>0.461 to 0.942</td>
</tr>
<tr>
<td>Lichens</td>
<td>0.098 ± 0.048</td>
<td>1.103 (1%)</td>
<td>0.927 to 1.280</td>
</tr>
</tbody>
</table>
Table 2.4. Model results for selected habitat features for a) warm (2005) vs cold (2006) springs, and b) nest versus random sites for white-tailed and rock ptarmigan in the southern Yukon Territory. For both a) and b) most variables had little influence on the log-likelihood and so we only show the models within 2AICc units of the top model. Variable names are as for Table 2-2. Lateral = % lateral cover. Matched pair logistic regression was used for nest-random comparisons and does not include an intercept.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Loge(L)</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Warm vs cold spring comparisons</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>White-tailed ptarmigan</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-26.13</td>
<td>54.37</td>
<td>0.00</td>
<td>0.18</td>
</tr>
<tr>
<td>Tshrub+Elev</td>
<td>3</td>
<td>-25.32</td>
<td>54.98</td>
<td>0.61</td>
<td>0.14</td>
</tr>
<tr>
<td>Tshrub</td>
<td>2</td>
<td>-25.60</td>
<td>55.54</td>
<td>1.17</td>
<td>0.10</td>
</tr>
<tr>
<td>Elev</td>
<td>2</td>
<td>-25.68</td>
<td>55.70</td>
<td>1.33</td>
<td>0.09</td>
</tr>
<tr>
<td>Gramin</td>
<td>2</td>
<td>-25.95</td>
<td>56.24</td>
<td>1.87</td>
<td>0.07</td>
</tr>
<tr>
<td><strong>Rock ptarmigan</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dshrub</td>
<td>2</td>
<td>-29.82</td>
<td>63.92</td>
<td>0.00</td>
<td>0.16</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-30.91</td>
<td>63.92</td>
<td>0.00</td>
<td>0.16</td>
</tr>
<tr>
<td>Rock</td>
<td>2</td>
<td>-30.39</td>
<td>65.06</td>
<td>1.14</td>
<td>0.09</td>
</tr>
<tr>
<td>Elev</td>
<td>2</td>
<td>-30.78</td>
<td>65.85</td>
<td>1.93</td>
<td>0.06</td>
</tr>
<tr>
<td>Aspect</td>
<td>2</td>
<td>-30.79</td>
<td>65.86</td>
<td>1.94</td>
<td>0.06</td>
</tr>
<tr>
<td>Slope</td>
<td>2</td>
<td>-30.80</td>
<td>65.89</td>
<td>1.97</td>
<td>0.06</td>
</tr>
<tr>
<td><strong>b) Nest-random models</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>White-tailed ptarmigan</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral</td>
<td>1</td>
<td>-10.94</td>
<td>24.00</td>
<td>0.00</td>
<td>0.26</td>
</tr>
<tr>
<td>Lateral+Lichen</td>
<td>2</td>
<td>-9.89</td>
<td>24.16</td>
<td>0.15</td>
<td>0.24</td>
</tr>
</tbody>
</table>
Table 2.4 (continued). Model results for selected habitat features for a) warm (2005) vs cold (2006) springs, and b) nest versus random sites for white-tailed and rock ptarmigan in the southern Yukon Territory. For both a) and b) most variables had little influence on the log-likelihood and so we only show the models within 2AICc units of the top model. Variable names are as for Table 2-2. Lateral = % lateral cover. Matched pair logistic regression was used for nest-random comparisons and does not include an intercept.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>$\text{Log}_e(L)$</th>
<th>$\text{AIC}_c$</th>
<th>$\Delta\text{AIC}_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lateral+Gramin</td>
<td>2</td>
<td>-10.27</td>
<td>24.92</td>
<td>0.91</td>
<td>0.16</td>
</tr>
<tr>
<td>Lateral+Dshrub</td>
<td>2</td>
<td>-10.39</td>
<td>25.16</td>
<td>1.15</td>
<td>0.15</td>
</tr>
<tr>
<td>Lateral+Heather</td>
<td>2</td>
<td>-10.72</td>
<td>25.82</td>
<td>1.81</td>
<td>0.10</td>
</tr>
<tr>
<td><strong>Rock ptarmigan</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral</td>
<td>1</td>
<td>-20.01</td>
<td>42.10</td>
<td>0</td>
<td>0.26</td>
</tr>
<tr>
<td>Lateral+Heather</td>
<td>2</td>
<td>-19.27</td>
<td>42.78</td>
<td>0.68</td>
<td>0.19</td>
</tr>
<tr>
<td>Lateral+Tshrub</td>
<td>2</td>
<td>-19.46</td>
<td>43.15</td>
<td>1.05</td>
<td>0.16</td>
</tr>
<tr>
<td>Lateral+Gramin</td>
<td>2</td>
<td>-19.80</td>
<td>43.84</td>
<td>1.74</td>
<td>0.11</td>
</tr>
<tr>
<td>Lateral+Lichens</td>
<td>2</td>
<td>-19.89</td>
<td>44.02</td>
<td>1.92</td>
<td>0.10</td>
</tr>
</tbody>
</table>
Table 2.5. Habitat differences between nest and random sites (measured as value at the nest site – value at the random site) for rock, white-tailed and willow ptarmigan in the southern Yukon Territory. Values indicate mean difference with standard error in brackets. n refers to the number of nest-random site pairs.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Rock ptarmigan (n=53)</th>
<th>White-tailed ptarmigan (n=35)</th>
<th>Willow ptarmigan (n=7)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overhead cover</td>
<td>9.43 ± 2.58</td>
<td>12.80 ± 5.14</td>
<td>35.14 ± 11.66</td>
</tr>
<tr>
<td>Lateral cover</td>
<td>24.15 ± 3.43</td>
<td>29.80 ± 4.48</td>
<td>49.68 ± 9.49</td>
</tr>
<tr>
<td>Dist shrub</td>
<td>0.74 ± 2.84</td>
<td>-7.30 ± 15.34</td>
<td>-0.76 ± 0.31</td>
</tr>
<tr>
<td>Rock</td>
<td>0.09 ± 2.83</td>
<td>9.50 ± 4.80</td>
<td>-0.93 ± 0.66</td>
</tr>
<tr>
<td>Graminoid</td>
<td>-1.98 ± 2.97</td>
<td>-4.20 ± 2.74</td>
<td>-35.00 ± 7.99</td>
</tr>
<tr>
<td>Tall shrub</td>
<td>2.97 ± 2.13</td>
<td>-3.70 ± 2.32</td>
<td>46.57 ± 8.54</td>
</tr>
<tr>
<td>Dwarf shrub</td>
<td>-3.79 ± 2.29</td>
<td>0.30 ± 3.68</td>
<td>-5.86 ± 3.34</td>
</tr>
<tr>
<td>Lichens</td>
<td>-0.31 ± 1.13</td>
<td>1.70 ± 1.40</td>
<td>0.39 ± 1.53</td>
</tr>
<tr>
<td>Heather</td>
<td>1.30 ± 2.10</td>
<td>1.20 ± 2.22</td>
<td>0.43 ± 0.61</td>
</tr>
<tr>
<td>Mean shrub hgt&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td>-0.36 ± 0.17</td>
<td></td>
</tr>
<tr>
<td>Mean stems within 1m&lt;sup&gt;a&lt;/sup&gt;</td>
<td></td>
<td>97.57 ± 11.20</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Tall shrubs were rarely present at both nest and random sites of rock and white-tailed ptarmigan, thus I only present values on shrub height and stem density for willow ptarmigan.
Figure 2.1 Surface area plot showing the probability that a nest site would be that of a white-tailed ptarmigan rather than a rock ptarmigan as a function of elevation and slope (top) and graminoids and lichens (bottom) (1 – probability white-tailed indicates the probability that it would be a rock ptarmigan nest site). Probabilities were based on the model averaged estimates in Table 3 with a sample of nests for 44 white-tailed ptarmigan and 58 rock ptarmigan. For each variable, I restricted the range of values to those observed during the study.
Figure 2.1 (continued) Surface area plot showing the probability that a nest site would be that of a white-tailed ptarmigan rather than a rock ptarmigan as a function of elevation and slope (top) and graminoids and lichens (bottom) (1 – probability white-tailed indicates the probability that it would be a rock ptarmigan nest site). Probabilities were based on the model averaged estimates in Table 3 with a sample of nests for 44 white-tailed ptarmigan and 58 rock ptarmigan. For each variable, I restricted the range of values to those observed during the study.
References


CHAPTER 3 – INFLUENCE OF CLIMATIC CONDITIONS ON TIMING OF BREEDING AND REPRODUCTIVE SUCCESS OF ROCK AND WHITE-TAILED PTARMIGAN

Introduction

For many north-temperate birds, timing of breeding is influenced by spring temperature (Wilson and Arcese 2003, Martin and Wiebe 2004). This response may be related to the effects of temperature on food abundance (Arcese and Smith 1988), availability of nesting habitat (Hannon et al. 1988, Madsen et al. 2007) and thermoregulatory costs of females, which may affect their allocation of effort to reproduction (Brown et al. 1999). Over the past few decades, spring temperatures have risen in many regions and with few exceptions, birds have responded by advancing their breeding dates (Dunn and Winkler 1999, Brown et al. 1999, Parmesan and Yohe 2003, Ludwig et al. 2006). Climatic conditions are also expected to become more variable as temperatures rise (IPCC 2007), which may lead to stronger year-to-year variation in breeding dates. Predicting how such variation will influence reproductive output for a population requires knowledge on 1) how temperature affects breeding date, 2) how breeding date affects reproductive output, 3) the influence of other factors, such as nest predation, on reproduction, and, 4) whether a species life history affects how they cope with variable climatic conditions. In this chapter, I will address these issues for sympatric rock and white-tailed ptarmigan.

Annual variation in timing of breeding can influence clutch size (Hendricks 2003), number of nesting attempts (Hannon et al. 1988, Wilson and Arcese 2003) and number of juveniles that survive to breed (Martin and Hannon 1988). However, these relationships are often complex and dependent on the influence of other factors that influence reproductive output. In a study of song sparrows (*Melospiza melodia*), Wilson and Arcese (2006) found that spatially-separate populations displayed synchronous timing of breeding as a consequence of a shared climate, but had different reproductive output due to variation in rates of nest predation and cowbird parasitism. Nest predation in particular is a key factor affecting avian reproduction (Ricklefs 1969) and must be considered simultaneously with climate if we are to understand the

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2 A version of this chapter has been submitted for publication.

determinants of reproductive output for a population. Nest predation rates may co-vary with weather because of effects on predator or prey behavior (Morrison and Bolger 2002, Rodríguez and Bustamente 2003, Collister and Wilson 2007), but are also influenced by other ecological factors such as the abundance of predators, prey density and the availability of alternative prey (Bety et al. 2002, Cain et al. 2006, Grand et al. 2006). If these ecological factors vary over the breeding season we may observe temporal patterns of nest predation within years (Dinsmore et al. 2002, Grand et al. 2006, Wilson et al. 2007a). Rates of nest predation might also vary over spatial scales because different habitats can influence predator abundance or hunting efficiency (Martin and Wiebe 1998, Stephens et al. 2005).

Very few studies have considered how congeneric species with similar ecology and habitat preferences respond demographically to annual variation in climatic conditions. In this chapter, I first examine how annual spring temperature affects timing of breeding for rock and white-tailed ptarmigan. Species that breed in tundra habitat are limited in their onset of breeding by timing of snowmelt (Hannon et al. 1988, Lindberg et al. 1997, Martin and Wiebe 2004). Thus, I predict that spring temperature in April and May, when individuals return to territories, should have a strong influence on when individuals of both species initiate breeding. I then consider how timing of breeding affects clutch size and the number of hatched young for both species. Declines in clutch size with delayed breeding are common for birds (Daan et al. 1988, Winkler and Allan 1996) and it is possible that smaller clutches may produced fewer hatched young. My study is unique in being able to compare whether this response is similar for two congeneric species in the same location. As I show, the two species respond differently, which suggests different life history strategies and different mechanisms for coping with variation in climatic conditions. My final objective is to examine what factors influence rates of nest predation. In chapter 2, I found that rock and white-tailed ptarmigan differ in selection of nest micro-habitat by elevation, slope and the ground cover of graminoids versus rock. I will examine whether the two species differ in nest survival and if so, whether this might be related to different habitat preferences.

**Methods**

My study area and general field methods were described in Chapter 1. Here, I add details relevant to the statistical analyses and techniques of this chapter.
Timing of breeding and reproductive output

I estimated the date of first egg (DFE) by observing nests during the laying stage, back-dating from date of hatch or floating a single egg if the nest was found after incubation had begun (Westerkov 1950). However, direct estimates of date of first egg may be biased because nests that fail before they are found are not accounted for. An approach to correct for this is the Horvitz-Thompson estimator, described in detail by Dinsmore et al. (2002). For every nest found, I used the top nest survival model (see next section) to calculate the probability that a nest initiated on the same day would have survived until the day that nest was found. This probability was then used to estimate how many other nests might have been initiated on the same day but failed before they were found. After applying this approach to each nest in the sample, I recalculated the estimate of mean initiation date each year. The mean date of first egg based on the Horvitz-Thompson method turned out to be within 1 day of the mean date from the field estimates, and therefore I only report the latter in the results.

I examined whether breeding dates were influenced by environmental conditions by regressing the mean date of first egg for both species against average spring temperature measured daily from April 13 through May 13 each year. Because temperature data were only collected at the study site after arriving there, I used Environment Canada daily weather data from Burwash Landing. Although temperatures at Burwash Landing may be higher than the study site given the lower elevation, the April-May conditions at Burwash Landing each year should be proportionately similar to the conditions at the study site. I chose the period April 13 to May 13 because May 14 was the earliest date of first egg and previous studies on ptarmigan have shown that temperatures in the month prior to breeding are influential in predicting onset of breeding (Hannon et al. 1988, Martin and Wiebe 2004).

For both species, I also examined how date of first egg influenced clutch size of the first attempt and number of chicks hatched annually. I analyzed relationships between weather, nest initiation, clutch size and number of hatched young using Bayesian methods implemented in winBUGS 3.0.3 (McCarthy 2007). Bayesian methods are an alternative to the more commonly used frequentist statistics. A posterior distribution for a parameter is estimated by incorporating prior information with maximum likelihood methods. If the prior distribution is flat (i.e. uninformative), the posterior distribution is determined entirely by the likelihood and in this case, the credible intervals around the Bayesian estimates are equal to the confidence intervals.
using frequentist statistics. However, because parameters are treated as random variables using Bayesian methods, the 95% credible interval is interpreted as the probability that population parameter lies within the specified interval. Because there is no estimate of the probability of the data given a null hypothesis, there are no p-values for these methods and results should be interpreted based on the estimate and magnitude of error associated with the credible intervals.

For the Bayesian statistics performed in Chapter 3 and 4, I used uninformative prior probabilities for each analysis. Prior information was not used because for many questions my aim was to compare variation in breeding traits and demographic traits among populations in different locations. Thus, I preferred a more conservative approach rather than incorporate information from populations in other locations, which may bias rather than aid parameter estimates in the context of this study. For each analysis, a total of 100,000 samples were run to generate parameter estimates after discarding an initial burn-in of 10,000. I specified a normal distribution for date of first egg, clutch size and mean number of young hatched per female annually, and a Poisson distribution for models comparing DFE against number of hatched young. Results presented include the parameter estimate along with the 95% credible interval.

**Nest survival**

To examine nest survival, I used the nest survival module in program MARK (White and Burnham 1999, Dinsmore et al. 2002). This model is a generalization of the maximum-likelihood estimator of Bart and Robson (1982) and estimates daily nest survival while allowing for individual, group and time-specific covariates. The model requires the following assumptions: 1) nests are correctly aged when found (if age is included), 2) nest fates are correctly determined, 3) nest visits do not influence subsequent nest survival, 4) nest fates are independent, and 5) homogeneity of daily nest survival rates (Dinsmore et al. 2002). I assigned nest fate for most cases (98.6%). For those nests of uncertain fate, I only used information up to the last date the nest was observed active and then classified the nest as successful over that period. I assumed nest fates were independent because ptarmigan are territorial and nests were well-dispersed throughout the study area. Two nests were believed to have failed because of human disturbance and were removed from the analysis.

I initially estimated daily nest survival (DNS) rates for each species and for all subsequent comparisons, with species included as an additive effect. I then considered models to ask if DNS varied by year, time in season, or age of the nest. My first model was a null model and assumed
constant survival with respect to time. Year was then added as a categorical variable to test for annual variation. I then explored models that allowed for daily nest survival to vary as a linear and a quadratic function of the age of the nest. Nest age effects would most likely be related to changes in parental behavior over the nest cycle (Martin et al. 2000, Grant et al. 2005, Wilson et al. 2007a). Because it is unlikely that relationships between daily nest survival and nest age would vary by year, I did not include year by age interactions. I also tested for linear and curvilinear effects of time of season, and because seasonal patterns might vary annually, I allowed for a time by year interaction with separate intercepts for each year.

