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The interactive effects of climate, social structure, and life history on the population dynamics of hoary marmots (*Marmota caligata*)

by

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Abstract

I used 8 years of mark-recapture data to test alternative hypotheses about the relative influence of winter climate, social structure, and life history on survival, reproduction, and population dynamics of hoary marmots (*Marmota caligata*) in the southwest Yukon. Climate, characterized by the mean winter Pacific Decadal Oscillation index (PDO), was strongly related to juvenile survival, more weakly linked with adult survival and fecundity, and did not appear to influence breeding probability. Group social structure had little influence on population dynamics. Variation in adult and juvenile survival affected the population growth rate more strongly than fecundity or breeding probability, but the relative influence of life history parameters changed from year to year. Comparisons between hoary marmots and other alpine mammals indicated that the average environment to which an animal is adapted, the strategies employed to survive winter, and life history constraints may all affect demographic sensitivity to winter climate.

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Chapter 1: Introduction

Context and rationale

The central objective of population ecology is to understand the mechanisms that influence population growth rates (Sibly and Hone 2002). Animal populations can be regulated by their environment, species interactions, and intrinsic characteristics of populations and individuals, or interactions between these factors (Forchhammer et al. 2001; Aars and Ims 2002; Sibly and Hone 2002; Agrawal et al. 2007). Regardless of the cause, a change in the growth rate of a population can always be attributed to specific demographic parameters (births, deaths, immigration and emigration) (Caswell 2001; Oli and Dobson 2003; Oli and Armitage 2004). However, a single factor such as weather can influence multiple life history traits simultaneously, sometimes in conflicting ways (Forchhammer et al. 1998). Identifying the population-level importance of ecological factors therefore requires integrating their influence across all life history traits, while simultaneously considering the influence of other processes.

There is an urgent need for population ecologists to improve their ability to predict the ecological impacts of climate change on wildlife and identify species that are most at risk, especially in arctic and alpine ecosystems (Post et al. 2009). Climate change already appears to be affecting animal populations around the world, and is likely to continue doing so (Parmesan and Yohe 2003). However, animals that live in cold environments (such as arctic and alpine habitat) may be affected most severely. Significant warming is already occurring in these regions, and future change is expected to be greater and more rapid than in most other parts of the world (Hassol 2005; Körner and Ohsawa 2006). In fact, examples of climate-induced extirpations of arctic and alpine animal populations are already beginning to accrue in the literature (Beever et al. 2003, 2010). Accurate prediction of such events requires an understanding of why some species and populations are more sensitive to environmental change than others. Unfortunately, unexplained variability in ecological responses is a common feature of climate change research in arctic and alpine habitats (Post et al. 2009). Part of this variability could be due to the fact that, despite low biodiversity, these ecosystems are home to animals with a diverse array of life history strategies and adaptations to life in a cold, harsh environment.

The genus *Marmota* (Family Sciuridae) provides a useful framework in which to investigate the effects of climate, life history, and other traits on the demography of animals in cold environments (Armitage 2007; Blumstein and Armitage 1998). In particular, marmots are well suited to studying the importance of social structure. There are 14 extant marmot species, 6 of which live in North America (Barash 1989). All 14 species hibernate, and with the exception of the woodchuck (*Marmota monax*), all are restricted to alpine and/or arctic habitats with cold, snowy winters (Barash 1989). However, the geographic ranges of individual species differ considerably in terms of the severity of environmental conditions (Davis 2005). In addition, *Marmota* species exhibit a wide range of social systems and social group sizes, from the solitary woodchucks to the hierarchical family groups of alpine marmots (*Marmota marmota*) (Barash 1989; Blumstein and Armitage 1998; Kyle et al. 2007).

Social structure is relevant for understanding how weather and climate change will affect marmots for several reasons. First, marmot social complexity is commonly viewed as an evolutionary consequence of harsh environmental conditions (Armitage 1999). Genetic relatedness among marmot species is correlated with the degree of similarity in climatic severity between the environments in which they evolved (Davis 2005). In addition, woodchucks are the only marmot species whose range includes temperate, low-latitude habitats, while alpine marmots, which show the greatest degree of social complexity in the genus, live only at or above tree line in regions with heavy snowfall (Farand et al. 2002). Second, large marmot social groups should enjoy a thermoenergetic advantage during hibernation (Boyles et al. 2008), because in most marmot species all social group members occupy the same hibernaculum (Blumstein and Armitage 1998). Finally, social complexity can have direct effects on marmot life histories as a result of social dominance and reproductive suppression (Wasser and Barash 1983). All of these patterns have been documented in populations of the alpine marmot (*M. marmota*), the most social species in the genus (Arnold 1988; Hackländer et al. 2003). However, the influence of social structure on population dynamics, and its importance relative to environmental conditions, appears to vary across the genus (Farand et al. 2002; Armitage and Woods 2003).

My research focused on the population dynamics of hoary marmots (*Marmota caligata*), the largest North American marmot species (Armitage 1999). In the Yukon Territory, near the northern extent of their range, hoary marmots hibernate for approximately 8 months during extremely cold, dark winters where temperatures routinely drop below -40°C (D.S. Hik et al., unpublished data). These conditions are arguably more severe than those experienced by any marmot species for which detailed demographic data were previously available (Farand et al. 2002; Schwartz and Armitage 2004; Bryant and Page 2005; Griffin 2008). Hoary marmots also live in relatively complex social groups (see Fig. 1-1), and are ranked near the high end of the marmot social complexity spectrum (Armitage 2007). However, both social structure and winter climate can be highly variable. For example, in the southwest Yukon, the timing of spring snowmelt differs by as much as a month from year to year (Fig. 1-2), social groups range in size from 2 to ~30 individuals, and both monogamous and polygynous mating systems have been observed (Kyle et al. 2007). This combination of a severe but variable environment and variable social structure made it possible to effectively compare alternative mechanisms of survival, reproduction and population growth.

Research objectives

The basic objectives of my study were to determine how environmental conditions, social structure, and life history interact to shape the population dynamics of hoary marmots, and to gain insight into how these factors affect marmots and socially hibernating animals in general. I was also motivated by interest in why some alpine mammals are more sensitive to climate than others, based on differences in behavior and life history.

Study species

Hoary marmots occur primarily in alpine habitat, although they can also be found in coastal tundra on the north slope of Alaska (Barash 1989). They are common throughout northwestern North America, and their range extends from the Cascade mountains of northern Washington to central Alaska south of the Yukon river (Gunderson et al. 2009). Like all marmots, they are generalist herbivores that feed on grasses, sedges, dwarf shrubs, and herbaceous plants (Hansen 1975). Despite their wide distribution, very little is known about the population dynamics of hoary marmots (Kyle et al. 2007). To date, only one other demographic study, on a population near the southern edge of the species' range, has ever been conducted. Most of that research was not published in the peer-reviewed literature, although parts were summarized in several book chapters (Barash 1989).

Hoary marmots take several years to reach adult size, and typically do not breed until their fourth year of life (Chapter 3). Young animals typically remain with their natal group at least until sexual maturity, at which point most males disperse, but most females and some males remain through adulthood (T.J. Karels, unpublished data; see Fig. 1-1). The disparity in dispersal between males and females is probably due to the existence of social hierarchy. In most social groups, only one dominant male will breed, but he may mate with several females (Kyle et al. 2007). Finally, hoary marmot social groups hibernate communally, providing a mechanism by which group size might influence thermoregulation and overwinter survival (Holmes 1984). Whether hoary marmot females practice reproductive suppression remains unknown, although some authors have speculated that they do (Wasser and Barash 1983).

The collared pika (*Ochotona collaris*): evaluating an alternative life history strategy

Collared pikas (Fig. 1-3) are another species of generalist alpine mammalian herbivores that are common in the southwest Yukon (Franken and Hik 2004). However, pikas are small (~160g) animals with limited fat reserves, and unlike marmots they do not hibernate (Krear 1965; Morrison et al. 2004). Instead, they rely on food caches or ‘haypiles’ accumulated during the growing season to survive the winter (Dearing 1997). They are also individually territorial, which allows individuals to defend their haypiles from theft by other pikas (Smith and Ivins 1986). Collared pikas have short life-spans (2-5 years), and low average probability of overwinter survival (< 0.5; Morrison and Hik 2007). Collared pika survival is correlated with the timing of snowmelt during the previous year, presumably because earlier onset of the growing season gives pikas more time to amass adequate haypiles (Morrison and Hik 2007; Morrison et al. 2004). Fecundity does not appear correlated with winter conditions, although it may be influenced by population density (Morrison and Hik 2007).

In the Yukon, collared pikas and hoary marmots share almost identical habitat requirements. Both species make their burrows in talus patches adjacent to meadows (Fig. 1-4), with haypiles and marmot burrows often literally on top of each other (V. Patil, personal observation). The same is true for American pikas

(*Ochotona princeps*)and yellow-bellied marmots (*Marmota flaviventris*) in Colorado (Barash 1973). Interspecific competition between collared pikas and hoary marmots may exist, but direct interactions occur infrequently (K. O'Donovan, unpublished data). Furthermore, pikas and marmots tend to forage at different distances from the edge of their home talus patches, which may reduce the need for exploitation competition (Barash 1973; Karels et al. 2004b; Morrison et al. 2004). Finally, pikas and marmots that share the same talus are obviously subject to similar weather and other environmental conditions.

However, differences in behavior and life history, especially in their behavioral adaptations to cold (i.e., hibernating versus food-hoarding) imply that the two species experience their environment differently. Pika and marmot populations at a long-term study site in the Yukon have been observed to fluctuate in abundance independently of each other (D.S. Hik, unpublished data). This unexplained variability, which may be due to differences in life history, behavior, physiology, or all three, was the initial motivation for current research on hoary marmot population dynamics. Comparisons between pika and marmot population dynamics are made throughout this thesis to illustrate how interspecific differences can result in different levels of demographic sensitivity to climate.

Study site

All fieldwork was conducted in the Ruby Range Mountains of the southwest Yukon Territory (138 ° W 62 ° N; Fig. 1-5), in a 4-km^2 valley at an elevation of 1650–1900 m. On average, the snow-free growing season was approximately 70 days with a mean July temperature of approximately 7°C (Hik et al. 2001). The terrain was mostly boulder fields (36%) and vascular plants (27%), the remainder being bare ground, mosses and lichens. Suitable habitat for both species was distributed between south-, east-, and west-facing aspects (Fig. 1-4). In mid-August, the peak biomass of available forage ranged from 42 g/m^2 adjacent to boulder fields, to 71 g/m^2 further into the meadows and was dominated by *Dryas octopetala*, *Carex* spp. and *Salix reticulata* (McIntire and Hik 2005). Thus, the amount of available forage here was considerably less than the 117 g/m^2 determined by Holmes (1979) in south-central Alaska in the only other study of high-latitude hoary marmot populations. Other herbivores sharing the same habitat include arctic ground squirrels (*Urocitellus parryii*), ptarmigan (*Lagopus* spp.), voles (*Microtus longicaudus, M. miurius, M. oeconomus, Cleithrionomys rutilus*), Dall sheep (*Ovis dalli dalli*), caribou (*Rangifer tarandus*), and grizzly bears (*Ursus arctos*). Potential marmot predators included golden eagles (*Aquila chrysaetos*), red fox (*Vulpes vulpes*), wolves (*Canis lupus*), wolverine (*Gulo gulo*), coyote (*Canis latrans*), and grizzly bears. Short-tailed weasels (*Mustela erminea*) have occasionally been observed to predate collared pikas, but are probably too small to pose a threat to juvenile marmots.

Marmot capture methods

From May to August 1999 to 2004, most marmots in the population were live-trapped, marked, and released. Live-traps of various sizes (Tomahawk Live Trap Company, Tomahawk, WI) were baited with human urine (Taulman 1989) and live vegetation from the adjacent alpine meadows, including sedges (*Carex* spp.) and herbs (e.g. *Artemisia* spp.), that are part of their normal diet (Hansen 1975; Holmes 1979). Juveniles emerged during a 2-wk period in early to mid-July and were captured upon emergence. At first capture, all marmots were marked in each ear using No. 3 monel tags (National Band and Tag, Newport, Kentucky) and a small piece of colored wire to facilitate individual identification at distances less than 50 m. A unique alphanumeric combination was lightly dyed (Clairol Hydrience, #52 Black Pearl, Clairol Canada, Montreal, Quebec or Nyanzol-D American Color and Chemical Corp., Charlotte, NC) into the fur above the tail of each animal to allow for individual identification at distances up to 200 m with binoculars. Colored wires were replaced annually, and faded dyed markings were reapplied as necessary at subsequent recaptures. Mass, zygomatic arch, and total length were measured at first capture each season, and mass was measured at each subsequent recapture within a season. Sex was determined by hand, and the ages of marmots captured after the first year of life were assigned using discriminant function analysis (DFA) and classification regression tree (CART) models of body size measurements (Karels et al. 2004a).

In 2007-2009, a subset of four social groups was trapped, representing approximately half the population of the valley. All measurements and marking techniques were identical to those used in the earlier census. Some juveniles were not trapped in 2008 and 2009 due to time constraints, but all litters were counted within a week of emergence, while juveniles remained within a few meters of their natal burrow. The 2009 trapping period spanned only two weeks, so trapping effort was systematically divided into four sessions that involved equal man-hours and effort, to allow for population size and detection probability to be estimated under a robust-design mark-recapture framework (Kendall and Pollock 1992; Lebreton et al. 1992).

Climate vs. weather: data and definitions

Weather generally refers to short-term variation in temperature and precipitation, while climate is defined as the average conditions in an environment over an extended period of time. Several decades of data are typically required to study climatic trends, so the length of my dataset precluded me from investigating the influence of long-term climate change on hoary marmots. I focused instead on year-to-year variation in winter temperature, precipitation, and snowpack, which I refer to collectively as 'winter climate'. Short-lived stochastic events like freeze-thaw cycles (Pruitt 1974; Vors and Boyce 2009) may also have been important for hoary marmots. However, I did not have temperature and snow-depth data of sufficient resolution to study such events.

Even where detailed weather data are available, it can be difficult to identify the specific variables that are ecologically relevant for a particular species (Stenseth and Mysterud 2005). One solution to this problem is to try correlating demographic patterns with a large number of variables (maximum temperature, minimum temperature, mean precipitation, cumulative total precipitation, etc.) (Schwartz and Armitage 2004). However, this shotgun approach risks producing statistically significant but spurious results. Multiple weather measurements can be condensed using principal components analysis or similar measures, but the initial choice of variables to be included may still be arbitrary (Stenseth et al. 2003).

I chose to measure winter climate using the Pacific Decadal Oscillation (PDO) index. PDO is a 20-30 year cyclic pattern of climate variation in the North Pacific Ocean that correlates well with temperature and precipitation throughout northwestern North America (Mantua and Hare 2002; Mantua et al. 1997). I estimated PDO using the mean PDO index from November to May (source: http://www.esrl.noaa.gov/psd/data/climateindices). The November-May range was chosen mainly for its biological significance as the period when marmots were hibernating. Mean winter PDO was negatively correlated with timing of spring snowmelt at my site (Morrison and Hik 2007), annual snow accumulation on nearby Mt. Logan (~100 km away; Moore et al. 2002), and snow depth at weather stations across the Yukon (Hegel et al. 2009). There is also a positive relationship between PDO and air temperature in the Yukon (Hegel et al. 2009). Finally, using winter PDO also allowed me to compare my findings with several other recent studies of animal populations in the Yukon that relied on the same climate index (Morrison and Hik 2007, Hegel et al. 2009, Loehr et al. 2010). The utility of large scale climate indices in ecological studies is well-documented. In fact, some authors argue that they are more ecologically relevant than any specific weather variables, because they effectively integrate the effects of all such variables (Stenseth et al. 2003; Stenseth and Mysterud 2005).

Chapter descriptions

In **Chapter 2**, I compared the effects of winter conditions and social structure on the overwinter survival of hoary marmots, while accounting for age and sex. My objectives were to determine whether large, complex social groups were better able to cope with more severe winters, and to compare the sensitivity of juvenile and adult marmots to winter climate. I also contrasted hoary marmot survival patterns with those of other alpine mammalian herbivores, and generated hypotheses to explain interspecific differences in survival.

Studies of animal demography often focus on survival, which is the easiest demographic parameter to model robustly (Caswell and Fujiwara 2004; Lebreton et al. 1992; Ozgul et al. 2007). Fecundity, breeding probability, and other reproductive parameters generally receive much less attention (Ozgul et al. 2007). In **Chapter 3**, I examined the causes and consequences of variation in hoary marmot breeding probability and other reproductive life-history parameters. In particular, this chapter addressed the phenomenon of biennial breeding, which, although rare in mammals, has been reported for eight marmot species including *M. caligata* (Barash 1974; Blumstein and Armitage 1999; Griffin et al. 2007). Like many unusual marmot traits, biennial breeding has been hypothesized as an adaptation for life in cold, unproductive environments (Barash 1974). However, the evidence for this behavior in marmots is scant, and satisfactory explanations for its persistence in wild populations are lacking (Griffin et al. 2007). As with survival, both winter climate and social structure can potentially influence aspects of marmot reproduction, so I investigated whether either or both of these factors explained why hoary marmots would skip breeding opportunities.

As already discussed, the importance of variation in individual demographic parameters cannot be measured without considering their integrated impact on population growth. In **Chapter 4,** I identified the age-classes and life history parameters that made the greatest contribution to variance in the growth rate of a hoary marmot population using two methods: matrix model Life Table Response Experiments (LTREs) and reverse-time mark-recapture modeling (Nichols et al. 2000; Caswell 2001). I conducted an identical analysis using data collected from collared pikas at the same location during an overlapping time period. My first objective was to determine the population-level importance of patterns in survival and reproduction that were uncovered in Chapters 2 and 3. By modeling the population dynamics of marmots and pikas simultaneously, I was also able to test predictions about relationships between life history and population growth, and to identify factors that contributed to differences in the population dynamics of the two species. Finally, this chapter had a major methodological component. Although the two retrospective population analyses I used serve similar purposes (Cooch et al. 2001), they have never been directly compared in the literature using empirical data. I tested the null hypothesis that the two methods should yield identical results. This chapter contains a discussion of how the underlying assumptions and theory behind each approach could affect it’s outcome, and reasons why one method might be preferred over the other.

Chapter 5 presents a synthesis of the preceding three data chapters. It addresses my original study objectives and summarizes the major findings of my research. It also contains suggestions for future research.