To examine the effects of habitat and temperature on daily nest survival, I added these variables to the top temporal models based on the results of the preceding analysis. Habitat models were run with and without species as an additive effect. In chapter 2, I found that rock and white-tailed ptarmigan differ in nest-habitat within the study site in relation to elevation, slope and the ground cover of graminoids, rock and tall shrubs. Therefore, I added each of these variables as well as lateral cover to the top temporal model. I also considered additive effects between these variables and, elevation and slope. Temperature was added to the best model that included time and habitat effects. Because temperature might be correlated with time of season, I also considered temperature in models without a seasonal trend. Unfortunately, I did not have data on daily precipitation, which might also influence nest survival (Dinsmore et al. 2002, Collister and Wilson 2007). I used Akaike’s information criterion for small samples (AICc, Burnham and Anderson 2002) to rank candidate models, and the ΔAICc and Akaike weights (w_i) to assess model uncertainty and evaluate the likelihood of each model. There is currently no suitable goodness of fit test for nest survival models in MARK (Dinsmore et al. 2002).

Results

Timing of breeding and reproductive output

I monitored the nests of 86 rock and 58 white-tailed ptarmigan over four years (Table 3.1). Across years, the mean date of first egg (DFE) for both species varied by about two weeks, with two earlier years (2004-2005) and two late years (2006-2007, Figure 3.1, 3.2, Table 3.1). Timing of breeding and spring temperature, although based on only four years of data, were negatively related (rock: $\beta_{\text{temp}} = -2.69$ (95% Cred Int: -4.04, -1.32), n=4; white-tailed: $\beta_{\text{temp}} = -4.05$ (95% Cred Int: -6.74, -1.50), n=4, Figure 3.2). The parameter estimates indicate that with each degree
rise in mean daily temperature, I would predict an advance in the mean date of first egg by 2.7
days for rock ptarmigan and 4 days for white-tailed ptarmigan. Despite the difference in onset of
breeding across years, cessation of breeding was relatively similar and showed little relation to
spring temperature for either species. As a consequence, the overall range of initiation dates was
greater in years when breeding began earlier (Table 3.1).

The mean clutch size of the first attempt for rock ptarmigan was 7.54 (95% Cred Int: 7.21,
7.88, n=68), while for white-tailed ptarmigan it was 7.16 (6.87, 7.44, n=45). For both species the
size of the first attempt decreased with later laying, but the rate of decline was considerably
steeper for rock ptarmigan (rock ptarmigan: $\beta_{DFE} = -0.131$ (95% Cred Int: -0.167, -0.095, Figure
3.3), n=68; white-tailed ptarmigan: $\beta_{DFE} = -0.039$ (-0.066, -0.011), n=45). For rock ptarmigan,
the regression equation predicts a mean clutch size of 9.41 (95% Cred Int: 8.83, 9.99) on the
earliest DFE of a first attempt (day 134), and only 6.0 (5.50, 6.50) on the latest (day 160). Over
the same time period, the equation for white-tailed ptarmigan predicts a change from a mean of
7.82 (7.27, 8.36) to 6.82 (6.45, 7.19). The relationship between date of first egg and number of
young hatched per female followed a similar pattern for both species (rock ptarmigan: $\beta_{DFE} = -$
0.038 (95% Cred Int: -0.059, -0.018), n=68; white-tailed ptarmigan: $\beta_{DFE} = -0.017$ (-0.033, -
0.002), n=46). The back-transformed estimates from the log model with a Poisson distribution
predict a mean for rock ptarmigan of 4.95 (3.64, 6.55) hatched young per female when date of
first egg was 134 declining to 1.84 (1.32, 2.46) when date of first egg was 160. Over the same
period, the decline for white-tailed ptarmigan ranged from 5.35 (3.97, 7.00) to 3.42 (2.73, 4.19).
Note that the mean estimates of hatched young per female will be lower than the average number
hatched per successful nest because many females fail to produce any young. For comparison,
the mean hatched young per successful nest was 6.14 (5.36, 6.98) for rock ptarmigan and 6.32
(5.47, 7.24) for white-tailed ptarmigan.

Nest survival – species and temporal trends

Forty-nine of 86 (57%) rock ptarmigan nests failed, one due to human disturbance. Of the
remaining 48, 39 appeared to have failed due to nest predators, 3 to adult predators and 5 to
abandonment/weather (1 unknown). Of 58 white-tailed ptarmigan nests, 27 failed (47%) with 21
due to nest predators, 5 to adult predators and 1 unknown. Nest survival was estimated using 142
of the 144 nests, and a total of 2033 exposure days. Mean estimates of DNS in each species with
no other predictors indicated slightly higher DNS in white-tailed (0.969, 95% Confidence Int:
0.955 to 0.979) than rock ptarmigan (0.961, 95% CI: 0.949 to 0.971). However, because of considerable overlap in confidence intervals, the species model had less support than the null model (Table 3.2, but see below). These estimates, when raised to the mean length of the nest cycle (29 days for both), suggest an average nest success of 40% for white-tailed ptarmigan and 32% for rock ptarmigan.

Among temporal models, I found little evidence that daily nest survival varied by nest age or year (Table 3.2a). Subsequent estimates of annual process variance (sigma) were 0.0059, which when converted to 2 standard deviations and raised to nest cycle length predict a range of annual nest survival from 0.24 to 0.50 for the two species overall. I was unable to generate species specific estimates of annual process variance. Season had little influence on daily nest survival when constrained to a single pattern across years, but models with a linear trend by year interaction had considerable support. When plotted, back-transformed estimates suggest that daily nest survival increased with date in 2004, decreased in 2006, and remained about constant in 2005 and 2007 (Figure 3.4). The linear trend model predicted that nest survival for each species and year equaled (rock and white-tailed ptarmigan, respectively): 2004 - 0.26, 0.39; 2005 - 0.24, 0.38; 2006 - 0.32, 0.45; 2007 - 0.59, 0.69. Incorporating species as an additive effect to year by time models improved model support ($\beta_{\text{white-tailed}} = 0.377, 95\% \text{ CI: } -0.144 \text{ to 0.899}$) and indicated that nest success of white-tailed ptarmigan was about 11 to 13% higher than rock ptarmigan.

**Nest survival - temperature and habitat effects**

To examine the effects of weather and habitat, I added these variables to a time by year model, and also considered temperature with a constant time model (Figure 3.4). Daily nest survival covaried positively with mean daily temperature (model averaged $\beta = 0.096 \pm 0.040$ (SE), Figure 3.5). Furthermore, models with constant time and temperature had far greater support than models with time*year and temperature, suggesting some of the seasonal patterns might be due to fluctuations in temperature. I did not find strong support for an influence of habitat on daily nest survival, although a model with the habitat variable ‘rock’ and year*time had a similar AICc value to a year*time only model (difference of 0.0357 units). The beta estimate for rock in that model was $0.0083 \pm 0.0061$ indicating a tendency for increasing daily nest survival in habitats with greater rock cover. There was also weak support for increasing
daily nest survival with greater lateral cover around the nest (model averaged $\beta_{\text{lat cover}} = 0.0065 \pm 0.0058$).

**Discussion**

**Environmental effects on timing of breeding and reproductive output**

During four years mean onset of breeding was similar in rock and white-tailed ptarmigan, but varied by about 2-3 weeks over the latter half of May and early June. Synchrony in the breeding of each species suggests that they are responding to the same environmental cues. In particular, onset of egg laying occurred earlier when spring temperatures in the month prior to breeding were warmer, similar to findings for many temperate zone birds including grouse (Forchhammer et al. 1998, Ludwig et al. 2006, Wilson et al. 2007b). Temperature may influence the onset of breeding by at least two mechanisms. First, warmer temperatures lead to more rapid snowmelt, thus increasing the availability of nesting and foraging habitat early in the season. Cotter (1999) suggested that rock ptarmigan in the Canadian Arctic began breeding shortly after snow cover declined to less than 50% of territory area, and similar effects of snow cover were noted for white-tailed ptarmigan in the Sierra Nevada of California (Clarke and Johnson 1992). Onset of breeding for other tundra species including willow ptarmigan, American pipits (Anthus rubescens), black brant (Branta bernicla) and pink-footed geese (Anser brachyrhynchus) are also influenced by snowmelt (Hannon et al. 1988, Lindberg et al. 1997, Hendricks 2003, Madsen et al. 2007). In Colorado, white-tailed ptarmigan appear to be more conservative and delay breeding until early June regardless of snow cover, perhaps as a precaution to avoid spring storms (Martin and Wiebe 2004). Thus, it is possible that response to spring conditions varies among geographic locations depending on the predictability of inclement weather. Temperature may also influence females directly through thermoregulatory costs. Prior to incubation, females gain up to 25% of their body mass and colder temperatures may lead to a delay in breeding if the increased energetic costs lower the available energy that can be devoted to reproduction (Wiebe and Martin 2000).

Delayed breeding may result in smaller clutches (Hannon et al. 1988, Hendricks 2003) and a reduced number of nesting attempts per year (Morrison and Bolger 2002, Wilson and Arcese 2003, Martin and Wiebe 2004), both of which may lower annual reproductive output. I observed that both species of ptarmigan laid smaller clutches as the onset of breeding was delayed.
However, both species also differed in their rate of decline in clutch size over time, despite experiencing the same conditions. Relative to white-tailed ptarmigan, clutch sizes of early rock ptarmigan nests were larger while those of late nests were smaller. This result appears to indicate a greater resilience for white-tailed ptarmigan under less favorable breeding conditions, perhaps related to differing allocation of effort to reproduction versus survival by the two species (Chapter 4).

**Effects of time and weather on nest survival**

Predators of nests and adults were the main direct cause of nest failure in both species (89% of failures for rock ptarmigan, 100% for white-tailed ptarmigan). Identifying the dominant nest predators is difficult, but I suspect most nest predation was due to red foxes and arctic ground squirrels, with lesser amounts from short-tailed and least weasels, and common ravens (*Corvus corax*). Avian predators, particularly golden eagles (*Aquila chrysaetos*), were indirectly responsible for nest failure after killing incubating females. Caution is needed when assigning causes of failure because nests that fail due to weather or are abandoned for other reasons may be scavenged before the next visit, thus giving the appearance of depredation (Etterson et al. 2007). The estimates of nest failure due to weather or abandonment presented here should therefore be considered as minima.

Initial estimates of nest survival for each species suggested an average 10% higher nest success for white-tailed ptarmigan as well as yearly variation for both species. Estimates of annual process variance predicted a range of nest success from 24 to 50% for the two species overall. Although results for 2007 were outside this range, those estimates were based on fewer nests due to a drop in population size for both species between 2006 and 2007. While this potentially reflects higher nest survival in years with lower densities, it may also be a sampling artifact. Nest survival of precocial ground-nesting birds tends to be low and is often under 50% (Dinsmore et al. 2002, Grant et al. 2005, Walker et al. 2005, Grand et al. 2006, Moynahan et al. 2007). Estimates for white-tailed ptarmigan in Colorado averaged 24% (Chapter 4), while for willow ptarmigan at Chilkat Pass, British Columbia and La Pérouse Bay, Manitoba, nest survival was 34 and 42% respectively (Wilson et al. 2007a). Apparent nest success for white-tailed ptarmigan in the Sierra Nevada was 36% (average over 6 years, Clarke and Johnson 1992), while for rock ptarmigan it was 50% in the Italian Alps (Scherini et al. 2003) and 53% in the Canadian
Arctic (Cotter 1999). However, because these latter three analyses used apparent nest success, these estimates may be biased high (Mayfield 1961, Bart and Robson 1982).

I found little support for an influence of nest age on daily nest survival, but did find an interactive effect between time of season and year. Seasonal changes in daily nest survival are likely driven by variation in ecological factors such as the abundance of alternative prey, requirements by predators for their own reproduction and the influence of weather (Schmidt and Whelan 1999, Grand et al. 2006, Mahony et al. 2006, Moynahan et al. 2007). These factors might not be temporally consistent across years, which may lead to annual differences such as those observed here. Because I did not measure predator activity or the abundance of alternative prey, I can only acknowledge that they may have played an undetected role in the seasonal patterns. However, I also found a positive effect of temperature on daily nest survival, which accounted for some of the variation in the seasonal trend.

Because weather resulted in very few cases of direct nest failure, it would appear that temperature indirectly influenced daily nest survival via effects on nest predation. This effect of weather may be common but go unrecognized in many cases (Rodriguez and Bustamente 2003, Collister and Wilson 2007). The direction of these relationships may depend on the type of predator-prey community and climatic conditions. Weather may influence predator behavior if colder temperatures or precipitation increase energetic demands or reduce the abundance of alternative prey. Both of these aspects were thought to be the cause of lower nest survival for loggerhead shrikes (Lanius ludovicianus) in Alberta during periods of cold and wet weather (Collister and Wilson 2007). In contrast, rufous-crowned sparrows (Aimophila ruficeps) in California had higher nest success in cool, wet weather potentially because it places thermoregulatory constraints on foraging by snakes, the dominant nest predator (Morrison and Bolger 2002). Weather might also influence nest predation through effects on prey behavior, such as if colder temperatures lowered nest attentiveness, which may increase nest detectability by predators (Martin et al. 2000, Wiebe and Martin 2000). In Montana, sage grouse (Centrocercus urophasianus) daily nest survival increased on the day of a rain event and decreased the following day, which may have been related to predator and prey behavior (Moynahan et al. 2007). In my study area, temperature and precipitation are probably correlated and the lower daily nest survival during cool weather may also be due in part to the effects of precipitation. Unfortunately, I did not have data to examine how rainfall affects nest survival.
Interspecific differences in nest survival

Different species may experience different nest success rates, even in the same environment (Grant et al. 2005, Stephens et al. 2005). My results indicate that nest success was 9 to 11% higher for white-tailed than rock ptarmigan. Territories of the two species are well dispersed throughout the study area, but they show differing nest-habitat preferences. White-tailed ptarmigan typically nested at higher elevations, on steeper slopes and in more rocky habitats, while rock ptarmigan were more common in sedge meadows at lower elevations (Chapter 2). Although I did not find strong effects of habitat, there was a tendency for higher daily nest survival in areas with greater rock cover, which may explain higher nest survival rates for white-tailed ptarmigan. The abundance of arctic ground squirrels was lower in more rocky areas, and these areas may be more difficult for red foxes to hunt in. In Colorado, Wiebe and Martin (1998) found higher nest success of white-tailed ptarmigan females on steeper slopes and suggested this might be because canids avoid these sites.

Conclusions

I found four key patterns in this chapter. First, rock and white-tailed ptarmigan show synchrony in the onset of breeding, which appears to be strongly determined by spring temperatures and its effect on snow cover. Second, clutch size and the number of young hatched declined with later laying in both species, but did so more strongly for rock than white-tailed ptarmigan. Third, seasonal patterns of nest survival varied by year and this may have been related to temperature. Finally, I found that daily nest survival was slightly higher for white-tailed than rock ptarmigan, perhaps because the more rocky habitats preferred by white-tailed ptarmigan provided additional protection from predators. Because both clutch size and number of young hatched were positively related to spring temperature, I suggest that warmer springs may enhance reproductive output overall. However, because rock ptarmigan appear to have a greater decline in reproductive effort as breeding is delayed, they may benefit to a greater extent from warm springs. In Chapter 5, I will use these results to examine how interspecific differences in response to spring conditions affect population growth rates for the two species.
Table 3.1. Descriptive nest statistics for a) rock and b) white-tailed ptarmigan in the Ruby Ranges, Yukon Territory, 2004-2007. Mean spring temperature refers to the average daily temperature from April 13 to May 13 from Burwash Landing 50km southwest of the study site. June 1 = day 152 in 2005 – 2007 and day 153 in 2004. Estimates for mean DFE, and mean number of young hatched were generated using Bayesian methods and values in brackets show the 95% credible intervals.