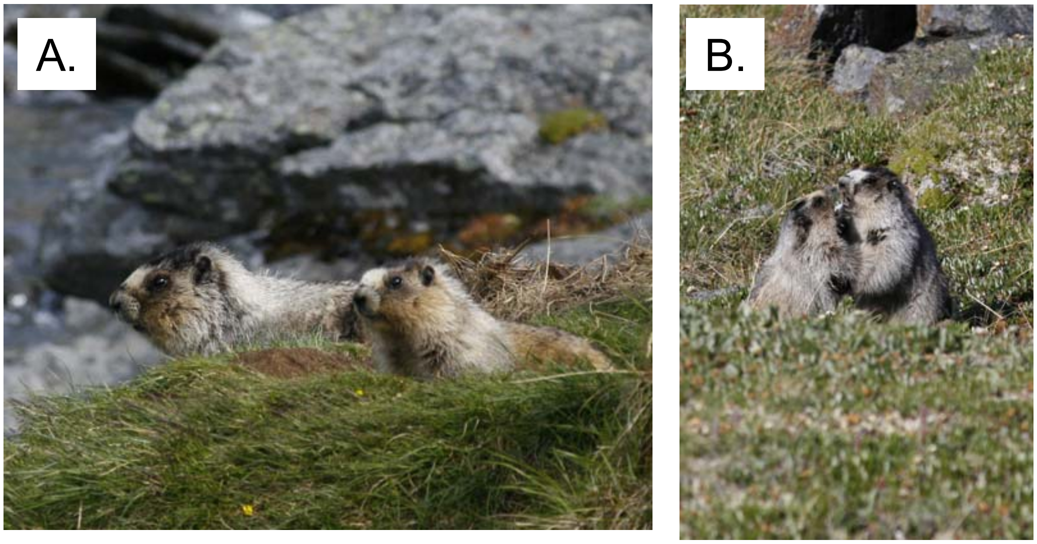

Figure 1-1: A) Adult female and yearling hoary marmot. Immature hoary marmots typically remain with their natal social group at least until sexual maturity, at which point most males disperse. B) Two adult (2-3 years old) hoary marmots ‘boxing’. Social group interactions are not restricted to mothers and their offspring. All members of a social group interact, usually in non-agonistic ways.

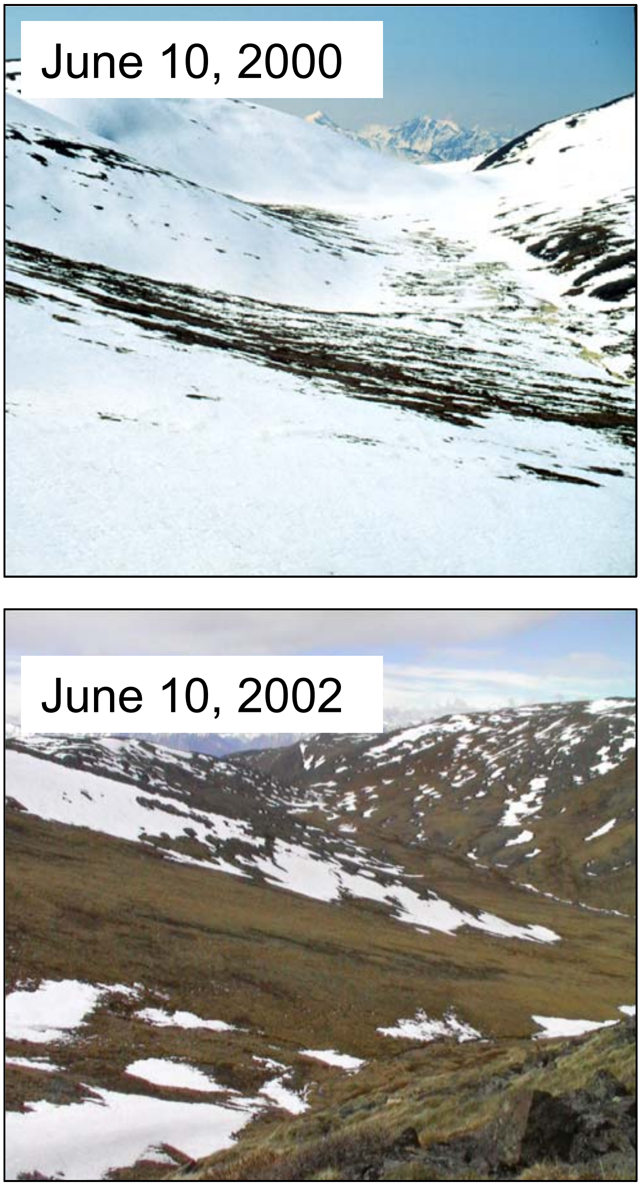

Figure 1-2: Annual variability in snow conditions in the Ruby Range, Yukon, Canada. Both pictures were taken from the same vantage point on the same date. (Courtesy of T.J. Karels).

Figure 1-3: Adult collared pika on talus in the Ruby Range, Yukon, Canada.

Figure 1-4: Typical hoary marmot habitat in the Ruby Range, Yukon, Canada, composed of talus interspersed with alpine meadows. The picture is taken from a south-facing patch of talus looking across to a west-facing patch. Hoary marmots and collared pikas inhabit south-, east-, and west-facing aspects in the study area.

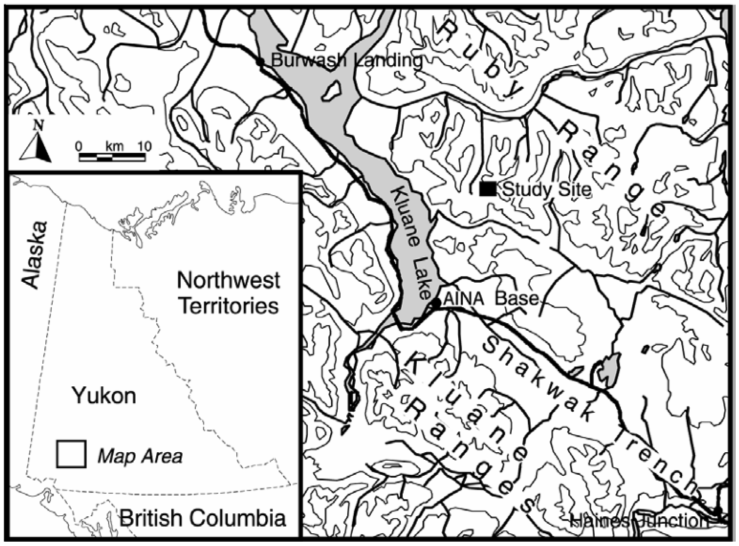

Figure 1-5: Location of hoary marmot study population within the Ruby Range mountains of southwest Yukon, Canada (138° W 62°N).

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Chapter 2. Winter weather vs. group thermoregulation: What determines survival in hibernating mammals?[1]

Introduction

Social structure can exert a powerful influence on the demography of a species. Both the benefits of sociality, which include protection from predators, joint territory defense, and opportunities for cooperative breeding, and the perceived costs, such as lost reproductive opportunities, have been well studied (Blumstein and Armitage 1998; Blumstein and Armitage 1999). However, whether the net effect of group living is positive, negative, or neutral can depend on spatial or temporal variability in environmental conditions, and may be more difficult to assess (Armitage 2007; Forchhammer et al. 1998).

In strongly seasonal environments such as arctic and alpine habitats, the ability to withstand extreme cold can be an important determinant of fitness (Armitage 2007; Willis et al. 2005). Sociality can be advantageous in these environments because individuals can huddle with group members, reducing exposed surface area and allowing them to conserve energy more efficiently (Arnold 1990; Boyles et al. 2008). Huddling efficiency should theoretically increase with group size, and is therefore a potential mechanism for expressing Allee effects because small groups may be less able to buffer the adverse effects of cold temperatures (Arnold 1990). Although numerous examples of this pattern exist, large group size and huddling behavior are by no means ubiquitous among

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mammals faced with cold winters, and the factors that regulate the effectiveness of these strategies as adaptations to cold remain poorly resolved (Boyles et al. 2008).

In particular, the role of group thermoregulation during hibernation has received little attention (Boyles et al. 2008). Although many species that hibernate do so in groups, group size and social structure have only been shown to affect hibernation survival in a few instances (Armitage 1999; Arnold 1990), while other factors such as physiology and microclimate have often been identified as being more important (Aars and Ims 2002; Armitage and Woods 2003).

In this chapter, I present the first detailed analysis of mechanisms that appear to determine overwinter survival for the hoary marmot (*M. caligata*), a poorly studied species distributed throughout northwestern North America. I also compare hoary marmot demography with that of other marmot species and other alpine animals (e.g. pikas, *Ochotona* spp.), and discuss potential explanations for variation in the effect of winter conditions on the survival of these species.

The objective of my analysis was to assess the relative importance of social structure, population density and winter climate, which I defined as the combined influence of temperature and precipitation patterns during a given winter, as determinants of hoary marmot survival. I hypothesized that winter intensity would be most important, while social structure would have a lesser effect, and would have the greatest influence on juvenile marmots, which are much smaller than other age-classes and therefore more susceptible to excessive heat loss (Winter Intensity Hypothesis). This hypothesis was based partly on observations of changes in marmot abundance in the southwest Yukon, and partly on speculation in earlier studies regarding the selective pressures that led to the evolution of sociality in marmots (e.g. Blumstein and Armitage 1998; Armitage 1999).

I also evaluated two alternative, but not mutually exclusive, hypotheses regarding the persistence of large, polygynous social groups. Given the poor quality of the surrounding habitat, large social groups may simply be a necessary consequence of delayed dispersal (Constraint Hypothesis) (Armitage 1999). On the other hand, if non-reproductive adults ('social subordinates') help by warming the burrow during hibernation (see Arnold 1990), then larger, more complex social groups could be an adaptation for surviving northern winters (Adaptation Hypothesis). This question has special significance for wildlife living in arctic and alpine habitats, where the winter climate is extremely harsh, and climate change is projected to occur more rapidly than in many other regions of the world (Hassol 2005; Post et al. 2009).

Methods

Trapping methods and detailed descriptions of the study site and hoary marmot biology can be found in Chapter 1. The following section describes additional field and analytical methods used in this study.

Social group assignment

Locations of trapped and observed marmots were recorded according to a north-orientated grid marked with wooden stakes at 50-m intervals. Observations were recorded by all field personnel. Observations and trapping locations were pooled and analyzed using the overlap routine in program Ranges V (Kenward and Hodder 1996) to determine social groupings. Marmots with > 75% overlap in the 95% kernel estimate (Worton 1989) of home range were assigned to the same social group. Social group assignments of individuals were verified continuously during the study from observations of behaviour (i.e. shared burrow use) and social interactions between individuals. Young of the year were assigned to the social group of their putative mother by observing behavioral interactions and shared burrow use, and those assignments were verified using genetic markers (Kyle et al. 2007). Only marmots that could be confidently assigned to a social group in the study area (i.e. non-transients) were included in analyses.

Parameters and candidate model set

I tested the influence of several intrinsic factors (sex, age, social group composition) and extrinsic factors (weather, food resources) by constructing 25 candidate linear models representing *a priori* biologically plausible combinations of these covariates and their interactions. I chose to include two age-classes in my models, corresponding to juveniles (animals less than one year old), and non-juveniles (all others). Size differences between yearling, two-year-old, and fully mature marmots exist (Barash 1989). However, I was particularly interested in assessing variation in the survival rate of juveniles, because this age-class has by far the the smallest energy reserves during hibernation (Armitage 2007). Juveniles are also the only age class that is strongly influenced by social thermoregulation in other marmot species (Arnold 1990). Because juveniles and yearlings do not disperse and exhibit essentially no sexual size dimorphism (Barash 1989; T.J. Karels, unpublished data), I suspected that sex effects might only apply to non-juveniles, and included models reflecting this hypothesis.

To test my primary hypothesis, winter weather was measured as the mean winter Pacific Decadal Oscillation (PDO) index. PDO is a 20-30 year cyclic pattern of climate variation in the North Pacific Ocean that correlates well with temperature and precipitation throughout northwestern North America (Mantua and Hare 2002; Mantua et al. 1997). I estimated PDO using the mean PDO index from November to May during 1) the winter in which survival was being assessed, and 2) the prior winter (i.e., a lagged effect) (source: http://www.esrl.noaa.gov/psd/data/climateindices). I chose to focus on winter values only, because I was primarily interested in survival during the belowground period for marmots, and because the same period was used to study the relationship between PDO and collared pika survival at my site (Morrison and Hik 2007). As discussed in Chapter 1, mean winter PDO was negatively correlated with timing of spring snowmelt at my site (Morrison and Hik 2007), and with measurements of snow depth throughout the Yukon (Hegel et al. 2009). The candidate model set included models containing non-lagged PDO only, lagged PDO only, and additive effects of both. The social environment was measured as both the total number of marmots within the social group (N_{group}) and the number of non-breeding marmots >2 years old (N_{sub}) at the end of the previous summer. Abbreviations and definitions for all covariates are listed in Table 2-1.

Survival and recapture modeling

I estimated recapture probabilities (ρ) and apparent survival rates (ϕ) using Cormack-Joly-Seber (CJS) models implemented in program MARK (White and Burnham 1999) using the RMark package for R (Laake and Rexstad 2007; R Development Core Team 2009). I evaluated the relative support for models using an information-theoretic approach (Akaike 1973; Burnham and Andersen 2002). The possibility of over-dispersion was accounted for by estimating $\hat{c}$ according to the bootstrapping procedure in program MARK (White and Burnham 1999), and the use of quasi-AIC values corrected for small sample sizes ($QAIC_C$) (Anderson et al. 1994). The estimate of $\hat{c}$ from a global survival model (TIME*AGE*SEX) was 1.33, suggested the presence of some over-dispersion, justifying my use of $QAIC_C$. The top model set was defined as those models where $\Delta QAIC_C < 10.0$.

I ranked models according to their Akaike weights (ω). The strength of evidence for models within a candidate set was compared with evidence ratios (Burnham and Anderson 2002), which are the ratio of ω values for pairs of models (evidence ratios are relative for individual pairs of models). The relative importance of each model covariate was estimated by summing the weights for all models that included that term (Burnham and Anderson 2002). Beta coefficients and associated standard errors for all parameters were averaged across the entire model set (Anderson 2008).

Results

Population abundance and trends

Based on trapping data, total marmot abundance across the study area increased from 66 marmots in 1999 to 146 in 2002 before declining to 80 individuals in 2004 (Fig. 2-1). Colony I had six individuals in 1999 but was extinct by 2001. Considerable inter- and intra-colony variation was observed in the relative abundances of sex- and age-classes (Fig. 2-2). Overall, 217 known-sex individual marmots from eleven social groups were captured and monitored over six years for a total of 509 marmot years.

Capture probability (ρ)

Only six marmots (1 adult male, 5 adult females) were overlooked in one year and seen again in subsequent years. One adult male was missed in 2003, one adult female was missed in 2000 and four adult females were missed in 2002. Mark – recapture models that included sex and age classes for ρ were not supported relative to a model that assumed a constant rate of recapture, suggesting that capture rate did not depend on sex or age. The recapture rate estimated by the top model was $\rho = 0.96 \pm 0.02$ (Estimate ± SE), indicating a high probability of recapture.

Apparent survival (ϕ) estimation

The top model set included 9 models, all of which contained both winter PDO and lagged winter PDO as covariates (Table 2-2). The best model included only those two covariates (Table2-2). The second best model, which included the effects of age, winter climate, and the number of subordinate adults, had similar support to the top model, which only contained the effects of age and winter climate (Table 2-2). However, the log-likelihood of the second-best model was slightly lower than that of the top model (551.4 vs. 556.46), despite the addition of two extra parameters, suggesting that the addition of those parameters (N_{sub} and AGE*N_{sub}) did not improve the model's fit (Burnham and Anderson 2002). The top three models were substantially supported ($\Delta QAIC_C \leq 2$, summed Akaike weight = .84), while support for the remaining models was considerably weaker ($\Delta QAIC_C \geq 4$) (Table 2-2). According to the sum of Akaike weights, the relative ranking of main effects across the entire candidate set was: PDO = PDO_{lag} > AGE > N_{sub} > N_{group} > SEX > VEG (Table 2-3). The effects of climate (as measured by PDO and PDO_{lag}) were supported more strongly than social group size or subordinate adult abundance. Both PDO and PDO_{lag} were negatively related to survival, while the number of subordinate adults and survival were weakly positively related (Table 2-3). The effect size (as measured by the beta coefficient) for the most recent winter was larger and less uncertain than that of the previous winter (Table 2-3). The effect of age on survival varied from year to year (Fig. 2-3). Finally, the relationship between winter PDO and survival was stronger for the juvenile age-class than for older individuals (Table 2-3). Winter

PDO values were significantly correlated with annual juvenile survival estimates from the model TIME*AGE (Fig. 2-4).

Discussion

Climate

The winter intensity hypothesis, which predicted that winter climate would affect survival more than social structure, was supported. In fact, average winter PDO appeared to be more important than any other covariate, including those reflecting differences in sex, age, and local habitat quality. In particular, juvenile survival was strongly correlated with PDO values (Fig. 2-4). Higher PDO values in the second half of the study corresponded with a substantial increase in juvenile mortality (Fig. 2-3). I was unable to directly model the effects of snowfall, snowpack depth, and temperature. However, PDO is highly correlated with snowmelt at my site, and with both snowpack and temperature elsewhere in the Yukon and throughout northwestern North America (Hegel et al. 2009; Mantua and Hare 2002; Moore et al. 2002; Morrison and Hik 2007). Indeed, indices like PDO appear to have more predictive power than specific temperature or precipitation variables, because they effectively integrate all such measures simultaneously (Hallett et al. 2004).

Although the strongest influence on survival came from the most recent winter, lagged PDO (t-1) was also important. Both PDO and PDO_{lag} were negatively correlated with survival, which suggests that the consequences of warmer-than-average winters can be cumulative. For juveniles, any cumulative effects of winter climate would have to operate through maternal effects (Sheriff et al. 2009). I do not have a sufficiently long time series to examine this phenomenon, but lagged climate effects have been observed in other northern species (Boonstra and Hochachka 1997; Forchhammer et al. 1998; Inchausti and Ginzburg 1998). They have not previously been addressed in the marmot literature.

Gender

The effect of sex on survival was weaker than expected. Hoary marmot adult males are more likely to disperse than females by the time they are reproductively mature (T.J. Karels, unpublished data), and apparent survival estimates do not distinguish death from permanent immigration. The true survival rate was therefore likely underestimated for adult males. I cannot estimate the magnitude of this bias, because I do not have data on pre- and post-dispersal male survival. If suitable habitat is available, the difference is likely to be small. For example, dispersing yellow-bellied marmots (*Marmota flaviventris*) in Colorado only experienced a 16% reduction in survival probability compared to philopatric individuals (Van Vuren and Armitage 1994). Because adult male hoary marmots can be up to 1.5 kg heavier than females, it is possible that the reduction in apparent survival was balanced by the effect of sexual dimorphism (Barash 1989; T.J. Karels, unpublished data).

Social group size and group thermoregulation/comparison with other marmot species

There was a relationship between the number of non-breeding adults (subordinates) and juvenile overwinter survival. However, while group thermoregulation was moderately supported relative to PDO, its effect size was smaller and more uncertain (Table 2-3). Overall, I found the greatest support for the constraint hypothesis, meaning that the persistence of large hoary marmot social groups is probably related more to the necessity of delayed dispersal than to the benefits of social thermoregulation (Armitage 1999). Although I anticipated that climate would have a dominant effect on hoary marmot survival, the effects of social group size were still weaker than expected. Multiple studies have shown that all members of a hoary marmot social group hibernate together (Barash 1974; Holmes 1984) and huddling during hibernation should reduce heat loss during arousals (Boyles et al. 2008). In addition, the average mass of juvenile hoary marmots is less than half that of adults, so juveniles should be more sensitive to the energetic costs of hibernation than other age classes (Armitage 2007).