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
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<tr>
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<td>3.74</td>
<td>5.14</td>
<td>0.23</td>
<td>1.46</td>
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<tr>
<td>(°C)</td>
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<td></td>
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<tr>
<td>a) Rock ptarmigan</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of nests</td>
<td>24</td>
<td>28</td>
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<td>7</td>
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<tr>
<td>Mean date of first egg</td>
<td>144.2</td>
<td>142.1</td>
<td>154.3</td>
<td>152.5</td>
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<td>(139.4, 144.7)</td>
<td>(153.1, 155.6)</td>
<td>(146.2, 159.0)</td>
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<tr>
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<td>162</td>
<td>159</td>
<td>160</td>
<td>168</td>
</tr>
<tr>
<td>Nest initiation range (days)(^a)</td>
<td>22</td>
<td>25</td>
<td>10</td>
<td>19</td>
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<tr>
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<td>2.20</td>
<td>4.71</td>
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<td>(2.24, 3.53)</td>
<td>(1.66, 2.82)</td>
<td>(3.24, 6.46)</td>
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<tr>
<td>b) White-tailed ptarmigan</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Number of nests</td>
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<td>7</td>
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<tr>
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<td>158.9</td>
<td>158.3</td>
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<td>(156.8, 160.9)</td>
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<td>(3.68, 5.73)</td>
<td>(2.01, 3.36)</td>
<td>(3.24, 6.46)</td>
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</table>

\(^a\) calculated from the date of first egg – date of last egg.
Table 3.2. Model selection results for nest survival of rock and white-tailed ptarmigan in the southern Yukon Territory (2004-2007). To better illustrate the patterns, I first show the results from the analysis of daily nest survival in relation to species, year, time of season and nest age (a). I then added habitat and temperature variables to the top temporal models (constant and year*time) from (a). Because (a) and (b) are from the same data set, AICc and deviance can be compared across the two, but the ΔAICc and wi refers only to the set of models within (a) and (b) separately. I compared 16 candidate models for (a) and 26 for (b) (four were the same in both). Only the top 10 models are shown in each case.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>wi</th>
<th>k</th>
<th>Deviance</th>
</tr>
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<td><strong>a) temporal models</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_{\text{constant}}$</td>
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<td>2</td>
<td>540.92</td>
</tr>
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<td>0.10</td>
<td>8</td>
<td>529.69</td>
</tr>
<tr>
<td>$S_{\text{nest age }+ \text{ species}}$</td>
<td>545.87</td>
<td>2.01</td>
<td>0.09</td>
<td>3</td>
<td>539.86</td>
</tr>
<tr>
<td>$S_{\text{time }+ \text{ species}}$</td>
<td>546.78</td>
<td>2.92</td>
<td>0.06</td>
<td>3</td>
<td>540.77</td>
</tr>
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Figure 3.1. Mean daily temperature (Celsius) across the breeding season at the study site in the southern Yukon Territory, 2004 to 2007.
Figure 3.2. Mean date of first egg laid for rock (dashed line, circles) and white-tailed ptarmigan (solid line, squares) versus mean daily temperature from April 13 to May 13 in the Ruby Range Mountains, Yukon Territory, 2004-2007. Each observation represents the average of all first nesting attempts for the two species in that year.
Figure 3.3. Change in first clutch size in relation to date of first egg for rock and white-tailed ptarmigan in the Yukon Territory, Canada. Solid and open circles refer to breeding attempts during the two warm (2004-05) and two cold (2006-07) seasons respectively.
Figure 3.4. Predicted daily nest survival in relation to time of season for rock (open circles) and white-tailed Ptarmigan (solid squares) in the southern Yukon Territory, 2004-2007. Figures were based on a model of year*time + species (3rd model in Table 3-2a) with each panel representing the pattern for a particular year: a) 2004 b) 2005 c) 2006 d) 2007. Nest survival was plotted for 29 days starting on day 8 in 2004, 2005 and day 18 in 2006, 2007. Note that back-transformation of linear trends with a logit transformation will tend to be curved. Day 1 corresponds to May 20.
Figure 3.5. Predicted daily nest survival in relation to mean daily temperature for rock (open circles) and white-tailed Ptarmigan (solid squares) in the southern Yukon Territory, 2004-2007. Figures were generated using the parameter estimates from the species + temp model in Table 2b.
References


CHAPTER 4 – COMPARATIVE LIFE HISTORY STRATEGIES OF ROCK AND WHITE-TAILED PTARMIGAN: DO SIMILAR ENVIRONMENTS LEAD TO CONVERGENT STRATEGIES?³

Introduction

A central issue in ecology is why populations and species differ in their allocation of effort towards reproduction versus survival (Lack 1968, Stearns 1983, Roff 1992). Across many taxa, species vary along a slow-fast continuum (Stearns 1983, Sæther 1988, Roff 1992, Ricklefs 2000). At the ‘slow’ end are longer-lived species characterized by high survival, a delayed age at sexual maturity and low annual reproductive effort. At the ‘fast’ end are shorter-lived species with low annual survival, rapid time to maturity and high annual reproductive effort. For birds and mammals, most life history diversification is thought to have occurred early in their evolutionary history, thus differences are often most pronounced among orders and families (Read and Harvey 1989, Owens and Bennett 1995). However, life history variation is also observed among congeneric species or populations of the same species across geographic locations, habitat types and elevations (Badyaev 1997, Ferretti et al. 2005, Frederiksen et al. 2005, Sandercock et al. 2005, Bears 2007). Because species’ traits are influenced by phylogeny comparative studies of closely related species provide a way to identify mechanisms leading to the diversification of life histories (Roff 1992, Martin 1995, Martin 2004). I will use this approach with three populations of ptarmigan in two separate locations to test hypotheses on the mechanisms driving avian life history evolution.

Among birds, several hypotheses for the evolution of alternative life histories have been proposed including body size (Read and Harvey 1989), food abundance (Lack 1947, Martin 1987), degree of seasonality (Ashmole 1963, Ricklefs 1980), nest predation (Skutch 1949, Slagsvold 1984, Arnold et al. 1987) and risk of adult mortality (Williams 1966, Roff 1992). Despite several decades of research the importance of these different mechanisms is still debated and it is likely that multiple mechanisms influence the strategies of species across locations (Lack 1947, Skutch 1948, Ricklefs 2000, Martin 2004). Many earlier studies focused on

³ A version of this chapter has been submitted for publication.
variation in reproductive effort by asking why avian clutch size varies across latitude. This emphasis on clutch size has recently been criticized as too narrow (e.g. Martin 2004). Other traits such as egg size and incubation length also contribute to reproductive effort and co-vary with clutch size (Rahn and Ar 1974, Ricklefs 2000, Figuerola and Green 2006, Martin et al. 2006). Moreover, the number of nest attempts may be a more accurate measure of reproductive effort than the clutch size for individual attempts. Life history studies that focus on multiple traits simultaneously should better illuminate the patterns underlying life history evolution in birds (Martin 2004).

In this study, I used a comparative approach to examine life history strategies of sympatric rock (Lagopus muta) and white-tailed ptarmigan (Lagopus leucura) in the same environment in the Yukon Territory (YK, 2004-2007), and a separate white-tailed ptarmigan population at the opposite end of the range in Colorado (CO, 1987-1996, K. Martin data). The two environments are similar in habitat structure and climatic conditions, but differ in latitude, elevation and community composition. Sandercock et al. (2005) previously examined life history strategies of white-tailed and willow ptarmigan (Lagopus lagopus) at three locations and concluded that reproductive effort was higher for populations with a greater risk of mortality on nests and females. In a review of North American game birds, Zammuto (1985) showed a negative correlation between longevity and clutch size suggesting mortality risk affects reproductive effort. In these comparisons, each population inhabited a unique location requiring inference across environments. By examining two species in sympatry, I was able to control for the potential influence of environment on life history. I first tested if the breeding biology of white-tailed ptarmigan in the Yukon was more similar to rock ptarmigan in the same location than to white-tailed ptarmigan in Colorado. I expected this comparison to help identify traits that exhibit a relatively plastic response to environmental differences versus those more constrained by phylogeny. With these results in hand, my second objective was to test which of the hypotheses below most consistently explained differences among the three populations. To do so, I compared the breeding traits of each population with their demographic rates and environmental differences.

Hypotheses
1) Food abundance. - David Lack (1947) suggested that food abundance constrains the number of young parents can nourish and thereby explains the observation that reproductive effort (i.e.
clutch size) increases with latitude, day-length, and a greater pulse of food at northern latitudes (see also Martin 1987). The elevation of the alpine zone decreases with increasing latitude with the result that seasonality of resources tends to be fairly consistent across latitudes (Martin 2001). Thus, it is not clear that food abundance would necessarily be higher in the Yukon. However, longer day lengths in the Yukon should allow females to acquire resources more quickly during the pre-breeding period thus allowing them to invest more in reproduction. If true, I expect clutch sizes and re-nest propensity to be similar for the two species in the Yukon, and both should be greater than for the Colorado population.

Ashmole (1963) introduced a second resource hypothesis dependent on the degree of seasonality relative to population density (see also Ricklefs 1980). Ashmole argued that populations are regulated by density-dependence during the non-breeding period when resources are scarce. As a result, populations in more seasonal northern environments will have greater resources per individual during breeding, which allows them to allocate more energy to reproduction. This hypothesis is difficult to test because we need a measure of the degree of seasonality in the two environments and more detailed knowledge on density and regulation of each population during the non-breeding period. Therefore, I will not consider this hypothesis further.

2) Nest predators. - An alternative set of hypotheses focus on the effects of nest predation on reproductive effort. Nest predation is the dominant cause of avian nest failure and thus an important source of natural selection (Ricklefs 1969). Environments with a high risk of nest predation may favor smaller broods that have a shorter period of exposure to predators and would allow a female to maintain reserves for re-nesting should the first attempt fail (Slagsvold 1984, Arnold et al. 1987). According to these hypotheses, I predict that populations with the lowest nest survival should invest less in the first nest attempt but have a greater re-nest propensity following failure.

3) Risk of adult mortality. - A high risk of adult mortality leads to strong selective pressure to develop quickly, reproduce early and increase allocation to each breeding attempt because the likelihood of future breeding opportunities is low (Williams 1966, Roff 1992). Many birds exhibit trade-offs between reproductive effort and adult survival (Saether 1988, Ghalambor and Martin 2001, Martin et al. 2006) and experimental studies on other taxa reveal how life history strategies can shift following a change in adult mortality (Reznick et al. 1990, Gasser et al.
According to this hypothesis, individuals within populations that are at greater risk of adult mortality should have greater annual reproductive effort because there is a lower likelihood of future breeding opportunities. This effort might be reflected in larger clutches, larger eggs or a greater re-nest propensity.

4) **Body size.** - Smaller bodied species tend to mature earlier and have higher annual reproductive effort than larger bodied species (Read and Harvey 1989). This relationship is related to mortality risk as a function of size (Sæther 1989), but may also be influenced by other physiological aspects (Nagy 1987). Average mass for females of the three populations differed by about 55g; rock ptarmigan were the heaviest while Yukon white-tailed ptarmigan were the lightest (Table 3-1). If this difference affects reproductive effort, investment should be greatest for Yukon white-tailed ptarmigan, intermediate for Colorado white-tailed ptarmigan and lowest for rock ptarmigan. In a previous ptarmigan study, Sandercock et al. (2005) found little evidence for an influence of body size on reproductive effort.

**Methods**

**Study area**

Detailed information on the Yukon study site is provided in Chapter 1. In Colorado, white-tailed ptarmigan were studied at four alpine sites (Loveland Pass, Guanella Pass, Colorado Front Ranges and Mount Evans, ~ 39°6’N, 105°7’W) over a 9-yr period (1987-1996). Habitat structure was relatively similar between the two sites with breeding habitat in Colorado consisting of alpine tundra with sedges, forbs, willow, coniferous shrubs (krummholz) and rock (Wiebe and Martin 1998). The elevation of the alpine zone in Colorado was considerably higher at 3300-4300m. Densities in Colorado were similar to those of white-tailed ptarmigan in the Yukon at about 1-2 pairs/km² (Braun et al. 1993). Data collection methods developed for my study in the Yukon followed the protocol previously developed by K. Martin for Colorado and thus are directly comparable between sites.

**Data analysis**

Parameter estimates for nest, brood, chick and adult survival were calculated using program MARK (White and Burnham 1999). For all other estimates I used Bayesian methods in WinBUGS 3.0.3 (McCarthy 2007). I specified normal distributions for all variables except re-nesting probability (binomial) and number of chicks hatched per female (Poisson). Estimates
were based on a run of 100,000 samples after discarding an initial burn-in of 10,000. In all cases, a burn-in of 10,000 samples was sufficient to achieve a stationary posterior distribution (McCarthy 2007). Further detail for each estimate is given below:

1) **Body Mass.** - Females were caught and weighed over approximately five weeks during the pre-laying period. Prior to breeding, females build energetic reserves to carry them through incubation and therefore, to estimate early spring mass, I conducted a regression of mass against days before egg laying. I compared models with both a linear and a quadratic relationship, and found the latter to have greater support in all cases (Deviance Information Criterion (DIC): quadratic model < 2 units of the linear model, Spiegelhalter et al. 2002). I then used the regression equations from the quadratic model to estimate the expected early spring mass at 30 d before laying for each population.

2) **Clutch size.** - Clutch size for first and second attempts was determined as the maximum number of eggs laid per nest using only completed clutches.

3) **Egg mass and clutch mass relative to body size.** - The width and length of a sample of eggs was measured for individual nests within each population. For each egg, I first determined egg volume, which was calculated as \( V = kLW^2 \) where \( k=0.49 \), \( L=\)length and \( W=\)width (Sandercock et al. 2005). Egg mass was then calculated as \( E = Vg \) where \( V \) is egg volume and \( g = 1.08g/ml \), the specific gravity of a chicken egg. Average clutch mass of each attempt was calculated as mean egg mass * mean clutch size. As an estimate of relative investment into each nesting attempt given the mass of females across the three populations, I divided average clutch mass by early spring body mass.

4) **Mean and duration of clutch initiation.** - For all females, I estimated mean date of first egg using first attempts from all individuals each year. The duration of clutch initiation was calculated as the number of days between the first and last clutch of the year for all nesting attempts.

5) **Incubation length.** - Length of incubation was determined by subtracting the date when incubation commenced from the date of hatch and was only done for nests where these dates were known with certainty. Incubation for ptarmigan typically begins with the laying of the penultimate egg (Braun et al. 1993), although some slight variation may occur (Wiebe and Martin 2000).
6) *Chick mass at hatch.* - To measure chick mass at hatch, I regressed mass against hours from hatch and compared a quadratic and a linear fit to the data. A linear model was a better fit for the Yukon birds (based on DIC as above), but a quadratic model was superior for Colorado because chicks were measured over a longer period. Growth of chicks initially followed a linear trend but after about one week, rose in a more exponential fashion. Using the best-fit models, I determined the predicted mass at hatch.

7) *Renest probability.* - The date of nest loss may affect whether a female will re-nest. Therefore, to predict re-nesting probability, I fit a generalized linear model (binomial distribution, logit link) of whether a female re-nested against the day of season when the first nest was lost. The stage of nest loss (i.e. day of incubation) may also influence re-nest probability but this is likely correlated with date of loss and it was not possible to consider both here.

8) *Chicks hatched/female.* - I estimated chicks per female as the average number of young a female hatched annually. Females only raise one brood per season.

9) *Nest, chick and brood survival.* - I used the nest survival module in program MARK (White and Burnham 1999, Dinsmore et al. 2002) to estimate nest, chick and brood survival for all three populations. For nest survival estimates, I used the results presented in chapter 3. To examine chick and brood survival, I fit models relating survival to chick age (linear, quadratic and cubic patterns). Broods were considered to have survived as long as 1 or more chicks remained. Because of synchrony in hatch dates and strong effects of chick age on survival, I was unable to simultaneously consider the effects of time of season on chick survival. Survival of individual chicks within broods is not likely independent. There is currently no suitable goodness of fit test for nest survival models (Dinsmore et al. 2002), but I estimated c-hat as the deviance of the global model/degrees of freedom. This measure of c-hat is positively biased and therefore estimates of model selection and variance will be conservative. However, this is the only suitable means for estimating overdispersion for chick survival. I then used c-hat to adjust AICc values (quasi AICc, Burnham and Anderson 2002) and sampling variance. The top model was used to estimate chick and brood survival to day 35.

10) *Adult survival.* - I also used program MARK to estimate annual survival of adult males and females. Although survival varies among years, my intention was to provide an indication of
the average survival within each population and so I present estimates from a model without year effects. However, I used the global model with sex and time to estimate c-hat using a bootstrap goodness of fit test. The estimate of c-hat was then incorporated into comparisons of support for candidate models (QAICc) and sampling variance.

Results

Environmental conditions

The Yukon and Colorado sites are separated by about 3250 km including a latitudinal gradient of approximately 2400 km (21.5 degrees, Table 4.1). The habitat was structurally similar between sites (although plant species vary), but the altitude of the alpine zone declines with increasing latitude and thus, the Yukon site was approximately 2000 m lower in elevation. Consistent with the latitudinal effect, mean day length during pre-breeding was approximately 3 h longer in the Yukon. Mean air temperatures during the breeding period (May through July) were similar at both sites (Table 4.1).