My results contrast with long-term studies of alpine marmot social groups, in which the presence of subordinate adults greatly increased juvenile survival (Arnold 1988; Arnold 1990). Although most marmot species live in seasonal environments with cold winters (Barash 1989; Table 2-4), and several species hibernate together some or all of the time (Armitage 2007), alpine marmots (*Marmota marmota*) are the only members of the genus for which social thermoregulation is crucial during hibernation (Armitage 1999; Arnold 1990). For example, group size has no measurable effect on juvenile overwinter survival in Yellow-bellied marmots (Armitage and Woods 2003). However, yellow-bellied marmots are the most energetically efficient hibernator in the genus, and their social groups are smaller and less variable in size than those of other alpine-dwelling marmots, which makes detecting group-size effects less likely (Armitage and Woods 2003). Two other North American species, Olympic marmots (*M. olympus)* and Vancouver Island marmots (*M. vancouverensis),* are similar to hoary marmots in terms of body size, physiology, and social structure, yet winter conditions do not appear to have a strong influence on survival for either species (Griffin 2008; Bryant and Page 2005; Nagorsen 1987). Olympic marmot mortality rates in Olympic National Park, WA, have apparently remained stable despite a dramatic decline in snowpack depth over the last 40 years (Griffin 2008), and most apparent overwinter mortality of Vancouver Island marmots can be attributed to predation in autumn (Bryant and Page 2005). However, both Olympic and Vancouver Island marmots are restricted to regions with mild winters and deep snowpack (Table 2-4). I suspect that variation in the causes of overwinter mortality between marmot species that are physiologically and socially similar, and the limited benefit of group hibernation at my study site, are both due to the importance of winter conditions (Table 2-4).

More specifically, the adaptive value of group thermoregulation during hibernation is probably limited by both the severity of winter temperatures and the availability of snowpack or other forms of thermal insulation. Winters in the Ruby Range, Yukon, are characterized by both extreme cold and shallow, variable snow cover (Table 2-4). Given that low PDO values imply deeper snow and later spring melt, inter-annual variability in snowpack is the most plausible explanation for the inverse relationship between PDO and hoary marmot survival in my study (see Mantua and Hare 2002; Morrison and Hik 2007). The hypothesis that winters with less snowfall are more energetically expensive for hoary marmots is further supported by preliminary field data showing a strong relationship between the number of arousals during hibernation and snow depth above the hibernaculum ($R^2 = 0.89$; T.J. Karels and D.S. Hik unpublished data). In contrast, the alpine marmot population studied by Farand et al. (2002) experienced winter snow depths of 140 cm ± 43 cm (mean ± SD). Deep snow cover at alpine marmot sites could promote a higher and more consistent burrow temperature, making inter-annual variation in social structure relatively more important.

Comparison with other alpine herbivores

Hoary marmots are by no means the only alpine animals for which winter climate exerts a dominant influence, particularly in the Yukon Territory. Gillis et al. (2005) found that population growth rate for Arctic ground squirrels at my study site was most sensitive to changes in adult and juvenile overwinter survival during hibernation, and although no specific relationship with PDO was reported, similar processes were likely responsible for the patterns observed. Non-hibernating animals in the region are also affected by winter conditions. At the same site, a recent study of collared pikas found a strong correlation between pika overwinter survival and lagged winter PDO, whereas population density appeared to have little effect (Morrison and Hik 2007). Similarly, PDO was significantly correlated with caribou calf recruitment across the Yukon Territory (Hegel et al. 2009), and was a better predictor of Yukon thinhorn sheep horn growth rates over the last 40 years than genetic variation or size-selective hunting pressure (Loehr et al. 2010). However, unlike hoary marmots, these species were all better off following high-PDO winters. As already discussed, spring snowmelt and the onset of vegetation growth occurred earlier in such years. For animals that do not hibernate, having adequate insulation may not be enough to survive the winter, and the opportunity to accumulate energy reserves during a long growing season beforehand may be more important. This is particularly likely for food-hoarding animals like pikas (Morrison and Hik 2007; Morrison et al. 2004). Deep snow can also act as a hindrance to larger animals like caribou by decreasing their mobility and making them more susceptible to predation (Hegel et al. 2009). On the other hand, warmer winters with less snow do not always benefit non-hibernating animals. For example, an increase in the frequency of freezing rain instead of snow and the resulting loss of available food due to ice cover have been implicated in the decline of several arctic caribou populations (Pruitt 1959; Vors and Boyce 2009). More generally, the influence of climate on population dynamics is likely to differ between species that have different behavioral and physiological traits for surviving the winter, even when they occupy similar habitats or niches.

Conclusions/implications for arctic climate change ecology

The Pacific Decadal Oscillation is a multi-decadal cyclic oscillation in sea surface temperature (Mantua and Hare 2002), so the declining survival rates that I observed cannot be attributed to long-term global warming. However, my results may still be useful when applied to the study of climate change at high latitudes. In a recent review, Agrawal et al. (2007) concluded that predictive ability in population and community ecology is currently hampered by a lack of understanding regarding the role of ‘abiotic and biotic context’. This issue is particularly relevant for the study of arctic and alpine animals, which show considerable, often unexplained, variation in their response to warming (Post et al. 2009). This study highlights three aspects of ecological context that may be important in understanding why closely related or ecologically similar species might react differently to climate change.

First, as my interpretation of interspecific differences between marmots suggests, the relative importance of extrinsic and intrinsic demographic influences should depend on the average environment a species or population is exposed to. Predicting the importance of social thermoregulation and other ‘intrinsic’ adaptations to the cold therefore requires understanding the range of environmental conditions for which those adaptations are optimized.

Second, both temperature and precipitation must be accounted for when studying the ecological effects of climate, something that can be accomplished effectively using large-scale climate indices like the PDO (Stenseth and Mysterud 2005). Marmots are obviously not the only group of arctic and alpine mammals that use snow for insulation. In many northern and alpine ecosystems, the effects of warmer winters on a particular species will depend on the degree to which that species is affected by snowpack depth as compared to temperature, and on the significance of growing season length vs. winter severity for that species. These differences are likely to be influenced in turn by the specific strategies, like hibernation, group thermoregulation and food-hoarding, which a species uses to survive the winter.

Finally, the effects of climate on survival are difficult to determine without considering life history. It may not seem particularly surprising that variation in winter and spring snow conditions affect juvenile hoary marmots more strongly than adults, given their relatively smaller size and mass. However, because of this interaction between age and climate, I would have concluded that the relationship between PDO and hoary marmot survival is much weaker than it appears to be had I failed to account for age-structure. Conversely, juvenile and adult collared pikas at my site benefited equally from high-PDO years with early snowmelt, probably because juveniles must acquire their own territories and haypiles during their first growing season (Morrison and Hik 2007). As a result, a comparison between pikas and marmots could have yielded misleading conclusions about the relative sensitivity of the two species to climate change if differences between their life cycles were ignored. Such dramatic differences between ecologically similar animals in a shared environment indicate that extrapolating the effects of climate change from one species to another is more difficult than previously acknowledged (see Chapter 4).

Table 2-1: Names, abbreviations and descriptions of covariates used in construction of hoary marmot survival and recapture models

Abbreviation	**Definition and Description**
PDO	Mean Pacific Decadal Oscillation from November to May in the winter during which survival is being assessed
PDO_{lag}	Mean Pacific Decadal Oscillation from November to May in the winter before survival assessment
AGE	Non-juvenile (>12 months), juvenile (<12 months)
N_{group}	Total number of marmots within social group
N_{sub}	Number of non-breeding adults (age > 2 years) within social group.
VEG	Mean vegetation biomass per colony based on data from 2002 and 2003. Means were used as relative measure of productivity among colonies
SEX	Female vs. Male
TIME	Annual variation (no trend)
1	No time variation (constant)
Non-Juv:	Denotes a parameter applied only to animals > 12 months old
Juv:	Parameter applied only to animals < 12 months old

Table 2-2: Summary of survival model selection for hoary marmots in southwest Yukon from 1999 to 2004. The model selection procedure used an information-theoretic approach and I provide the number of estimable parameters (K), QAIC corrected for small sample size ($QAIC_C$), difference between $QAIC_C$ and the $QAIC_C$ value of the best model ($\Delta QAIC_C$), model weight (ω), quasi-deviance (QDeviance), and overdispersion parameter ($\hat{c}$). Model parameter abbreviations are described in Table 1. A '*' denotes full interaction between two covariates (both main effects and an interaction term). Where main effects are shown in parentheses, the model includes interaction between the inside and outside of the parentheses, but only additive effects within. For example, the top model could also be written as $AGE + PDO + PDO_{lag} + AGE*PDO + AGE*PDO_{lag}$. Only models with $\Delta QAIC_C < 10$ are shown. Covariate descriptions are contained in Table 2-1.

Model	**K**	**$QAIC_C$**	**$\Delta QAIC_C$**	**ω**	**QDeviance**	**$\hat{c}$**
$AGE*(PDO+PDO_{lag})$	7	432.65	0.00	0.39	85.71	1.33
$AGE*(PDO+PDO_{lag}+N_{sub})$	9	433.02	0.37	0.32	414.60	1.33
$AGE*(PDO+PDO_{lag}+N_{group})$	9	434.72	2.07	0.14	416.31	1.33
$AGE*N_{sub}*(PDO+PDO_{lag})$	13	436.87	4.22	0.05	410.01	1.33
Non-Juv:$SEX*(PDO+PDO_{lag})$, **Juv**: $N_{sub}*(PDO+PDO_{lag})$	12	436.97	4.32	0.04	412.23	1.33
$VEG*(PDO+PDO_{lag})$	7	438.43	5.78	0.02	424.17	1.33
$AGE*N_{group}*(PDO+PDO_{lag})$	13	439.14	6.49	0.02	412.28	1.33
$PDO+PDO_{lag}$	4	440.38	7.73	0.01	99.61	1.33
$N_{group}*(PDO+PDO_{lag})$	7	441.96	9.31	0.00	427.70	1.33

Table 2-3. Akaike weights (ω), model-averaged Beta coefficient estimates (β), unconditional standard errors (SE), and lower and upper bounds of 95% confidence intervals (LCL and UCL) for all parameters and interaction terms used to model variation in hoary marmot survival in Southwest Yukon between 1999 and 2004 (see Table 2). Asterisks denote beta coefficients whose confidence intervals do not include zero. Model-averaging, standard errors, and confidence interval calculations follow Anderson (2008).

	ω	**β**	**SE**	**LCL**	**UCL**	
Main effects						
PDO	1.00	-1.36	0.43	-2.20	-0.52	*
PDO_{lag}	1.00	-0.45	0.40	-1.24	0.34	
AGE	0.97	-0.58	0.72	-1.98	0.83	
N_{sub}	0.41	0.08	0.15	-0.22	0.38	
N_{group}	0.17	-0.01	0.02	-0.05	0.03	
SEX	0.04	0.03	0.06	-0.09	0.14	
VEG	0.02	0.01	0.03	-0.04	0.07	
Interaction Terms						
AGE*PDO	0.95	1.21	0.47	0.28	2.14	*
AGE*PDO_{lag}	0.95	-0.15	0.40	-0.93	0.64	
AGE*N_{sub}	0.37	-0.08	0.13	-0.34	0.17	
AGE*N_{group}	0.14	0.01	0.02	-0.03	0.04	
N_{sub}*PDO	0.09	-0.03	0.06	-0.14	0.09	
N_{sub}*PDO_{lag}	0.09	0.04	0.08	-0.12	0.20	
AGE*N_{sub}*PDO	0.05	0.01	0.03	-0.04	0.06	
AGE*N_{sub}*PDO_{lag}	0.05	-0.01	0.03	-0.08	0.05	
SEX*PDO	0.04	0.02	0.01	0.01	0.04	*
SEX*PDOlag	0.04	0.00	0.01	-0.01	0.02	
N_{group}*PDO	0.02	0.00	0.00	0.00	0.00	
N_{group}*PDO_{lag}	0.02	0.00	0.00	0.00	0.00	
VEG*PDO	0.02	0.00	0.00	0.00	0.00	
VEG*PDO_{lag}	0.02	0.00	0.00	0.00	0.01	
AGE*N_{group}*PDO	0.02	0.00	0.05	-0.10	0.10	
AGE*N_{group}*PDO_{lag}	0.02	0.00	0.01	-0.01	0.01	

Table 2-4: Summary of social systems, latitude, elevation, and winter conditions at major long-term study sites for common alpine-dwelling North American and European marmot species. '*' denotes a column modified from Armitage (2007).

Species	**Social System***	**Latitude**	**Elevation (m)**	**Mean Jan. Temp (C)**	**Winter Snow Depth (cm)**	**References**
Yellow-bellied (*M. flaviventris*)	Female matrilines	38° 57'	2800-3000	-10	108 ± 40 (Jan mean ± SD)	Schwartz and Armitage 2005; Rocky Mountain Biological Lab (www.RMBL.org)
Hoary (*M. caligata*)	Restricted Family	61° 12'	1600	-26.25	10 - 60 (Jan range)	Kyle et al. 2007; I. Myers-Smith, unpublished data; Environment Canada weather archives (http://weatheroffice.gc.ca)
Olympic (*M. olympus*)	Restricted Family	48° 05'	>1400	-1.25	135- 183 (Feb mean, 1385-1600 m)	Griffin 2008; Natural Resources Conservation Service Snow Course Data (http://www.wcc.nrcs.usda.gov/)
Vancouver Island (*M. vancouverensis*)	Restricted Family	49° 24'	700-1400	-2.8	259 ± 91 (Mean max annual depth ± SD)	Bryant and Page 2005; Environment Canada weather archives (http://www.weatheroffice.gc.ca); Taylor 1997
Alpine (*M. marmota*)	Extended Family	45° 29'	2300-3800	-5.8 (daytime)	140 ± 43 (Jan. mean ± SD)	Farand, Allaine and Coulon 2002

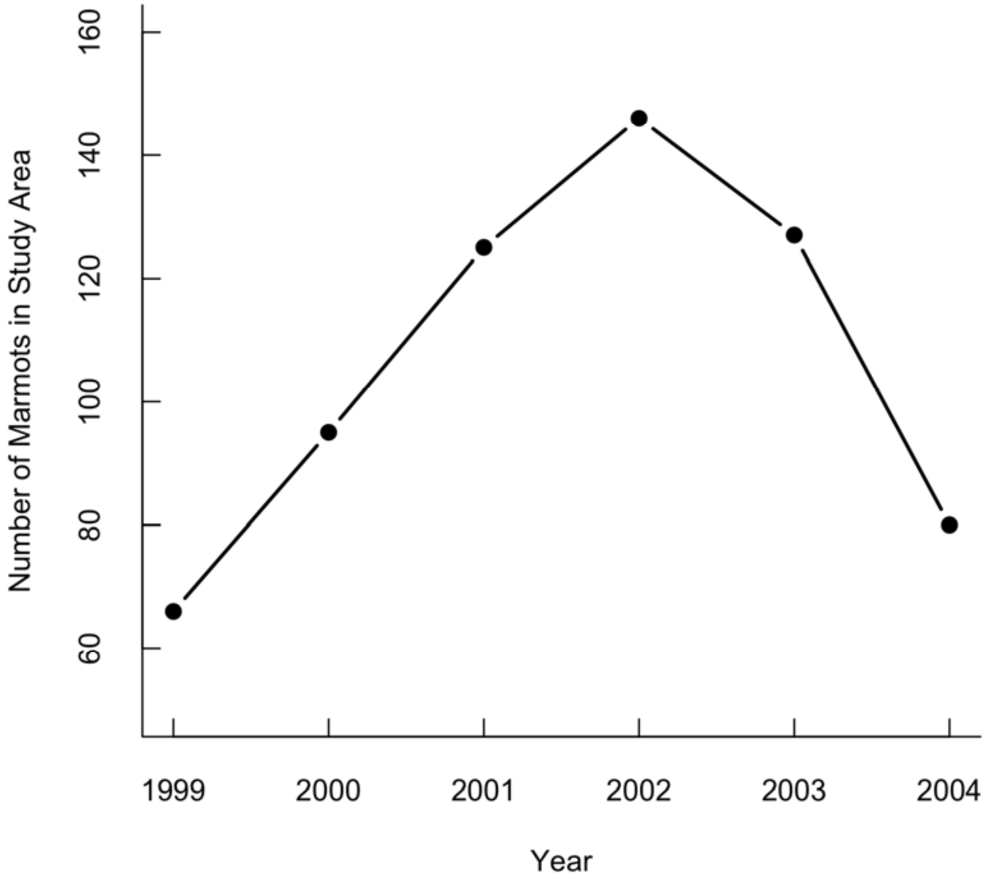

Figure 2-1: Population abundance of hoary marmots from 1999 to 2004 in an alpine valley in southwest Yukon. Abundance estimates were derived from an intensive mark – recapture study in which >96% of all living individuals were recaptured annually.

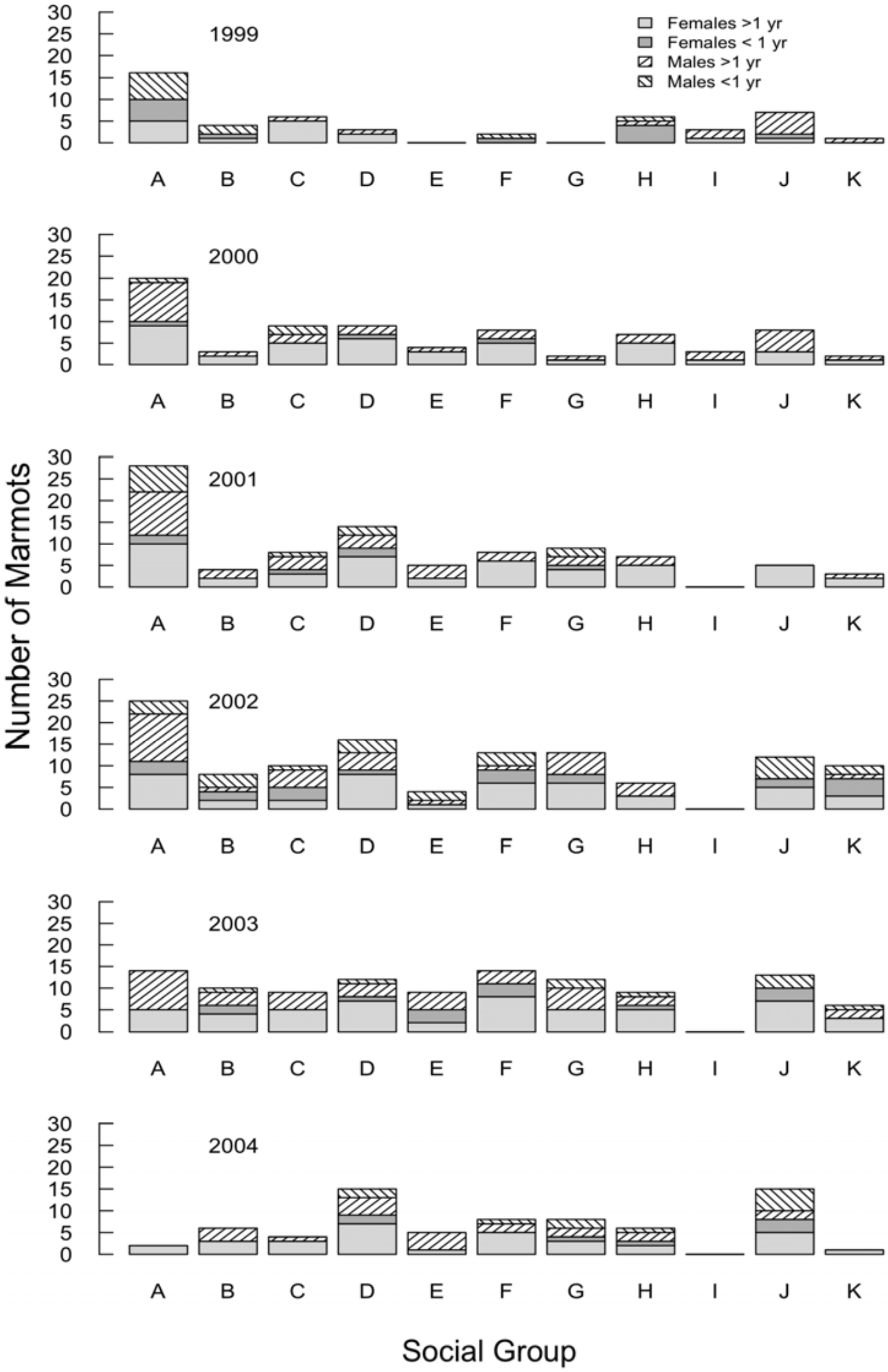

Figure 2-2: Abundance of hoary marmots live-trapped within an alpine valley in southwest Yukon, 1999-2004, stratified by sex, age (juvenile or older), and colony (A-K). Colony I contained no marmots from 2001 to 2004.