Body size and breeding traits

Female white-tailed ptarmigan in Colorado weighed an average 37 g more in early spring than Yukon females and 17 g less than rock ptarmigan females (Table 4.2). Female mass for all three species increased over the 30 d pre-breeding period with the greatest relative gain for rock ptarmigan (25.5% of pre-breeding mass), followed by Colorado white-tailed ptarmigan (20.5%) and Yukon white-tailed ptarmigan (19.1%, Figure 4.1). Several breeding traits were more similar between rock and white-tailed ptarmigan in the Yukon than between the two white-tailed ptarmigan populations. Both species of ptarmigan in the Yukon had larger first clutches, but smaller eggs and smaller chicks at hatch than Colorado white-tailed ptarmigan (Table 4.2). This suggests a partial trade-off in clutch size and egg mass, but Yukon rock and white-tailed ptarmigan still invested 5 and 7% more of their spring body mass, respectively, into first nesting attempts than Colorado females. Clutch sizes for the second nest attempt were similar among all three ptarmigan populations.

Incubation period ranged from 21 to 26 days overall and were shortest for rock ptarmigan, intermediate for Yukon white-tailed ptarmigan and longest for Colorado white-tailed ptarmigan. However, credible intervals for Yukon white-tailed ptarmigan overlapped the other two populations. Both white-tailed ptarmigan populations were more likely than rock ptarmigan to
renest following failure with the greatest potential among Yukon white-tailed ptarmigan (Figure 4.2). Average onset of initiation is about 10 days later in Colorado and dates need to be scaled for comparison. In the Yukon, white-tailed ptarmigan maintained a high renest probability for an additional 10 to 15 days longer than rock ptarmigan. White-tailed ptarmigan in Colorado showed a similar renesting probability to their Yukon conspecifics but with a more continuous decline in probability over time.

**Demographic rates**

Daily nest survival (DNS) and annual nest success was higher in the Yukon than in Colorado with no overlap in confidence intervals (Table 4.3). In the Yukon, white-tailed ptarmigan had higher daily nest survival than rock ptarmigan and a predicted 8 to 12% higher nest success (Table 4.3, Chapter 3), despite overlap in the confidence intervals. The mean number of chicks hatched per female followed the same pattern with the highest rates for Yukon white-tailed ptarmigan (3.92), intermediate rates for rock ptarmigan (2.87) and the lowest rates for Colorado white-tailed ptarmigan (1.77). There were no overlap in the credible intervals for hatched young (Table 4.3). Re-nesting contributed 18% of the annual hatched young for Yukon white-tailed ptarmigan, 8% for rock ptarmigan and 24% for Colorado white-tailed ptarmigan. The predicted survival of chicks and broods to day 35 was almost identical for rock and Yukon white-tailed ptarmigan, and both were about 7-8 (brood survival) and 14-17 (chick survival) percent higher than estimates for Colorado white-tailed ptarmigan. For all three populations, chick survival increased steadily during the first two weeks post hatching, and then leveled off over the following three weeks of observation.

Although hatched young, nest survival and chick survival tended to be more similar within than between environments, adult survival rates showed an opposite trend. Rock ptarmigan in the Yukon had markedly higher annual adult survival than either white-tailed ptarmigan population (Table 4.3). Mean survival of female white-tailed ptarmigan was similar between Colorado and Yukon, whereas Colorado males survived about 10% better than Yukon males (Table 4.3).

**Discussion**

**Breeding trait convergence in a common environment**

Theory predicts that under a common environmental influence, certain ecological and morphological traits may be more similar among different species than to their own ancestors...
elsewhere (Cody and Mooney 1978, Schluter 1986). However, phylogenetic history may restrict trait evolution and therefore, to test for convergence one must also account for phylogenetic constraints on change. Using this approach, Jennions and Telford (2002) found evidence for life history convergence among guppy populations as a consequence of the presence or absence of predators. Convergent life histories were also noted among geckos where the traits of one species (Homonota darwini) were more similar to phylogenetically distant species from similar latitudes than to congeneric species across latitudes (Ibargüengoytía and Casalins 2007). In this study, I first tested for evidence of an environmental influence on the evolution of breeding traits in ptarmigan by asking if values for white-tailed ptarmigan in the Yukon were more similar to sympatric rock ptarmigan than to another population of their own species in Colorado. As predicted, some breeding traits did show convergence, particularly in the case of trade-offs in clutch size versus egg mass. In the Yukon, rock and white-tailed ptarmigan laid larger first clutches but smaller eggs and hatched smaller chicks compared to Colorado white-tailed ptarmigan. On Vancouver Island, white-tailed ptarmigan have a mean clutch size of 6.2 eggs, which is intermediate to the Yukon and Colorado, although more similar to the latter (Martin and Forbes 2001). An increase in clutch size and decrease in egg mass with latitude has also been reported for rock ptarmigan (reviewed in Holder and Montgomerie 2008, see also Scherini et al. 2003). Among blue grouse, coastal populations have larger eggs but smaller clutches than interior populations (Zwickel and Bendell 2005). Overall, this finding suggests an environmental mechanism influencing characteristics of the first nest attempt. Before considering how these patterns relate to predictions from the hypotheses discussed previously, I consider the extent to which traits appear to co-vary.

Interpretations of geographic patterns of clutch size, egg mass, chick size and incubation length must consider the potential for co-variation among traits. Clutch size and egg mass are negatively correlated across a range of species and environments (Lack 1967, Sæther 1988, Blackburn 1991, Martin et al. 2006). For precocial species like ptarmigan, constraints on resource acquisition may limit the amount of energy females allocate to each nesting attempt and selection favoring larger clutches may necessarily require smaller eggs (Monaghan and Nager 1997, Figuerola and Green 2006). My data suggested such a trade-off for ptarmigan although it did not balance completely as the two species in the Yukon still invested more energy into the first nesting attempt (Table 4-2). This indicates that other ecological factors such as level
of nest predation or likelihood of juvenile or adult mortality might influence this relationship (e.g. Martin et al. 2006).

For birds generally, the length of incubation is positively correlated with egg size (Rahn and Ar 1974, Ricklefs and Starck 1998, Figuerola and Green 2006). This relationship is in part due to longer development times for larger chicks, but also because taxa that lay larger eggs tend to produce more precocial young (Boersma 1982, Martin 1987). At our sites, incubation length only showed partial convergence as lengths tended to be shorter in the North but Yukon white-tailed ptarmigan were intermediate between rock and Colorado white-tailed ptarmigan, perhaps suggesting some degree of species-specific constraint. Larger eggs and chicks at hatch may be one reason why incubation lengths were longer in Colorado. High altitude also slows embryonic development and this may have prolonged incubation in Colorado (Martin et al. 1993).

**Ecological mechanisms and first nest investment**

Clutch size typically increases with latitude in birds (Lack 1947, Klomp 1970, Dhondt et al. 2002). Although many ecological and physiological hypotheses have been proposed for the evolution of clutch size, there is no consensus on why latitudinal clines exist (Lack 1947, Skutch 1949, Monaghan and Nager 1997, Cooper et al. 2005). Greater food abundance or longer foraging periods at northern latitudes may allow females to invest more in first clutches and was long thought to be a key mechanism. For precocial species like ptarmigan, this effect might manifest in a female’s ability to acquire food prior to breeding. As predicted, the two populations in the Yukon had greater first nest investment, but I also predicted that they should have a greater re-nest propensity and that was not the case for rock ptarmigan. If resource abundance was a key mechanism we likely would have observed more rapid rates of mass gain during the pre-breeding period for the two Yukon populations. While rates of mass gain were highest for rock ptarmigan, Colorado white-tailed ptarmigan had slightly higher rates than Yukon white-tailed ptarmigan. This suggests that ptarmigan in Colorado were not more constrained in building up energetic reserves prior to breeding. Although these results appear to indicate food abundance is not likely a mechanism behind these differences, we would need additional data on food quality to verify that this is indeed the case.

For precocial species, small clutches lower the period of exposure for the nest and allow females to maintain investment for future attempts (Skutch 1949, Slagsvold 1984, Arnold 1987). Hypotheses on the effects of nest predation on clutch size are consistent with patterns among
closely related species and populations of the same species (Ferretti et al. 2005, Sandercock et al. 2005, Martin et al. 2006), but fail to explain the broad geographic patterns across north-temperate, tropical and south-temperate systems (Martin 2004). In terms of first nest investment, my findings were in line with this hypothesis; Yukon white-tailed ptarmigan had the highest and least variable nest survival, and the greatest investment, while Colorado white-tailed ptarmigan with the lowest nest survival invested the least. Rock ptarmigan were intermediate in both respects. Predation rates on nests and chicks may be positively correlated (as for the Colorado site) and in such cases, smaller clutches with larger eggs and chicks at hatch might act to enhance chick survival (Martin 1987, Grant 1991, Blomqvist et al. 1997). I also predicted that populations with the lowest nest survival might have a greater re-nest propensity but did not observe this. Although white-tailed ptarmigan in the Yukon had far higher nest survival than those in Colorado, individuals from the two populations re-nested at similar rates.

The level of adult mortality is also an important factor affecting reproductive investment across taxa (Williams 1966, Roff 1992). Adult mortality did not appear to be a factor behind differences in first clutch and egg size in this study. Yukon rock and white-tailed ptarmigan had similar clutch and egg sizes, yet differed in adult survival by 15-20%, while the two white-tailed ptarmigan populations differed in clutch and egg sizes yet had similar survival. However, first nest investment only explains part of an individual’s overall reproductive effort. Measures of clutch mass relative to body mass indicate that within all three populations, the additional investment via re-nesting would be far greater than the average difference in investment in the first attempt across populations. With the high energetic costs of producing and incubating another clutch, and the added predation risk for the remainder of the breeding period, re-nesting may be one of the most costly strategies and therefore a good indicator of reproductive effort. Re-nesting may also be an important component of seasonal reproductive output (Martin et al. 1989). Both white-tailed ptarmigan populations were more likely to re-nest than rock ptarmigan. In chapter 3, I also showed that clutch sizes of rock ptarmigan decline more quickly over time compared to white-tailed ptarmigan. These patterns indicate lower seasonal reproductive effort for rock ptarmigan compared to white-tailed ptarmigan and are consistent with expectations that reproductive effort declines when the probability of survival is higher (Sæther 1988, Reznick et al. 1990, Gasser et al. 2000, Ghalambor and Martin 2000). These results were also in line with expectations that smaller bodied species, who may have higher mortality, have a greater
investment in seasonal reproduction. This finding illustrates that the life history strategies of ptarmigan may be influenced by multiple environmental factors and the mechanism leading to larger clutches and smaller eggs with increasing latitude are different than the mechanisms that influence the overall allocation of seasonal reproductive effort via a prolonged breeding season.

**Variation in adult survival among sympatric rock and white-tailed ptarmigan**

Careful interpretation of local survival estimates is needed because they do not account for permanent emigration. Males of both species show strong fidelity to breeding territories (Choate 1983, Unander and Steen 1985, Braun et al. 1993) and were nearly always observed on the same territory each year in my study. Females are slightly less philopatric. In Colorado, between 2 and 6% of white-tailed ptarmigan females returned to their previous breeding area (Martin et al. 2000). Female rock ptarmigan typically return to the same breeding area but may switch territories (Holder and Montgomerie 2008). In my study, many females were radio-collared, which also allowed me to conduct extensive surveys (~100 km² around the study area) for breeders that dispersed to other sites. Only one female of each species was found to have moved out of the immediate study area into an adjacent valley. Patterns of adult survival are also consistent with the age structure, which was biased towards older individuals (after second year) for rock ptarmigan but younger individuals (second year) for white-tailed ptarmigan (Chapter 5).

Greater reproductive investment in response to higher mortality risk due to external factors (e.g. predators, climatic conditions) may further lower survival because of the costs of reproduction. The higher reproductive effort by white-tailed ptarmigan likely reflects this effect. However, I believe the inter-specific difference to be more strongly influenced by the susceptibility of individuals of the two species to predation, climatic conditions or disease. A longer breeding season should primarily influence females who bear the additional costs of egg-laying, incubation and chick-rearing. Male white-tailed and rock ptarmigan have similar breeding behaviors. While male white-tailed ptarmigan may stay on territories longer given the greater re-nest propensity of females, this effect should be slight and would not likely contribute to the substantially lower survival relative to male rock ptarmigan. In this case, an intriguing question is why two related species in the same location are affected differently by the same set of environmental conditions. One possibility is that they differ in susceptibility to the same predator community, perhaps because of size or behavioral differences. The two species might also respond differently to climatic conditions, or select different winter habitats that influence
mortality. Such differences may not necessarily be reflective of each species as a whole. Populations may vary in annual survival across different parts of the range, which may in turn influence their allocation to reproductive effort (Nichols and Haramis 1980, Dhondt 2001, Frederiksen et al. 2005, Sandercock et al. 2005, Folk et al. 2007).

Conclusions

Despite more than six decades of research, there is still much debate on why avian life history traits vary across geographic locations. This may be partly due to the fact that multiple life history and demographic traits must be considered simultaneously (many of which covary) and different mechanisms may influence traits even in the same environment (Martin 2004). My results suggest two mechanisms influence breeding strategies of ptarmigan. The first affects how individuals invest in the first attempt (i.e. quantity vs quality of eggs) and in this respect, the two species in the Yukon were more similar than the two white-tailed ptarmigan populations at opposite ends of the range. The influence of nest and chick predators was most consistent with this observation. The second mechanism affects the likelihood of maintaining breeding effort across the season and in this respect, the two species in the same environment had different strategies. Maintenance of reproductive effort appears to be a more direct measure of the costs of reproduction than clutch size given the energetic requirements of a second attempt and the risks of renesting. This finding was consistent with predictions on a trade-off between adult survival and seasonal reproductive effort. In Chapter 5, I will examine how these differences influence population growth, sensitivity and response to climate change for rock and white-tailed ptarmigan in the Yukon.
Table 4.1. Location, environmental conditions and ptarmigan density at the study sites in the Yukon (2004-2007) and Colorado (1987, 1989-1996).

<table>
<thead>
<tr>
<th></th>
<th>Yukon</th>
<th>Colorado</th>
</tr>
</thead>
<tbody>
<tr>
<td>Latitude</td>
<td>61.1°N</td>
<td>39.6°N</td>
</tr>
<tr>
<td>Elevation (m)</td>
<td>1475 – 2200</td>
<td>3350 - 4250</td>
</tr>
<tr>
<td>Average breeding season temperature (°C)¹</td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>3.1</td>
<td>2.2</td>
</tr>
<tr>
<td>June</td>
<td>8.6</td>
<td>7.6</td>
</tr>
<tr>
<td>July</td>
<td>9.0</td>
<td>10.6</td>
</tr>
<tr>
<td>Day length pre-breeding (hrs per day)²</td>
<td>17.9 ± 0.06</td>
<td>14.8 ± 0.02</td>
</tr>
<tr>
<td>Density (pairs/square km)</td>
<td>Rock: 2-6</td>
<td>1-2</td>
</tr>
<tr>
<td></td>
<td>White-tailed: 1-3</td>
<td></td>
</tr>
</tbody>
</table>

¹Temperature data for Colorado were recorded at the Mount Evans Research Station (by the National Oceanic and Atmospheric Administration) from 1971-2000. There were no long-term weather stations at the Yukon site and those data represent the monthly means averaged over 2004-2007.

²Day length during the pre-breeding period was calculated for the 14-day period prior to the mean laying date (following Sandercock et al. 2005)). For the Yukon, the mean laying date was the average for the two species.
Table 4.2. Body size and breeding traits of rock and white-tailed ptarmigan populations (YK = Yukon (2004-2007), CO = Colorado (1987-1996). Unless noted otherwise, estimates were generated using Bayesian calculations in WinBUGS (vers 3.0.3) and include the population mean and 95% credible interval. Estimates that were predicted based on model equations are noted with an asterisk (see methods for further detail).