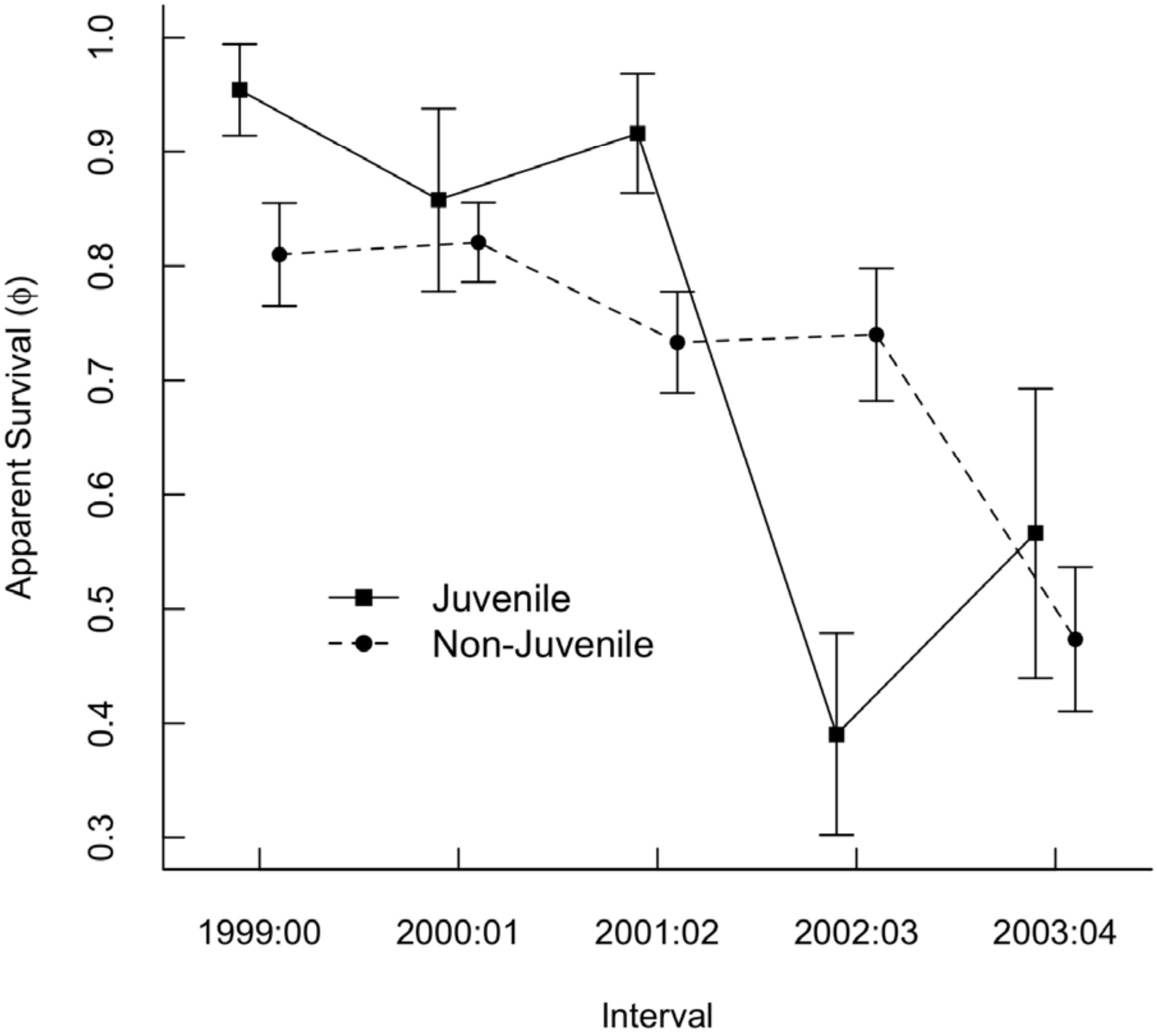

Figure 2-3: Model-averaged apparent survival (ϕ, $\bar{x} \pm 1$ SE) of juvenile and non-juvenile (> 1 yr.) hoary marmots in southwest Yukon from 1999 to 2004 based on a constant rate of recapture and all three models with substantial support ($\Delta QAIC_C \leq 2$).

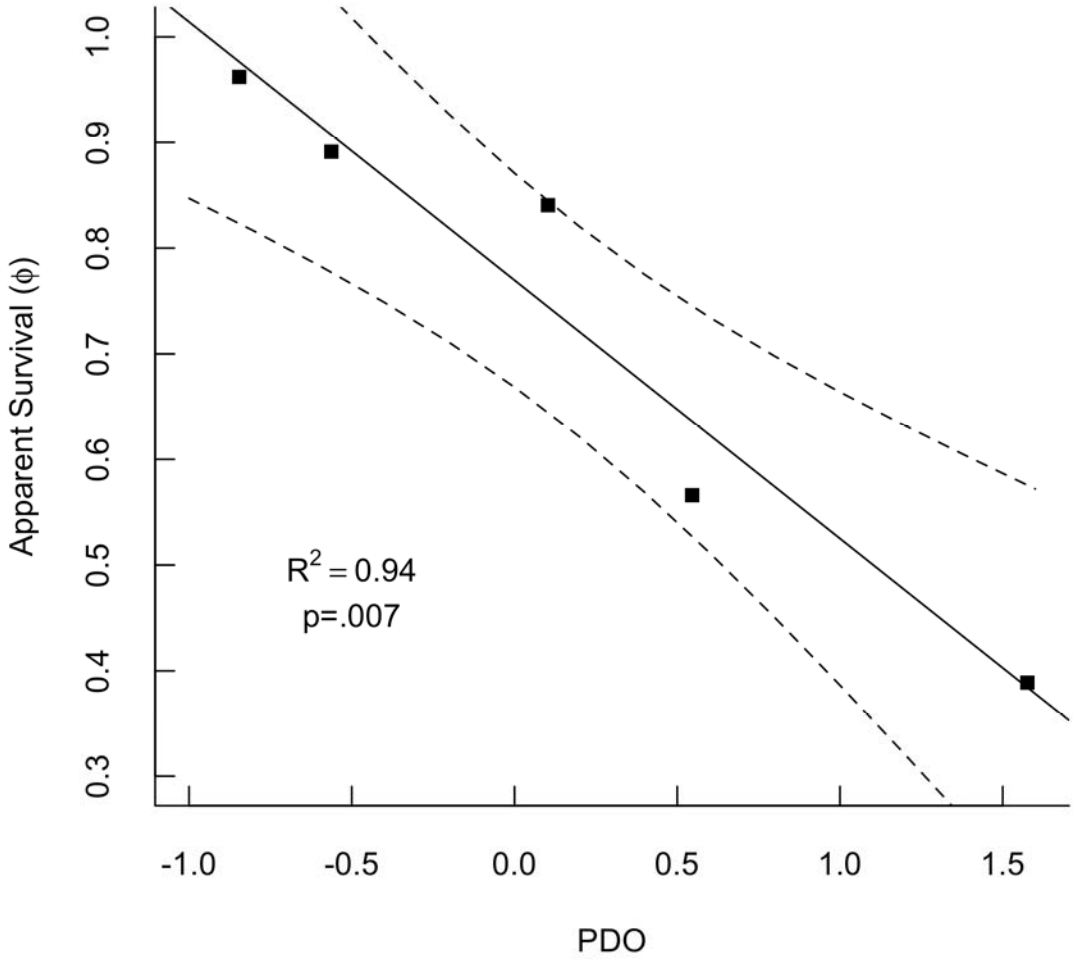

Figure 2-4: Linear regression of mean winter Pacific Decadal Oscillation (PDO) versus annual estimates of juvenile hoary marmot survival in southwest Yukon from 1999 to 2004, from a model in which age-specific survival estimates were not constrained by linear covariates. Dotted lines represent 95% confidence intervals.

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Chapter 3. Do evolved, ecological, or social constraints affect hoary marmot reproduction? An analysis of a presumed biennial breeder

Introduction

Biennial breeding, or reproductive skipping, is an uncommon vertebrate life history strategy that is characteristic of a few groups of long-lived birds and mammals (Heezik et al. 1994; Chastel 1995; Blumstein and Armitage 1999; Dane 2002). Most biennial-breeding species live in harsh, unproductive environments such as arctic and alpine habitat, and this behavior is generally explained as a consequence of environmental constraints on reproduction. (Wasser and Barash 1983; Chastel 1995; Jouventin and Dobson 2002; Griffin et al. 2007). However, harsh environments can also be highly stochastic (Wingfield and Kitaysky 2002; Schwartz and Armitage 2004; Martin and Wiebe 2004). In such situations, a conservative life history strategy involving biennial breeding may be maladaptive, because animals that skip one reproductive opportunity may not live long enough to reproduce in the future (Benton et al. 1995).