<table>
<thead>
<tr>
<th></th>
<th>Rock ptarmigan (YK)</th>
<th>White-tailed ptarmigan (YK)</th>
<th>White-tailed ptarmigan (CO)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female pre-breeding</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>massa (g)</td>
<td>411 (370 - 453)</td>
<td>357 (341 - 373)</td>
<td>394 (387 – 402)</td>
</tr>
<tr>
<td>Clutch size:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st attempt</td>
<td>7.54 (7.21 - 7.88)</td>
<td>7.16 (6.87 - 7.44)</td>
<td>5.88 (5.72 - 6.04)</td>
</tr>
<tr>
<td>2nd attempt</td>
<td>5.09 (4.60 - 5.58)</td>
<td>5.11 (4.16 - 6.66)</td>
<td>4.78 (4.54 - 5.01)</td>
</tr>
<tr>
<td>Egg mass (g)</td>
<td>19.47 (18.87 - 20.06)</td>
<td>18.73 (18.34 - 19.12)</td>
<td>20.48 (20.30 - 20.66)</td>
</tr>
<tr>
<td>Avg clutch mass (g):</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st attempt</td>
<td>146.80</td>
<td>134.11</td>
<td>120.42</td>
</tr>
<tr>
<td>2nd attempt</td>
<td>99.10</td>
<td>95.71</td>
<td>97.89</td>
</tr>
<tr>
<td>Clutch mass/pre-breeding body mass</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1st attempt</td>
<td>0.357</td>
<td>0.376</td>
<td>0.306</td>
</tr>
<tr>
<td>2nd attempt</td>
<td>0.241</td>
<td>0.268</td>
<td>0.248</td>
</tr>
<tr>
<td>Mean date of initiationb</td>
<td>May 28 (May 22 - June 3)</td>
<td>May 31 (May 20 - June 8)</td>
<td>June 9 (June 3 - June 26)</td>
</tr>
<tr>
<td>Duration clutch initiation (days)b</td>
<td>19.1 (10 - 25)</td>
<td>27.5 (19 - 42)</td>
<td>31.7 (23 - 45)</td>
</tr>
<tr>
<td>Incubation length (days)</td>
<td>22.5 (22.0 - 23.0)</td>
<td>23.3 (22.5 - 24.2)</td>
<td>23.7 (23.5 – 24.0)</td>
</tr>
<tr>
<td>Chick mass at hatch (g)</td>
<td>11.85 (10.81 - 12.89)</td>
<td>11.18 (10.57 - 11.80)</td>
<td>12.68 (12.39 - 12.98)</td>
</tr>
</tbody>
</table>

a pre-breeding refers to mass 30 days before egg laying

b values in brackets indicate the range in annual mean DFE and duration of clutch initiation (all attempts) over the study periods (n=4 for each species in the Yukon, n=7 for Colorado)
Table 4.3. Demographic rates of rock and white-tailed ptarmigan populations (YK = Yukon site (2004-2007), CO = Colorado site (1987, 1989-1996)). Estimates of nest, brood and chick survival were calculated using Program MARK and values represent the mean and 95% confidence interval. Estimates based on predictions from the best MARK model are shown with an asterisk*. Number of chicks hatched per female was calculated using WinBUGS with the 95% credible interval in brackets.

<table>
<thead>
<tr>
<th></th>
<th>Rock ptarmigan (YK)</th>
<th>White-tailed ptarmigan (YK)</th>
<th>White-tailed ptarmigan (CO)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily nest survival</td>
<td>0.961 (0.949 - 0.971)</td>
<td>0.969 (0.955 - 0.979)</td>
<td>0.953 (0.945 - 0.959)</td>
</tr>
<tr>
<td>Predicted annual nest success*</td>
<td>0.32</td>
<td>0.40</td>
<td>0.24¹</td>
</tr>
<tr>
<td>Hatched young / female</td>
<td>2.87 (2.50 - 3.26)</td>
<td>3.92 (3.39 - 4.49)</td>
<td>1.77 (1.56 - 1.99)</td>
</tr>
<tr>
<td>Predicted brood/chick survival to day 35*</td>
<td>0.74 / 0.55</td>
<td>0.73 / 0.52</td>
<td>0.66 / 0.38</td>
</tr>
<tr>
<td>Adult female survival</td>
<td>0.62 (0.50 - 0.73)</td>
<td>0.43 (0.21 - 0.69)</td>
<td>0.44 (0.37 - 0.51)</td>
</tr>
<tr>
<td>Adult male survival</td>
<td>0.73 (0.61 - 0.82)</td>
<td>0.49 (0.26 - 0.72)</td>
<td>0.59 (0.53 - 0.65)</td>
</tr>
</tbody>
</table>

¹This estimate is lower than that previously determined by Sanderock et al. (2005) who calculated apparent nest success.
Figure 4.1. Change in mass (grams) in relation to days before the date of first egg (DFE) for Yukon rock ptarmigan, Yukon white-tailed ptarmigan and Colorado white-tailed ptarmigan.
Figure 4.2. Probability of renesting in relation to date of loss for the first nest for rock and white-tailed ptarmigan in the Yukon Territory (top figure) and white-tailed ptarmigan in Colorado (bottom figure). The average onset of breeding is delayed by about 10 days in Colorado and the x-axis is shifted to allow comparison. Error bars show the 95% credible intervals for predictions of the logistic regression model.
References


Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91:430-455.


CHAPTER 5 – INFLUENCE OF LIFE HISTORY STRATEGIES ON SENSITIVITY, POPULATION GROWTH AND RESPONSE TO CLIMATE VARIATION FOR ROCK AND WHITE-TAILED PTARMIGAN POPULATIONS

Introduction

Climate change is expected to result in higher mean temperatures for many regions as well as greater annual variability in weather conditions (Christensen et al. 2007). An important question is how will these changes affect animal populations (Walther et al. 2002, Parmesan and Yohe 2003). Both theoretical and empirical studies indicate that a species’ life history has implications for the response of populations to variation in demographic rates such as reproductive output and annual survival (Sæther and Bakke 2000, Morris and Doak 2002, Clark and Martin 2007). Thus, a first step in predicting climate change effects for any particular population is to estimate the sensitivity of population growth ($\lambda$) to changes in these rates. This can be accomplished using projection matrix models (Leslie 1945, Wisdom and Mills 1997, Caswell 2001, Beissinger et al. 2006). Across species, the influence of demographic rates on $\lambda$ varies depending on where they lie along a life history continuum. Populations of short-lived species that mature early and have high annual reproductive effort tend to be most sensitive to variation in the reproductive rates and juvenile survival, while those of longer lived species who mature late and have low annual reproductive effort, tend to be more sensitive to variation in adult survival (Sæther and Bakke 2000, Oli and Dobson 2003, Clark and Martin 2007).

An understanding of how life history affects population dynamics can then help us forecast how a directional change in temperature or precipitation might affect population growth, assuming that weather, demographic rates and population growth are linked. To examine these scenarios, matrix population models can be combined with empirical data on the relationship between climatic variables and demography for the population of interest (Caswell 2001, Morris and Doak 2002). For example, Reed et al. (2007) used this approach to show that deer mice ($Peromyscus maniculatus$) populations in Kansas could not persist if average annual precipitation declined by more than 11%. Climate models also predict that temperature and

4 A version of this chapter will be submitted for publication.
precipitation may become more variable (Christensen et al. 2007). If this leads to greater variation in demographic rates it will likely destabilize population growth (May 1974, Lande 1993). Greater stochasticity raises the likelihood that for any given year, the population may be reduced either to absolute extinction, or to some threshold size below which other factors such as demographic stochasticity, Allee effects or inbreeding may prevent a recovery (Gilpin and Soulé 1986, Lande 1993, Stephens and Sutherland 1999, Morris and Doak 2002). Saltz et al. (2006) used matrix models to show how a predicted increase in the variability of precipitation might lead to greater fluctuations in population size and a higher extinction risk for Asiatic wild ass in Israel (see also Hilderbrand et al. 2007). Models could also be used to predict the impacts of climate change by examining how climate affects predator-prey relationships, patterns of density-dependence or the extent to which demographic rates co-vary (Sæther 1997, Grant and Benton 2000, Ezard et al. 2006).

In this study, I developed a matrix population model to examine how life history variation affects sensitivity, stochastic population growth and susceptibility to climate variation of sympatric rock and white-tailed ptarmigan in the southern Yukon Territory, Canada. In chapter 4, I showed that relative to rock ptarmigan, white-tailed ptarmigan invest more heavily in reproductive effort and have greater productivity, but lower annual survival and an age structure biased towards younger females. Based on these findings, I predicted that white-tailed ptarmigan should be relatively more sensitive to changes in reproductive rates and juvenile survival, while rock ptarmigan would be more sensitive to variation in adult survival, particularly of older age classes. I also considered how differences in life history strategies might influence the response to climate change for each species through two types of analyses. I first used Canadian Regional Climate Models (Plummer et al. 2006) to forecast expected changes in breeding season climate by 2050. Using information on how reproductive rates for both species vary with temperature (Chapter 3), I then conducted simulations using the population model to predict how growth rates of each species might be affected. Many populations are also influenced by more extreme events that are not typically included in stochastic models. These events are referred to as ‘catastrophes’ and are infrequent but very influential in the dynamics and persistence of populations (Lande 1993, Mangel and Tier 1994, Ludwig 1999, Martin et al. 2000). During my study, the abundance of both species dropped by approximately 50% between 2006 and 2007, likely due to a combination of severe weather and high avian predation on adults. Within the
general study region, populations of many species, including willow ptarmigan (*Lagopus lagopus*), are tied into the snowshoe hare cycle (Krebs et al. 2001a, Martin et al. 2001) and it is possible that the decline was related to this. As a separate analysis, I considered how frequently these events could occur before populations of rock and white-tailed ptarmigan would decline ($\lambda < 1$).

**Methods**

**Estimation of model parameters**

Most demographic rates used in population models were previously estimated for reproductive and life history analyses in chapters 3 and 4. These rates include the number of young hatched, clutch size, probability of renesting, and, nest, chick and adult survival. With a few exceptions, most variables in this analysis were separately determined for second-year and after second-year birds. Because of the ASY-biased age structure for rock ptarmigan, I had insufficient data for a proper estimate of SY hatched young. Data for white-tailed ptarmigan indicated that SY females hatched about 20% fewer young than ASY females and this difference is similar to average estimates for these two species elsewhere (Weeden 1965, Steen and Unander 1985, Sandercock et al. 2005a). Based on this, I specified rock ptarmigan SY females as hatching 20% fewer young than ASY females. Among ptarmigan generally, the probability of renesting is also age dependent with 2 and 3 year-old females showing a greater propensity to renest than 1-yr old females (Sandercock et al. 2005a). I calculated the observed renest probability for all birds combined and adjusted by age assuming SY females had a 20% lower renest propensity than ASY females. Among grouse generally, there is often little difference in nest survival among age classes (Sandercock et al. 2005a, Pitman 2003, Moynahan et al. 2007) and therefore I assumed constant nest survival with age for both species. Nest survival was estimated separately for first and second nest attempts.

I was only able to estimate juvenile survival for the first few months during the chick stages (June through August) and both species had similar rates with a mean of 0.52-0.55 over this period (Chapter 4). To determine annual juvenile survival, I needed to combine these values with an estimate from September through April. Hannon and Martin (2006) report that average survival of juvenile willow and white-tailed ptarmigan from September to the following spring ranges from 0.45-0.55. There are no detailed studies of juvenile survival in rock ptarmigan. To parameterize the population model, I assumed an average of 0.5, which when combined with my
data would yield an average annual rate of about 0.27. However, because of uncertainty in this estimate, I ran most model projections with mean values of juvenile survival ranging between 0.22 and 0.32. This variation allowed me to consider how population growth rates of the two species differ if they have different levels of juvenile survival, which may be the case given the higher survival of adult rock ptarmigan. There was no support for models with differential survival of SY and ASY individuals for either species and I used the sex-specific means for combined age classes.

**Deterministic population model**

To analyze population growth rates, I used female-based Leslie matrix models (Leslie 1945, Caswell 2001, Morris and Doak 2002, Beissinger et al. 2006) calculated in Matlab Vers 7.1 (Mathworks 2005). Variation in the size and age-structure of a population from time $t$ to time $t + 1$ can be computed from:

$$n_{t+1} = An_t$$

where $n$ is a vector describing the age, stage or size-structure of the population and $A$ is a population projection matrix. I used a two-age pre-breeding model with second-year (SY) and after-second year (ASY) females as the two classes:

$$A = \begin{bmatrix} HY1*S0 & HY2*S0 \\ S1 & S2 \end{bmatrix}$$

where $HY1$ and $HY2$ are the number of female young hatched annually by SY and ASY females, $S0$ is the survival rate of juveniles from hatch to the following breeding season, and $S1$ and $S2$ are the survival rates of adult SY and ASY females respectively. Figure 1 shows a life cycle diagram corresponding to this matrix. The age-structured population vector was:

$$n_t = \begin{bmatrix} n1 \\ n2 \end{bmatrix}$$

where $n1$ and $n2$ are the number of SY and ASY individuals at time $t$ respectively. Using this initial deterministic model, we can repeatedly multiply $n$ by $A$, which yields a series of vectors that differ by a scalar equivalent to the population growth rate $\lambda_1$ (the dominant eigenvalue). From $\lambda_1$, I determined $r = \log(\lambda_1)$, the intrinsic rate of population growth as well as the subdominant eigenvalue ($\lambda_2$), reproductive value ($v$, left eigenvector) and the stable-age distribution ($w$, right eigenvector). I also determined the average number of female offspring produced per female over her lifetime (net reproductive rate, $R_0$) as:
\[ Ro = \sum_{x=0}^{n} s_x \cdot f_x \]

where \( s_x \) is the probability of survival to age \( x \) and \( f_x \) is the fecundity of females at age \( x \). After determining the net reproductive rate for both species, I calculated the generation time as:

\[ T = \frac{\ln(Ro)}{\ln(\lambda)} \]

Matrix models are also useful for calculating the sensitivity of \( \lambda_1 \) to absolute changes in the demographic rates (Caswell 2001, Morris and Doak 2002, Beissinger et al. 2006). Specifically, we can calculate the sensitivity \( (S_{a_{ij}}) \) of \( \lambda_1 \) to matrix element \( a_{ij} \) as:

\[ S_{a_{ij}} = \frac{\partial \lambda}{\partial a_{ij}} \]

In cases where a matrix element contains multiple rates (as for the fecundity term in \( A \) above), it is more informative to estimate the sensitivity of \( \lambda_1 \) to the rates that comprise each element (i.e. lower level sensitivities). This is achieved by differentiating the matrix element with respect to the vital rate of interest and applying the chain rule (Caswell 2001). When the scale of demographic rates differ, it can be difficult to compare the effects of absolute changes in each rate on \( \lambda_1 \). Elasticity analyses are useful in this case because they rescale the sensitivity values and measure the proportional change in \( \lambda_1 \) in response to a proportional change in rate \( r_i \):

\[ E_{r_i} = \frac{\partial \lambda_1}{\lambda_1} \cdot \frac{\partial r_i}{r_i} \]

I also calculated the lower level sensitivities and elasticities to the multiple reproductive components that comprise the number of young hatched annually (clutch size, nest success, and the probability of renesting). For this, I used a second deterministic model based on a projection matrix \( B \) with the following structure:

\[
B = \begin{bmatrix} F1 & F2 \\ S1 & S2 \end{bmatrix}
\]

For rock ptarmigan, \( F_1 \) and \( F_2 \) are equal to:

\[
F_1 = [C_1_s \cdot ns_1 + (1-ns_1) \cdot r_1_s \cdot C_2 \cdot ns_2] \cdot S_0 \cdot 0.5 \\
F_2 = [C_1_a \cdot ns_1 + (1-ns_1) \cdot r_1_a \cdot C_2 \cdot ns_2] \cdot S_0 \cdot 0.5
\]

where \( C_1_s \) and \( C_1_a \) are the size of the first clutch for SY and ASY females respectively, \( C_2 \) is the size of the 2nd clutch (equal for both age groups), \( ns_1 \) and \( ns_2 \) is nest success for the first and second attempt respectively, \( r_1_s \) and \( r_1_a \) are the renest probabilities for SY and ASY females, and \( S_0 \) is juvenile survival. Fifty percent of the young were assumed to be female and therefore
estimates are multiplied by 0.5. Equations for white-tailed ptarmigan are the same except ASY females were assumed to have a probability of renesting a second time:

$$F_s = [C_1s \cdot n_{s1} + (1 - n_{s1}) \cdot r_{1s} \cdot C_2 \cdot n_{s2}] \cdot S_0 \cdot 0.5$$

$$F_a = [C_1a \cdot n_{a1} + (1 - n_{a1}) \cdot r_{1a} \cdot C_2 \cdot n_{a2} + (1 - n_{a1})(1 - n_{a2}) \cdot r_{1a} \cdot r_{2a} \cdot C_2 \cdot n_{a2}] \cdot S_0 \cdot 0.5$$

where $r_{1a}$ and $r_{2a}$ are the ASY renest probabilities for 2nd and 3rd attempts. If a 3rd attempt was initiated, I assumed clutch size and nest success was the same as for the second attempt. The contributions of second and third nests to the average fecundity of an age group depends on the probability that a female can initiate multiple attempts. For this to be the case, she must have failed once ($1 - n_{s1}$) for a 2nd attempt or twice ($1 - n_{s1})(1 - n_{s2}$) for a 3rd attempt. Furthermore, to initiate a third attempt at probability $r_2$, she must have already renested once at probability $r_1$. These probabilities need to be included to properly weight the contributions from second and third attempts given their lower frequency relative to first attempts. For both species, survival of SY and ASY females are represented by $S_1$ and $S_2$ as for matrix $A$.

**Stochastic population model**

I introduced environmental stochasticity to the model by allowing demographic rates to be drawn at random from a specified distribution and simulated 1000 population trajectories each for 25 years following the approach of Morris and Doak (2002). For this analysis, I used projection matrix $A$ because of its simpler structure. Estimates of hatched young for the fertility estimate is a more direct measure of reproductive output because it represents the sum total of all the lower level inputs in matrix $B$. Estimates of reproductive output using the lower level rates is very similar to the actual number of hatched young. The number of hatched young were randomly drawn from a stretched beta distribution with mean and variance equal to the observed values across the four years. The maximum and minimum values for this distribution were assigned based on likely upper and lower limits for the two species. Annual survival of second year and after-second year females were assumed equal and drawn from a beta distribution with mean and variance approximated from field data. Annual juvenile survival was also drawn from a beta distribution but simulations were run with a mean rate of 0.22, 0.27 and 0.32 to incorporate the uncertainty described earlier. Empirical survival estimates are apparent estimates where some individuals are lost because of permanent emigration. As I noted in Chapter 4, this is likely to be very low for breeding adults and should only have a slight influence on estimates of $\lambda$. To correct for this, we would need to incorporate a measure that accounts for the rate of
breeding dispersal (immigration and emigration) across the study area, but that was not available here.

To include the potential effects of covariation in the vital rates on population performance (Morris and Doak 2002, Boyce et al. 2006, Ezard et al. 2006), I allowed rates to be correlated within years. Because only 3 and 4 years of data were available for survival and fecundity respectively, it was not possible to examine correlations among demographic rates and therefore, I assigned correlations based on likely values given the species biology. Within-year correlations between SY and ASY fecundity and, between SY and ASY survival are likely strong and I assigned a correlation coefficient (r) of each = 0.9. Annual survival rates of juveniles and adults (combined SY and ASY) may also be correlated although the relationship could vary. A negative relationship might be observed if there are strong density-dependent effects of adults on juveniles, while a positive relationship may be more likely if environmental conditions affect all age groups equally. To represent this range of possibilities, I ran the model with juvenile-adult survival correlations = -0.5, 0 and 0.5, and evaluated how each affected population growth. I assumed there were no within-year correlations between the reproductive and survival components. Between-year correlation might occur when factors such as climatic conditions, predator abundance, disease or food supply are temporally autocorrelated (Royama 1992, Morris and Doak 2002). However, because of the difficulty in identifying these effects given short term data, I assumed there were no between-year correlations in this analysis. Density dependence is also a key process in population dynamics (Arcese et al. 1992, Royama 1992, Morris and Doak 2002), but is difficult to incorporate in matrix projection models because many years of data are required to identify the functional relationship (Caswell 2001, Morris and Doak 2002). Rather than assume what this relationship might be, I chose not to include density dependence here.

**Effects of variation in breeding season climate on population dynamics**

I also investigated the effects of a change in breeding season climatic conditions on population growth rates of each species. I used the Canadian Regional Climate Model (CRCM) 3.6 produced by the Canadian Centre for Climate Modelling and Analysis (Plummer et al. 2006) to create scenarios for future climate by 2050.

*Scenario 1.* I first estimated the influence of a change in mean spring (April-May) temperature on population growth. In chapter 3, I showed that warmer temperatures lead to earlier breeding, larger clutches and a greater number of young hatched. The CRCM model was used to estimate
change in mean spring temperatures in the study area from now until 2050 and predicts about a 1.4°C rise over that period (Plummer et al. 2006). To incorporate this effect in the first scenario, I used the previously determined relationships between timing of breeding and spring temperature to estimate the predicted change in breeding date relative to the average during the study. I then used the relationship between breeding date and number of hatched young to estimate how the number of hatched young might change over time. This estimate was incorporated in projection matrix A and I simulated 5000 runs of stochastic population growth each over 25 years. All parameters were drawn from the same distributions as noted earlier and for this analysis, I assumed there was no change in the variance. I also calculated the percent of runs that ended up below a quasi-extinction threshold equal to 20% of the starting population size of 50 females.

Scenario 2. Climate change models also suggest an increase in annual variability of temperature and precipitation for much of western North America (Christensen et al. 2007), although predictions of variability are less certain than those for a directional change. Increased climate variability in spring should result in greater variation in the annual number of hatched young as observed in Chapter 3. To examine this, I compared stochastic population growth when the annual variability in hatched young increased by 25 and 50% above current levels, assuming the same mean change as for Scenario 1.

Scenario 3. To examine how populations of each species respond to severe events such as that observed in 2006, I parameterized three projection matrices with values of hatched young and adult survival as observed in 2004, 2005 and 2006. For this type of analysis, a particular matrix element always occurs with the other elements in that year and it may be more appropriate to assume that juvenile survival was higher than average in the two good years and lower in the severe year. Hannon and Martin (2006) note that ptarmigan juvenile survival from independence to recruitment tends to be about 15-25% lower than adult survival. Therefore, to estimate juvenile survival for each of the three years, I used annual measures of chick survival through August and assumed survival from September through April to be 20% of adult survival. Because of the uncertainty in this parameter, I also ran a separate set of analyses using the original average of 0.27 for both species. I then ran model simulations where the frequency of the severe year varied between 10 and 50 percent. For each case, 1000 population trajectories were run for 25 years and I examined the population growth rate and probability of quasi-extinction as for scenario 1.
Results

Deterministic model results

Asymptotic population growth rates of rock ptarmigan were approximately stable at $\lambda=1.013$, while those for white-tailed ptarmigan were lower at $\lambda=0.957$ (Table 5.1). The stable age distribution indicated that ASY females were the dominant age class for rock ptarmigan (61%), while for white-tailed ptarmigan there was a lower proportion of ASY females (45%). This age structure was similar to that observed over the course of the study where ASY females comprised 64% of known breeders for rock ptarmigan but only 48% for white-tailed ptarmigan. The net reproductive rate of a female rock ptarmigan was 1.036 and thus approximately at replacement levels ($R_o=1$), while rates for white-tailed ptarmigan were below this level at 0.919. Generation times were about 0.7 years longer for rock ptarmigan than white-tailed ptarmigan.

To examine sensitivity and elasticity, I decomposed the hatched young term into the underlying reproductive components. Predicted population growth rates for both species were very similar to earlier estimates using hatched young in the fecundity term (rock ptarmigan: $\lambda=1.002$, white-tailed ptarmigan: $\lambda=0.961$, deterministic model result based on $S_0 = 0.27$ and no juvenile-adult survival correlation). $\lambda$ was most sensitive to changes in juvenile survival for both species, although relatively more for white-tailed ptarmigan (Figure 5.2). Survival of the first nest attempt was the next most sensitive for both species, followed by ASY and SY survival for rock ptarmigan and the reverse for white-tailed ptarmigan. Sensitivities to all other reproductive rates were low for both species. The elasticity analysis showed a different pattern for the two species. For rock ptarmigan, ASY survival was the most influential followed by juvenile survival. Reproductive rates for the first attempt had much higher elasticities than those for the second attempt and rates for ASY females were considerably more influential than those for SY females. For white-tailed ptarmigan, juvenile survival had the highest elasticity. Survival of the first nest attempt and SY annual survival were also influential as was first clutch size of both age groups. In contrast to rock ptarmigan, rates from SY females were slightly more influential than those from ASY females and elasticities for the second attempt were higher (Figure 5.2).

Stochastic model results

Predicted population growth rates with a stochastic model were approximately 2 and 4% lower than deterministic predictions for rock and white-tailed ptarmigan respectively (Table 5.2). Population growth rates also varied depending on juvenile survival ($S_0$) and the correlation
between juvenile and adult survival (including SY and ASY females). For rock and white-tailed ptarmigan, respectively, $\lambda$ decreased by about 0.135 and 0.18 as mean juvenile survival rates declined from 0.32 to 0.22. For both species, a positive correlation between juvenile and adult survival depressed $\lambda$, while a negative correlation enhanced it (Table 5.2). Lambda of white-tailed ptarmigan was slightly more responsive than that of rock ptarmigan to a change in the juvenile-adult survival correlation. Under this level of stochasticity, with $S_0 = 0.27$ and no adult-juvenile survival correlation, 14% and 77% of simulated rock and white-tailed ptarmigan populations respectively were predicted to be less than 20% of the starting population size (50 females) at the end of a 25-year period (Figure 5.3).

**Effects of change in breeding season climate on population growth rates**

The average date of first egg (DFE) for rock and white-tailed ptarmigan across the four years was 27 May and 30 May (Chapter 3). The expected average DFE assuming a 1.4°C rise in temperature was 23 May for rock ptarmigan and 24 May for white-tailed ptarmigan. This shift would be less than the variation observed over the four study years where average April-May temperatures varied over a 4.91°C range and mean annual DFE varied from 21 May to 2 June for rock ptarmigan and 19 May to 7 June for white-tailed ptarmigan. Thus, my empirical estimates can provide a measure of how change in spring temperature affects reproduction assuming all else is equal. A 1.4°C rise in mean spring temperatures led to an approximate 14% increase in the mean number of female hatched young for rock ptarmigan and a 10% increase for white-tailed ptarmigan. The enhanced reproductive output in turn increased $\lambda$ for both species by about 0.05 and reduced the percent of populations expected to be below the quasi-extinction threshold after 25 years (Figure 5.3). Increasing the annual variability in the number of hatched young had only a minor influence on population growth rates of both species (Figure 5.3).

**Influence of severe years**

The persistence of both species in relation to the frequency of severe years depended on the manner in which juvenile survival was specified (Table 5.3 shows the range of parameter estimates for each year). When I used the average estimate of 0.27 in the matrix, severe years could be no more frequent than 0.21 for rock ptarmigan and 0.32 for white-tailed ptarmigan to maintain stable populations ($\lambda \geq 1$, Figure 5.4). When juvenile survival was calculated in relation to observed annual differences and as a function of adult survival, estimates for rock ptarmigan ($S_0=0.35$) were considerably higher than for white-tailed ptarmigan ($S_0=0.24$). Under these
conditions, rock ptarmigan had greater resilience and could maintain a stable population even if severe years were as frequent as 0.36, while they could be no more frequent than 0.24 for a stable white-tailed ptarmigan population. Over the course of the study, only one of the four years had this level of severity (0.25 frequency), but without long-term data it is unclear how often these events occur.

**Discussion**

**Influence of life history on parameter sensitivity**

This study allowed for a comparison of how two closely related and sympatric species differ in the influence of the demographic rates on λ, given that at this location, rock ptarmigan have a slower life history than white-tailed ptarmigan (Chapter 4). I found that adult survival had the highest elasticity for rock ptarmigan, while juvenile survival and the reproductive rates were relatively more influential for white-tailed ptarmigan. Moreover, demographic rates of older females had a greater elasticity for rock ptarmigan, while those of younger females did for white-tailed ptarmigan. These results are in accordance with general theory on how life history affects λ for a range of taxa (Heppell et al. 2000, Sæther and Bakke 2000, Clark and Martin 2007). A previous study on willow (*Lagopus lagopus*) and white-tailed ptarmigan also found that juvenile survival and the reproductive rates were relatively more influential for populations that have greater investment in reproduction but lower adult survival (Sandercock et al. 2005a). Heppell et al. (2000) found that mammals that matured early and had high reproductive rates tended to have higher fecundity elasticities and lower survival elasticities. Oli and Dobson (2003) further showed that the importance of the reproductive parameters on λ declined as maturation was delayed and reproductive rate was decreased. Incorporating the importance of different demographic rates on λ has become an important tool in management plans for species of concern (Beissinger and Westphal 1998, Heppell et al. 2000) and variation in life history strategies is clearly an aspect that must be considered.

An important question is to what extent are these findings characteristic of rock and white-tailed ptarmigan populations generally. I showed in Chapter 4 that white-tailed ptarmigan in the Yukon tend to have higher reproductive effort than those in Colorado, although there was little evidence for differences in annual survival. I also suggested that the tendency for a reproduction-survival trade-off between rock and white-tailed ptarmigan in the Yukon may be related to how
each responds to the environmental conditions of this location and might vary elsewhere. There has been little study on how life history strategies and demographic rates vary across the range of a species. Those studies that have been conducted often find inter-population variation. Willow ptarmigan in sub-arctic habitats at La Pérouse Bay, Manitoba, appear to invest more in reproduction but have lower survival than their counterparts in subalpine habitats at Chilkat Pass, British Columbia (Sandercock et al. 2005b). Northern bobwhite (*Colinus virginianus*) populations in the northern part of the range tend to have lower adult survival but greater reproductive output than those in the south (Folk et al. 2007). Some of the most revealing studies are for seabirds due to their long history of demographic study (Frederiksen et al. 2005, Harris et al. 2005). North Pacific kittiwakes (*Rissa tridactyla*) survive better but are less fecund than individuals of the same species in the north Atlantic, perhaps as a consequence of milder winter conditions in the Pacific or more favorable breeding conditions in the Atlantic (Coulson 2002, Frederiksen et al. 2005). Rock and white-tailed ptarmigan might experience similar types of variation across their respective ranges, which may influence reproductive effort. Future research that examines how and why demographic rates of ptarmigan vary across their range would be valuable for predictions of how climate change may influence ptarmigan populations.

**Juvenile survival – an uncertain yet crucial demographic rate.**

Juvenile survival is one of the most difficult demographic rates to measure in birds and yet my results suggest it is a highly influential parameter for ptarmigan populations. A change in the mean estimate from 0.32 to 0.22 with no change in the variance strongly affected $\lambda$ of both species, but especially that of white-tailed ptarmigan. Other studies on ptarmigan and grouse have also found juvenile survival to be an important determinant of population growth rates and/or the number of birds observed at the start of the next breeding period (Weeden and Theberge 1972, Steen and Erikstad 1996, Sandercock et al. 2005a). Similar results have been noted for other short-lived birds (e.g. passerines, Clark and Martin 2007). For ptarmigan generally, dispersal and external recruitment, which is almost entirely by juveniles, is key to regional population persistence and the recovery of local populations following declines (Martin and Hannon 1987, Giesen and Braun 1993, Martin et al. 2000).

The first two weeks after hatch appears to be a particularly risky period with high mortality from predators and cold/wet weather (Steen et al. 1988, Ludwig et al. 2006). Hatching is often synchronous depending on timing of breeding and therefore, conditions during a short period in
early summer might be influential of recruitment to the population the following year. Chicks are also dependent on insects for protein and thus, optimal hatch dates should coincide with periods of peak insect abundance (Lack 1968). If due to climate change, the phenology of plant growth, insect emergence and ptarmigan hatch dates change at different rates, it may have consequences for chick survival (e.g. Ludwig et al. 2006). The period from independence to recruitment is less well studied but survival rates of juveniles during this period are often 15-25% lower than adults (reviewed in Hannon and Martin 2006). Predation appears to be the dominant cause of mortality, but other factors such as weather or food abundance may interact with predators (Smith and Willebrand 1999, Hannon and Martin 2006, Bowker et al. 2007).

**Response of populations to changing climatic conditions**

Global climate change models predict that spring (April-June) temperatures in the region will rise by about 1.4°C by mid-century (Plummer et al. 2006, Christensen et al. 2007). Using the projection matrices combined with empirical data, I found that population growth rates of both species responded similarly and are expected to increase by about 0.05. This increase was slightly reduced following greater variability in spring conditions. I showed earlier that white-tailed ptarmigan populations were more sensitive to changes in the reproductive rates and thus predicted that their lambda should respond more strongly to a rise in spring temperature. However, as I found in Chapter 3, rock ptarmigan have a stronger positive relationship between temperature and the number of hatched young, and although less sensitive to variation in the reproductive rates, this may balance out the response of $\lambda$ to a rise in temperature. My simulations also showed that populations of the two species would be approximately stable over the long-term as long as severe events, which simultaneously depress reproduction and survival, occurred at a frequency of less than once every four years.

A key assumption in using matrix models in this manner is that the demographic rates are only responding to a change in temperature, while all other environmental influences are constant (e.g. Beissinger et al. 2006). This may be unlikely. Because nest predators are a key determinant of reproductive output, accurate predictions would require knowledge on how climate warming would influence behavior, abundance and composition of the predator community. Greater reproductive effort also incurs costs (Jacobsen et al. 1995, Monaghan and Nager 1997) and an interesting question is how would greater effort due to more favorable spring conditions influence annual survival for the two species. We would also need to incorporate how
changes in winter climate might affect populations, especially since $\lambda$ is sensitive to juvenile and adult survival for both species. Climate models predict that by mid-century, winter temperatures in the region will rise by about 2°C while precipitation will increase by 10-20%. The combined effect of these changes is expected to reduce winter snowpack by about 25% (Christensen et al. 2007). Earlier studies on grouse have found both positive and negative effects of snow-depth on adult survival (Wang et al. 2002, Moynahan et al. 2006) and thus, how rock and white-tailed ptarmigan would be affected by this change is uncertain. Any model predictions would also need to incorporate the influence of avian predators as they are typically the dominant factor affecting survival (Braun and Rogers 1971, Nielsen et al. 1999, Valkama et al. 2005).

Grouse and ptarmigan populations cycle in many areas, which presents the question of how will climate change affect the dynamics of cyclic populations (Ranta et al. 2004, Ludwig et al. 2006). It is still unclear as to what drives population cycles, but proposed mechanisms include direct and alternative predator-prey relationships (Angelstam et al. 1984, Nielsen 1999, Korpimäki and Krebs 1996, Krebs et al. 2001a), parasites (Hudson et al. 1999), and, genetic factors and social behavior (Chitty 1967, Watson 1967). The mechanism that initiates a decline at the population peak may also differ from that which accelerates the decline and affects the amplitude of the cycle (Nielsen 1999). In the boreal forest of Canada, the snowshoe hare (Lepus americanus) cycle is produced by an interaction between food supplies and predation pressure from multiple species (Krebs et al. 2001b). There is debate as to whether climate change might disrupt grouse and ptarmigan population cycles (Williams et al. 2004, Ims et al. 2008). For grouse and other species such as voles, the cycle periods become shorter from north to south and eventually collapse (Hanski 1991, Cattadori and Hudson 1999). A proposed mechanism for this collapse is that there is a greater diversity of generalist predators further south whose abundance are not directly linked to any one prey species as they are in northern regions. As a consequence, there is a more direct rather than a delayed influence of predators on prey abundance and this limits the extent to which cycles can develop (Hanski et al. 1991). Theoretical models also show that cycles can disappear through period lengthening (Royama 1992). A current hypothesis is that climate change might disrupt cycles if more variable climatic conditions, particularly in winter, exert a stronger influence on populations and over-ride the delayed density dependent mechanisms that allow cycles to develop (Ims et al. 2008). How these events might influence rock and white-tailed ptarmigan populations in the study area is unclear and would require a
multi-decadal study on the extent to which they cycle and the mechanisms causing cycles. A greater empirical and theoretical emphasis on how climate change affects ptarmigan populations and the extent of cycling is an exciting possibility for future research.
Figure 5.1. Basic life cycle for rock and white-tailed ptarmigan as represented in the population projection matrix. Juv=Juveniles, SY=second year, ASY=after second year, HYs and HYa are the number of hatched young for SY and ASY females, Sj = juvenile survival to age 1, Ss and Sa are the annual survival rates of SY and ASY females. For a matrix model with a pre-breeding census, the elements in the top row of the matrix are the product of the HY and Sj terms.
Figure 5.2. Sensitivity (top) and elasticity (bottom) of survival and fecundity for rock and white-tailed ptarmigan. Rates include first clutch sizes for SY (C1S) and ASY (C1A) females, 2nd clutch size (C2), nest success of first (NS1) and second attempts (NS2), first renest probabilities for SY (R1S) and ASY (R1A) females, second renest probabilities for ASY females (R2), juvenile survival (S0), and, second year (S1) and after-second year (S2) survival.
Figure 5.3. Cumulative probability of quasi-extinction in relation to breeding season climatic conditions for (a) rock ptarmigan and (b) white-tailed ptarmigan. Quasi-extinction was defined as 20% of the starting population size of 50 breeding females after 25 years. Future mean conditions were generated using Canadian Regional Climate Models (mean temperature by 2050) and include an increase in annual variability of hatched young by 25 and 50% above current levels.
Figure 5.4. Predicted lambda of rock and white-tailed ptarmigan populations in relation to the frequency of severe years. Models were run with three projection matrices representing rates from 2004-2006. Solid circles refer to calculations of juvenile survival as a proportion (20%) of adult survival. Open circles refer to juvenile survival assuming a constant rate of 0.27. Values for all parameters are shown in Table 5-3.
Table 5.1. Asymptotic matrix properties for rock and white-tailed ptarmigan. Values are the point estimates based on a deterministic model using projection matrix A with the mean values in Appendix.

<table>
<thead>
<tr>
<th>Matrix property</th>
<th>Rock ptarmigan</th>
<th>White-tailed ptarmigan</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asymptotic population growth rate (λ)</td>
<td>1.013</td>
<td>0.957</td>
</tr>
<tr>
<td>Stable age distribution (w):</td>
<td></td>
<td></td>
</tr>
<tr>
<td>second year / after second year</td>
<td>0.39 / 0.61</td>
<td>0.55 / 0.45</td>
</tr>
<tr>
<td>Weighted reproductive value (v):</td>
<td></td>
<td></td>
</tr>
<tr>
<td>second year / after second year</td>
<td>1.00 / 1.09</td>
<td>1.00 / 1.14</td>
</tr>
<tr>
<td>Net reproductive rate (Ro)</td>
<td>1.036</td>
<td>0.919</td>
</tr>
<tr>
<td>Generation time (T)</td>
<td>2.61</td>
<td>1.90</td>
</tr>
</tbody>
</table>
Table 5.2. Deterministic and median stochastic growth rates of rock and white-tailed ptarmigan based on matrix model projections. Models were run with three values of juvenile survival and three levels of within year correlation between juvenile and yearling/adult survival. Within year fertility and annual survival rates of yearlings and adults were assigned a correlation of 0.9. All other pairwise comparisons were assumed to have no correlation. See methods for additional detail on the model.

<table>
<thead>
<tr>
<th>Juvenile survival</th>
<th>Correlation</th>
<th>Deterministic lambda</th>
<th>Stochastic lambda (sd)</th>
<th>Deterministic lambda</th>
<th>Stochastic lambda</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.22</td>
<td>0.5</td>
<td>0.917 (0.046)</td>
<td></td>
<td>0.818 (0.056)</td>
<td></td>
</tr>
<tr>
<td>0.22</td>
<td>0</td>
<td>0.944</td>
<td>0.923 (0.039)</td>
<td>0.864</td>
<td>0.826 (0.053)</td>
</tr>
<tr>
<td>0.22</td>
<td>-0.5</td>
<td>0.928 (0.033)</td>
<td></td>
<td>0.836</td>
<td>0.836 (0.045)</td>
</tr>
<tr>
<td>0.27</td>
<td>0.5</td>
<td>0.985 (0.048)</td>
<td>0.902 (0.063)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.27</td>
<td>0</td>
<td>1.013</td>
<td>0.993 (0.042)</td>
<td>0.957</td>
<td>0.910 (0.056)</td>
</tr>
<tr>
<td>0.27</td>
<td>-0.5</td>
<td>0.999 (0.033)</td>
<td>0.923 (0.050)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.32</td>
<td>0.5</td>
<td>1.052 (0.048)</td>
<td>0.997 (0.065)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.32</td>
<td>0</td>
<td>1.082</td>
<td>1.062 (0.044)</td>
<td>1.048</td>
<td>1.000 (0.061)</td>
</tr>
<tr>
<td>0.32</td>
<td>-0.5</td>
<td>1.065 (0.038)</td>
<td></td>
<td>1.008</td>
<td>1.008 (0.057)</td>
</tr>
</tbody>
</table>
Table 5.3. Mean parameter estimates for rock and white-tailed ptarmigan during two years of high productivity and survival (representing 2004-05), and one severe year of low productivity and survival (representing 2006). These parameters were used in matrix projection models to predict population persistence under varying frequency of the severe year (see Figure 5-4).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Rock ptarmigan</th>
<th>White-tailed ptarmigan</th>
</tr>
</thead>
<tbody>
<tr>
<td>SY hatched young (female)</td>
<td>1.34</td>
<td>1.21</td>
</tr>
<tr>
<td>ASY hatched Young (female)</td>
<td>1.68</td>
<td>1.52</td>
</tr>
<tr>
<td>Juvenile survival (method 1)</td>
<td>0.40</td>
<td>0.48</td>
</tr>
<tr>
<td>Juvenile survival (method 2)</td>
<td>0.27 (all years)</td>
<td>0.27 (all years)</td>
</tr>
<tr>
<td>Adult female survival</td>
<td>0.67</td>
<td>0.74</td>
</tr>
</tbody>
</table>
References


CHAPTER 6 - CONCLUSIONS

Thesis summary

Understanding what factors influence the distribution and abundance of animal populations has been of special interest recently due to expected effects of global climate change on populations, particularly those in ecosystems such as northern tundra where change will be most rapid (Hassol 2004, Christensen et al. 2007). Although complex, attempts to disentangle these impacts have involved a multi-disciplinary approach involving studies of habitat selection, physiology, behavior, population biology, and, community and landscape ecology. My thesis focused on how the environment affects habitat selection, demography, life history strategies and population dynamics of sympatric rock and white-tailed ptarmigan in northern alpine habitats. My results further our understanding of population ecology of tundra birds by showing how the environment affected reproduction and shaped life history strategies in two species of sympatric ptarmigan. These results were used to predict how populations of each species may respond to climate change in terms of reproductive rate and population growth, although definitive predictions await more detailed study, especially of the non-breeding period and linkages to predator and food effects.

My study showed that three species of ptarmigan segregate during the breeding season based on landscape features such as elevation and slope, and type of ground cover, particularly tall shrubs, graminoids and rock (Chapter 2). Ptarmigan display intra and interspecific territoriality, and results suggest strongly that interspecific competition limits access to breeding habitat, particularly for rock and white-tailed ptarmigan. I also found that when spring snow cover limits available habitat, individuals do not adjust and select different habitat types, but rather delay breeding until suitable habitat is available. This finding confirms research on other tundra bird species that have found similar results (Hendricks 2003, Martin and Wiebe 2004). Climate change has the potential to influence every aspect examined in this thesis, but in my opinion, the most dramatic effect will be a reduction in the distribution of rock and white-tailed ptarmigan across the region as a consequence of rising tree and shrub lines. The potential effects on willow ptarmigan are more complex and dependent on the relative movement of conifers into the subalpine and willows into the alpine.
Warmer spring temperatures enhanced reproductive success of both species via multiple mechanisms (Chapter 3). During the pre-breeding period, warmer temperatures advance breeding date leading to larger clutches and greater numbers of hatched young. This result is commonly observed for a range of bird taxa throughout the northern hemisphere (e.g. Visser et al. 1998, Martin and Wiebe 2004, Ludwig et al. 2006, Madsen et al. 2007, Wilson et al. 2007). An unexpected finding was that the decline in clutch size with delayed breeding was much stronger for rock ptarmigan than for white-tailed ptarmigan. This was only the first of several results showing how two closely related and sympatric species might have different strategies for coping with the same environmental conditions. Warmer temperatures also enhance nest success, but few nests fail directly due to weather suggesting this influence operates indirectly on the behavior of ptarmigan or nest predators. As I noted in Chapter 3, this result is likely common but had been difficult to study prior to the implementation of advanced nest survival models (Dinsmore et al. 2002, Shaffer 2004). By allowing us to treat weather as a covariate, we can examine that influence even when nest predators are the ultimate cause of failure.

The results from chapter 3 initially suggest that rising spring temperatures may be a benefit to reproductive output of ptarmigan in the region, but several issues should be noted. First, shifts in the breeding dates of birds need to match phenological changes of other aspects of the environment (e.g. plant flowering, insect abundance). If there is a mis-match in timing, it may be costly for chicks (Visser et al. 1998). Second, greater stochasticity in annual reproductive output can depress lambda. Although my modeling results only suggested a slight influence of increased variability in the number of hatched young, it is possible that I underestimated the extent of stochasticity due to climate change (Christensen et al. 2007). If greater, this effect may counteract any benefits individuals gain from warmer average conditions. Third, nest predators are an integral component of reproductive success and to make predictions on future impacts of climate on ptarmigan, we need to recognize how the predator and alternative prey community will change. This brings us back to the notion that the study of climate change effects is a multi-disciplinary effort. Fourth, any benefits of warmer springs for these two species in the short term may be countered by a loss of habitat in the long-term. All of these points emphasize how we need to consider both direct and indirect effects of climate change on populations. Finally, understanding long-term responses to climate change will require further study on the potential for adaptation. In the short term, plastic responses of individuals can allow them to cope with
changing conditions, but long-term adjustment requires adaptation, which requires adaptive variation within the population. Only a couple studies have thus far measured the extent of plastic versus adaptive responses to changing climatic conditions (Reale et al. 2003, Charmantier et al. 2008). Further studies on this topic for ptarmigan would be valuable.

Debate on the mechanisms driving life history evolution have been ongoing since Lack, Skutch and Moreau raised the question of why clutch sizes increase with latitude (Moreau 1944, Lack 1947, Skutch 1949). Part of the difficulty in answering this and related questions may be that no single mechanism accounts for life history variation across all species and geographic locations. My study strongly supports this notion (Chapter 4). Patterns of reproductive investment in the first nest attempt appear to converge in a common environment. As a result, rock and white-tailed ptarmigan in the Yukon had larger clutches, smaller eggs and shorter incubation periods than white-tailed ptarmigan in Colorado. This observation was most consistent with hypotheses on how nest predation affects the quantity and quality of reproductive investment into the first nest. A more surprising result was that despite co-existing in the same environment, an alternate mechanism led to a more rapid decline in reproductive effort over time for rock ptarmigan relative than white-tailed ptarmigan. Rock ptarmigan had higher adult survival than white-tailed ptarmigan and the differential allocation of reproductive effort for the two species was consistent with how we expect extrinsic age-specific mortality to influence reproduction (Stearns 1983, Reznick et al. 1990, Gasser et al. 2000). This finding also suggested that two congeneric species might have differing susceptibility to the same environmental conditions and has important implications for understanding life history evolution across populations and conservation strategies for threatened populations.

Life histories influence population dynamics of a species and my modeling results in Chapter 5 are consistent with earlier observations in that 1) species with a faster life history are more sensitive to variation in the reproductive rates and juvenile survival (Sæther and Bakke 2000, Oli and Dobson 2003), 2) increased environmental stochasticity lowers population growth rates and makes them more susceptible to extinction (Lande 1993), and 3) positive covariation among demographic rates lowers population growth rates (Morris and Doak 2002, Ezard et al. 2006). While I predicted that white-tailed ptarmigan might respond more strongly to a change in breeding season climate because of greater sensitivity to reproductive variation, I actually found a similar change in lambda for both populations. Although lambda for rock ptarmigan is less
sensitive to change in the reproductive rates, they show greater variability in the number of hatched young from warm to cold years (as shown in Chapter 3). This highlights a key point in the use of matrix models for conservation in that the overall influence of a particular demographic rate is a combination of the sensitivity of lambda to that rate and the extent to which that rate varies (Caswell 2001, Morris and Doak 2002).

The results of my study also revealed that predictions on climate change impacts for these two species will require further research on what limits their populations during the non-breeding period. For most bird species, the non-breeding period is when most mortality occurs (Newton 1998) and therefore, this result would apply to almost any bird species for which juvenile and adult survival are key factors influencing lambda. White-tailed ptarmigan populations might be affected more strongly if there was a relatively greater influence of climate change on juvenile survival, while rock ptarmigan may be respond more strongly if the effect was greatest on adult survival. As noted earlier however, the influence of a demographic rate on lambda is a combination of sensitivity of lambda to changes in that rate and the extent to which those rates vary. My study provided information on the former but we have far less information on the latter, especially for juvenile survival. Another intriguing question that deserves further study is how will climate change influence population cycles of ptarmigan in northern regions (Williams et al. 2004, Ims et al. 2008)

**Future directions**

As the first detailed demographic study of rock and white-tailed ptarmigan in northwest North America, my research answered a number of questions related to how environments influence life history strategies, demography and population dynamics. However, this work also raised several new questions that would be valuable areas for additional research. Over the past several decades there has been considerable effort in furthering our understanding of what determines reproductive effort in north temperate birds. Far less research has been directed towards the non-breeding season, even though this may be a more important period in terms of population limitation (Sherry and Holmes 1996, Sillett and Holmes 2002). For northern resident birds, the winter period is logistically difficult to work in, particularly for arctic and alpine species. In addition, the non-breeding period is at least twice as long as the breeding period making it more difficult to conduct extensive field work especially given other academic commitments for many researchers. These same issues have affected our ability to study migrant
species during the non-breeding season, but there are additional difficulties. Perhaps the most important is the difficulty in tracking individuals throughout the annual cycle, which limits our ability to link factors affecting individuals during breeding, migration and on the wintering grounds (Webster and Marra 2005).

Despite some of the difficulties of conducting research during the non-breeding period, I strongly believe that this is an area where further emphasis is needed if we are to improve our understanding of population ecology and enhance our ability to make predictions on how populations might be affected by climate change. Below I outline several studies on ptarmigan that would be valuable contributions to the field of life history evolution and population ecology. I discuss these studies in the context of my research in the Ruby Ranges, but this is not necessary as they apply to grouse and ptarmigan throughout their range. Many of the questions and results would also extend to birds generally and similar studies could be conducted on other taxa elsewhere.

1. How do environmental conditions influence annual survival rates of rock and white-tailed ptarmigan?

One of the most interesting findings from this study was that two congeneric species appear to differ in susceptibility to the same environmental conditions. As I noted in chapter 4, part of the higher mortality of white-tailed ptarmigan is likely related to their increased reproductive investment, which carries costs for the individual (Jacobsen et al. 1995). However, it is unlikely that this accounts for all of the observed pattern because males showed the same survival differences and yet appeared to have similar reproductive investment. Answering this overall question would involve several objectives. First, we need to recognize whether the breeding costs of males are similar between the two species. I suggest a study to measure the change in male body condition (mass corrected for overall size) from the pre-breeding to the post-breeding period as an index of reproductive energy expenditure. This should involve several comparisons including change in condition between 1) territorial breeders of the two species, 2) territorial breeders versus territorial non-breeders (i.e. males without females) within each species and 3) males whose females re-nest versus those whose do not. This last question in particular would help us estimate whether male white-tailed ptarmigan incur a cost from a longer breeding season. A complement to this study, which could easily be done simultaneously, would be a focus on breeding behavior of males of the two species and whether this affects territory.
settlement. Despite four years of study, it was not clear which of these two species was socially
dominant to the other. Although approximately 25% smaller, male white-tailed ptarmigan were
aggressive and frequently defended territories or mates against male rock ptarmigan (S. Wilson,
pers. obs.). Further research in this area would help our understanding of the level of
interspecific competition among these species, which ultimately has implications for population
abundance if tundra habitat declines (Hassol 2004).

A second overall aim would be to track a sample of radio-marked males and females of each
species year-round to identify the sources and timing of mortality. In particular, it would be
useful to test whether breeding and non-breeding mortality differs between the two species
within each sex. Given their extended breeding season and the risks associated with incubation
(Wiebe and Martin 1998, S.Wilson unpublished data), we might expect that average May
through July survival rates should be lower for white-tailed ptarmigan. Identifying the cause of
mortality can be difficult, but information from kill sites can be used as evidence and genetic
analyses of scat could be used to determine the proportion of rock, white-tailed and willow
ptarmigan in the diets of avian and mammalian predators (Prugh 2005). We should also keep in
mind that while predation is often the main direct cause of failure, other factors such as weather,
food limitation and disease might increase susceptibility to predators (Newton 1998). Disease
appears to be particularly important for survival of red grouse (Lagopus lagopus scoticus,
Hudson et al. 1995) but less so for ptarmigan in North America, although further study is needed
(Hannon et al. 1998). Climate change might exacerbate disease impacts by allowing disease
agents to thrive in new areas (Naugle et al. 2004), increasing growth rates of parasite populations
(Hudson et al. 2006) or increasing the susceptibility of individuals to disease following a
reduction in condition from other causes (e.g. food abundance, Newton 1998). When individuals
are captured, we can estimate body condition and collect blood samples to measure parasite load.
This information can then be used as covariates in survival models. Radio-collared adults could
also be monitored throughout the fall and winter to determine if rock and white-tailed ptarmigan
occupy the same types of habitat during the non-breeding period. If not, differential habitat
selection might be a factor behind interspecific differences in mortality.

Finally, it would be extremely valuable to examine the extent to which demography differs
across locations depending on how individuals cope with the particular environmental conditions
in that area. Although we often compare differences in demographic rates among individuals
within a population, there has been little study on the extent of variation across populations. As Frederiksen et al. (2005) suggests, this is likely related to the difficulty of collecting detailed demographic data across multiple sites. Those studies that have been conducted across locations often find evidence for geographic variation in demography, which may in turn shape reproductive effort (Frederiksen et al. 2005, Sandercock et al. 2005a). While the environmental conditions of the southern Yukon may be more favorable for survival of rock ptarmigan, those in a different environment may favor survival of white-tailed ptarmigan potentially leading to the opposite life history pattern from the one observed here. Further research in this area (perhaps through collaborative meta-analyses) would be extremely valuable. Ptarmigan are a useful group for this type of study because they are typically year-round residents thus allowing us to directly link environmental conditions at different times of the annual cycle to their life history and demography. Many other resident birds could be studied in a similar manner. At present, this is a more difficult question for migrants because we do not know where breeding populations winter and where wintering populations breed. However, as our understanding of migratory connectivity is enhanced, similar studies for those species will be very beneficial.

2. Dispersal patterns and causes of juvenile mortality

My results in chapter 5 as well as several other ptarmigan studies indicate juvenile survival is strongly influential for population dynamics of ptarmigan (Sandercock et al. 2005b, Hannon and Martin 2006). This has also been found for other short-lived birds such as passerines (Clark and Martin 2007). These findings are disconcerting because juvenile survival is one of the least well known and difficult demographic rates to study. This is primarily due to the fact that most juveniles disperse from natal areas and re-locating them is difficult (Greenwood and Harvey 1982, Hannon and Martin 2006). Earlier studies on ptarmigan have typically found that juvenile females disperse further than males and that external recruitment is key for population persistence in fragmented habitats (Giesen and Braun 1993, Martin et al. 2000). Survival rates of independent juveniles (September to April) is typically lower than adults, but there is considerable variation across studies (Smith and Willebrand 1999, Hannon and Martin 2006).

Studies of juvenile ecology tend to split up the the first year between pre and post-independence and further studies on both of these periods would be valuable. The first two weeks after hatch are a period of high mortality and is also when cold and wet weather can have a considerable impact on chicks (Kastdalen and Wegge 1991, Ludwig et al. 2006). My study
revealed a rapid increase in daily survival as chicks age over the first 3 weeks, but additional study on the causes of mortality would be useful. In particular, I suggest studies focus on 1) daily movements of chicks and what habitat types brood hens select during this time, and 2) how daily chick survival varies with weather conditions, both mean temperatures and the extent of extreme weather.

The post-independence period has received less study and I suggest future studies be focused around two main topics. First, for both species, how far do juveniles disperse and do the rates differ among the two sexes? This could be accomplished by radio-collaring a sample of chicks in late August and monitoring their movements over the next couple months as well as at the start of the following breeding season to identify where they finally settle to breed. In Colorado, juvenile male and female white-tailed ptarmigan tended to remain near the natal areas through fall and winter before dispersing to more distant breeding locations in mid to late April (Martin et al. 2000). Rock ptarmigan breeding habitat is more fragmented in the study region because the ridgelines at higher elevations, which connect different valleys, tend to be more suitable white-tailed ptarmigan habitat. Thus, by following dispersal movements of both species we would be able to address basic ecological questions on distance and sex-specific patterns and improve our understanding of how alpine habitat fragmentation affects dispersal patterns. A second focus during the post-independence period should be on the extent, timing and causes of juvenile mortality. This study would be similar to that proposed earlier for adults, but would provide critical information on juveniles that are necessary for population predictions. Throughout most of chapter 5, I assumed that juvenile survival rates would be similar for the two species. This was true during the pre-independence period, but because adult rock ptarmigan have higher survival than adult white-tailed ptarmigan, it is quite likely that juvenile rock ptarmigan might as well. This will only be answered through accurate estimates of juvenile survival and determining causes of mortality. The answer to this question would add an invaluable component to our understanding of ptarmigan life history evolution, and indeed, life history strategies in general.
References


Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish. Ibis 91:430-455.


Appendices

Appendix 1. Common dwarf shrub, woody shrub, forb and lichen species associated with rock, white-tailed and willow ptarmigan nesting habitat in the southern Yukon Territory. Values in brackets show the average percent occurrence across plots although many uncommon species are not uniformly present across plots. For tall shrubs, dwarf shrubs and lichens, I include the species or genus if their average percentage was greater than 0.2. For forbs, I show the 10 most common species around the nests of each.

<table>
<thead>
<tr>
<th>White-tailed ptarmigan</th>
<th>Rock ptarmigan</th>
<th>Willow ptarmigan</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tall shrubs</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Salix pulchra</em> (0.86)</td>
<td><em>Salix pulchra</em> (8.6)</td>
<td><em>Betula glandulosa</em> (45.21)</td>
</tr>
<tr>
<td><em>Salix glauca</em> (0.60)</td>
<td><em>Betula glandulosa</em> (0.63)</td>
<td><em>Salix pulchra</em> (24.43)</td>
</tr>
<tr>
<td><em>Potentilla fruticosa</em> (0.22)</td>
<td><em>Salix glauca</em> (0.46)</td>
<td><em>Salix glauca</em> (3.64)</td>
</tr>
<tr>
<td><strong>Dwarf shrubs</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dryas octopetala</em> (13.81)</td>
<td><em>Dryas octopetala</em> (6.85)</td>
<td><em>Vaccinium vitas-idaea</em> (1.18)</td>
</tr>
<tr>
<td><em>Salix arctica</em> (3.18)</td>
<td><em>Salix reticulata</em> (6.52)</td>
<td><em>Salix reticulata</em> (0.89)</td>
</tr>
<tr>
<td><em>Salix reticulata</em> (2.69)</td>
<td><em>Salix polaris</em> (1.49)</td>
<td><em>Empetrum nigrum</em> (0.36)</td>
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<tr>
<td><em>Salix polaris</em> (1.76)</td>
<td><em>Salix arctica</em> (1.47)</td>
<td><em>Ledum decumbre</em> (0.36)</td>
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<tr>
<td><em>Potentilla biflora</em> (0.34)</td>
<td><em>Vaccinium uliginosum</em> (0.47)</td>
<td><em>Vaccinium uliginosum</em> (0.07)</td>
</tr>
<tr>
<td><em>Pyrola grandiflora</em> (0.17)</td>
<td><em>Vaccinium vitas-idaea</em> (0.41)</td>
<td><em>Salix arctica</em> (0.04)</td>
</tr>
<tr>
<td><em>Vaccinium vitas-idaea</em> (0.14)</td>
<td><em>Salix barclayi</em> (0.35)</td>
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<tr>
<td><em>Potentilla hyperbactica</em> (0.13)</td>
<td><em>Pyrola grandiflora</em> (0.21)</td>
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</tr>
<tr>
<td><em>Potentilla fruticosa</em> (0.10)</td>
<td><em>Potentilla biflora</em> (0.11)</td>
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<tr>
<td><strong>Forbs</strong></td>
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<tr>
<td><em>Silene acaulis</em> (0.62)</td>
<td><em>Artemisia arctica</em> (1.12)</td>
<td><em>Petasites frigidus</em> (1.39)</td>
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<td><em>Artemisia arctica</em> (0.43)</td>
<td><em>Polygonum bistorta</em> (1.06)</td>
<td><em>Mertensia paniculata</em> (0.71)</td>
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<td><em>Saxifraga bronchialis</em> (0.32)</td>
<td><em>Dodecatheon frigidum</em> (0.75)</td>
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<td><em>Parrya nudicaulis</em> (0.26)</td>
<td><em>Petasites frigidus</em> (0.70)</td>
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<td><em>Saxifraga davinica</em> (0.23)</td>
<td><em>Anemone parviflora</em> (0.45)</td>
<td><em>Valeriana sitchensis</em> (0.25)</td>
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<td><em>Oxytropis nigrescens</em> (0.22)</td>
<td><em>Valeriana sitchensis</em> (0.23)</td>
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<td><em>Petasites frigidus</em> (0.13)</td>
<td><em>Gentiana algida</em> (0.21)</td>
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<tr>
<td><em>Anemone parviflora</em> (0.12)</td>
<td><em>Castilleja hyperborea</em> (0.20)</td>
<td><em>Cardamine purpurea</em> (0.07)</td>
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<tr>
<td><em>Polygonum bistorta</em> (0.11)</td>
<td><em>Silene acaulis</em> (0.17)</td>
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<tr>
<td><strong>Lichens</strong></td>
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<tr>
<td><em>Flavocetraria spp.</em> (6.49)</td>
<td><em>Flavocetraria spp.</em> (5.01)</td>
<td><em>Cladina spp.</em> (0.82)</td>
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<tr>
<td><em>Cladina spp.</em> (2.93)</td>
<td><em>Cladina spp.</em> (1.52)</td>
<td><em>Flavocetraria spp.</em> (0.68)</td>
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<td><em>Stereocaulon spp.</em> (1.30)</td>
<td><em>Stereocaulon spp.</em> (1.17)</td>
<td><em>Peltigera spp.</em> (0.54)</td>
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<tr>
<td><em>Thamnolia vermicularis</em></td>
<td><em>Thamnolia vermicularis</em> (0.69)</td>
<td><em>Dactylina arctica</em> (0.21)</td>
</tr>
<tr>
<td><em>Dactylina arctica</em> (0.31)</td>
<td><em>Dactylina arctica</em> (0.64)</td>
<td><em>Cladonia spp.</em> (0.18)</td>
</tr>
</tbody>
</table>

* Salix spp. likely include hybrids
Appendix 2. Parameter estimates used in deterministic and stochastic projection models. SY and ASY refer to second year and after-second year respectively. Clutch size, nest success and renest probability were only used in deterministic models and so variance was not incorporated. Only ASY female white-tailed ptarmigan were assumed to have a probability of a 3rd nest attempt. Because of uncertainty in juvenile survival, a range of estimates were used (see text for further detail).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Rock ptarmigan</th>
<th>White-tailed ptarmigan</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>variance</td>
</tr>
<tr>
<td>SY hatched young (female)</td>
<td>1.26</td>
<td>0.18</td>
</tr>
<tr>
<td>ASY hatched young (female)</td>
<td>1.58</td>
<td>0.28</td>
</tr>
<tr>
<td>1st clutch size SY/ASY</td>
<td>7.10 / 7.67</td>
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<tr>
<td>2nd clutch size (SY=ASY)+</td>
<td>5.43</td>
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</tr>
<tr>
<td>1st nest success (SY=ASY)</td>
<td>0.314</td>
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</tr>
<tr>
<td>2nd nest success (SY=ASY)</td>
<td>0.430</td>
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<tr>
<td>1st renest probability SY/ASY</td>
<td>0.26 / 0.33</td>
<td></td>
</tr>
<tr>
<td>2nd renest probability (ASY)</td>
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</tr>
<tr>
<td>Juvenile female survival</td>
<td>0.22 – 0.32</td>
<td>0.01</td>
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<tr>
<td>Adult female survival (SY=ASY)</td>
<td>0.62</td>
<td>0.01</td>
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Appendix 3. UBC Animal Care Permit

THE UNIVERSITY OF BRITISH COLUMBIA

ANIMAL CARE CERTIFICATE

Application Number: A05-0450

Investigator or Course Director: Kathy M. Martin

Department: Forest Sciences

Animals:

Birds - Other Ptarmigan 260

Start Date: April 1, 2005

Approval Date: March 17, 2008

Funding Sources:

Funding Agency: UBC VPR Research Development Fund
Funding Title: Support for an NSERC - International Polar Year award entitled "Climate forcing of alpine tundra ecosystems"

Funding Agency: UBC Overhead Recovery
Funding Title: Support for an NSERC - International Polar Year award entitled Climate forcing of alpine tundra ecosystems in southwest Yukon: a Canadian contribution to the International Polar Year

Funding Agency: Natural Sciences and Engineering Research Council of Canada (NSERC)
Funding Title: Kluane Lake Research Station

Funding Agency: Natural Sciences and Engineering Research Council of Canada (NSERC)
Funding Title: Northern Alpine Research Laboratory igloos

Funding Agency: Natural Sciences and Engineering Research Council of Canada (NSERC)
Funding Title: Avian ecology and climate variability in Kluane alpine ecosystems

Funding Agency: Natural Sciences and Engineering Research Council of Canada (NSERC)
Funding Title: Climate variability monitoring for northern alpine bird research
Appendix 3 (continued). UBC Animal Care Permit

<table>
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<td>Ecology of alpine and forest birds</td>
</tr>
<tr>
<td>UBC Grants from Federal Departments</td>
<td>Potential effects of climate change on breeding biology and population dynamics of rock and white-tailed ptarmigan in the southwest Yukon</td>
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<tr>
<td>UBC Grants from Federal Departments</td>
<td>Potential effects of climate change on breeding biology and population dynamics of rock and white-tailed ptarmigan in the Yukon Territory</td>
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<tr>
<td>UBC Grants from Federal Departments</td>
<td>Effects of climate change on breeding biology and population ecology of alpine ptarmigan</td>
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<tr>
<td>UBC Grants from Federal Departments</td>
<td>Potential effects of climate change on breeding biology and population dynamics of rock and white-tailed ptarmigan in the Yukon Territory</td>
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<td>UBC Grants from Federal Departments</td>
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<td>UBC Grants from Federal Departments</td>
<td>Effects of climate change on breeding biology and population ecology of alpine ptarmigan</td>
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</tbody>
</table>

Unfunded title: N/A

The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility.

Office of Research Services and Administration
102, 6190 Agronomy Road, Vancouver, BC V6T 1Z3
Phone: 604-827-5111 Fax: 604-822-5093