Most research on biennial breeding has involved long-lived seabird species with small clutch sizes (Heezik et al. 1994; Chastel 1995; Jouventin and Dobson 2002). For example, most albatross species can live for 40 years or more and lay only one egg at a time (Jouventin and Dobson 2002). Reproductive skipping may be beneficial for these species because their life histories prioritize parental investment in a limited number of young. Biennial breeding has not been well-studied in mammals, or in animals with less extreme K-selected life histories. Among mammals, it is most common in the genus *Marmota*. Of the fourteen extant marmot species, ten have been reported to skip one or more years when breeding (Blumstein and Armitage 1999). Although marmots are capable of living 10-15 years in the wild, adult survival rates can vary widely from one year to the next (Chapter 2; Bryant and Page 2005; Schwartz and Armitage 2004; Griffin 2008) Litter sizes are typically around 3-4, but can be as large as 7 in some species (Schwartz et al. 1998; Allaine et al. 2000). Three alternative but not mutually exclusive hypotheses could explain biennial breeding in marmots: the Evolved Constraint hypothesis, the Ecological Constraint hypothesis, and the Social Constraint hypothesis.

The Evolved Constraint hypothesis, which is similar to the explanation proposed for albatrosses, predicts that biennial breeding in marmots is a highly canalized evolved strategy for minimizing the costs of reproduction in a harsh environment. This hypothesis is difficult to test directly. However, it implies that biennial breeding is an essentially obligate behavior, leading to the prediction that annual breeding should be extremely rare, and that females who breed twice in a row should incur a heavy fitness cost (Weimerskirch et al. 1987). There is a physiological cost to reproduction for some marmot species. Breeding adult female hoary and Olympic marmots spend more time foraging, stay active later in the fall, and have lower average immergence mass than non-breeders (Barash 1980). However, the impact of this energetic loss on survival and lifetime fitness has not been determined.

Both Olympic and hoary marmots are supposedly biennial breeders, but annual breeding has been anecdotally observed in both species (Kyle et al. 2007; Griffin et al. 2007). It is unclear how common such events are, but frequent annual breeding would imply that the reproductive strategies of marmots are more flexible than previously believed. This leads to the Ecological Constraint hypothesis, which predicts that biennial breeding in marmots may only occur when the environment is too unproductive or the animal's condition is too poor to support more frequent reproduction. Animals that live in harsh environments often have plastic life histories that allow them to mitigate the costs of bad years while taking advantage of good years (Wingfield and Kitaysky 2002). Such plasticity would make sense for alpine-dwelling marmot species, because their habitats can be extremely variable (Schwartz and Armitage 2004). Based on this hypothesis, previous breeding state should still have an effect on current breeding probability (based on the physiological costs described in Barash 1980), but this effect should not be absolute. The Ecological Constraint Hypothesis also leads to the prediction that the probability of breeding for all females should be a function of environmental conditions. However, the effects of climate and breeding history could be additive or interactive. Finally, under this hypothesis there could still be a survival cost to reproduction, but it should either be attenuated or compensated for by change in another demographic variable during unusually 'good' years.

Because marmots are social animals, reproductive skipping may also be caused by competition between females (the Social Constraint Hypothesis). Dominant females suppress reproduction by subordinates in both alpine and yellow-bellied marmot social groups (Armitage and Schwartz 2000; Hackländer et al. 2003). In alpine marmots, this behavior leads to higher survival among the dominant female's offspring, which benefit from the presence of non-breeding subordinate adults during hibernation (Arnold 1990). There is speculation in the literature that most or all marmot species that supposedly breed biennially practice reproductive suppression, but suppression has been difficult to document in wild populations (Wasser and Barash 1983; Griffin et al. 2007). If this hypothesis is true, the average probability of breeding should decrease as the number of mature females per group increases (Blumstein and Armitage 1998). Reproductive suppression may also result in decreased breeding probability for younger females, especially in larger groups (Armitage and Schwartz 2000).

I studied the breeding patterns of hoary marmots in the Yukon, Canada using multi-state mark-recapture models. This study was the first formal analysis of variation in breeding probability in a marmot species classified as a biennial breeder. My main objectives were to determine the probability of annual and biennial breeding, and to evaluate the relative support for the three hypotheses described above. To help address my hypotheses, I also quantified the survival cost associated with reproduction, and compared this cost with the physiological costs (slower mass accumulation in summer, lower body mass at immergence) described by Barash (1980), and with the influence of winter climate on survival. Finally, I examined sources of variation in litter size and average social group fecundity to determine whether the processes that governed breeding probability also influenced other reproductive life history traits.

Methods

Basic hoary marmot biology, a description of the study site, and field sampling methods are described in Chapter 1. Additional information about hoary marmots that is pertinent to these analyses, and descriptions of the data sets and analytical methods used, are presented below.

Study species

Hoary Marmots show more plasticity in mating systems than most other alpine-dwelling marmots (Kyle et al. 2007; Blumstein and Armitage 1999). Although dominant females may suppress reproduction by subordinates or practice infanticide, multiple litters per social group, from multiple females, are common (Kyle et al. 2007). Typically, social groups contain only one dominant male, who fathers all offspring. At my study site, extra-pair paternity was relatively infrequent, and the timing of juvenile emergence suggests that most reproduction occurs prior to emergence from hibernacula in the spring (Kyle et al. 2007).

Data set

All analyses were based on trapping data collected between 1999 and 2004. I could not definitively assign all litters to parents or determine the breeding status of all females in 2007-2009, so these data were excluded from my CMR analyses. However, the number of litters, and the number of juveniles per litter, were counted for all four social groups trapped in 2007-2009. There is no evidence that hoary marmot females produce more than one litter per year (Barash 1975), so I used the number of litters as an estimate of the number of breeding females in those years.

From an initial dataset of 217 marmots trapped between 1999 and 2004, I created a second, more limited dataset consisting only of female marmots two years old or older (n=76). I excluded yearlings from this dataset because hoary marmots are not reproductively mature until age two, and generally do not reproduce until age three. In each year, I classified marmots as breeders or non-breeders based on two criteria: genetic parentage assignment and evidence of lactation during capture. Finally, I generated an encounter history for each animal in which the individual was considered present if sighted or captured at least once that year.

Multi-state CMR analysis framework

I analyzed my data using multi-state capture-mark-recapture (Lebreton et al. 1992; Nichols et al. 1994). This involved constructing a set of candidate models to explain variation in three parameters: Survival (S), detection probability (p), and a 'movement' parameter describing the probability of moving into the 'Breeder' state (Ψ). Before analyzing the data, I conducted a goodness of fit (GOF) test using program U-CARE (Choquet et al. 2009). Because I did not detect significant lack of fit in a fully time- and group-dependent global model, I was able to use Akaike's Information Criterion corrected for sample size (AIC_C)

to compare models (Burnham and Anderson 2002). Based on previous analyses, p was modeled as a constant. The mean detection probability was 0.96 ± 0.02 (SE) (Chapter 2).

Candidate model set

Probability of breeding

I selected the models in my candidate model set to represent all alternative hypotheses about the effects of age, social structure, climate, and previous breeding state on the probability of an individual choosing to breed. Age effects were included because I expected that older, more experienced marmots would be more likely to attempt reproduction than those which had recently matured. Previous breeding state was constrained to affect only older (> 3 year) marmots, because two-year-olds generally do not breed. Only 2 two-year-olds reproduced during the course of the study, and these individuals were excluded to simplify analyses. For indices of winter climate, I used the mean PDO index from November to May during both the most recent winter and the winter from the year before (i.e., a lagged effect). My candidate model set included models containing non-lagged PDO only, lagged PDO only, and additive effects of both. The social environment was measured as i) the total number of non-juvenile marmots within the social group (Group), and ii) the number of reproductively mature females in the group (Ad. fem). Both covariates would be negatively related to breeding probability if reproductive suppression were common in the population. A complete list of covariates used, as well as their abbreviations, is given in Table 3-1.

Survival

Survival models included only three covariates: winter PDO, winter PDO lagged by one year, and current breeding state. Previous survival analyses suggested that winter climate was by far the dominant influence on survival; however, these analyses did not include breeding state. I therefore chose this simplified model set in order to test the cost-of-reproduction hypothesis while accounting for the large influence of climate on survival.

CMR analyses / evaluation of fit

I constructed all analyses using program MARK and the RMark package in R (Laake and Rexstad 2007; R Development Core Team 2009). I ranked models using AIC_C (Akaike et al. 1973), and evaluated the relative importance of covariates by summing their AIC_C weights across the entire model set (Burnham and Anderson 2002). I also model-averaged Ψ and S across the entire model set (Burnham and Anderson 2002; Anderson 2008). Finally, I used the averaged Ψ values to predict the number of breeding females in 2007-2009. These predictions were compared with the estimated number of breeders from those years to test the generality of my results.

Fecundity models

I used generalized linear mixed models (GLMM's) to examine the effects of winter PDO, lagged winter PDO, group size, and group*climate interactions on three measures of hoary marmot fecundity. The three response variables were juveniles per social group (n = 66), average fecundity (juveniles per adult female w/in group; n=66), and litter size using a dataset of all litters with known mothers (n = 41). Error distributions were chosen after testing for conformity to a Poisson distribution (Scrucca 2004). Random effects were included based on likelihood ratio tests using the most parameterized fixed-effects model in each model set (Bolker et al. 2009). Results of overdispersion tests, the error distributions and the random effects used for each response variable are shown in Table 3-2. In all cases, I ranked models and calculated the relative support for individual variables using AIC_C. Beta-coefficients were model-averaged, and unconditional standard errors for those coefficients were estimated by bootstrapping with 1000 replications. The covariates used in all models are listed in Table 3-1.

Results

Breeding probability

Group size and winter climate were weak predictors of Ψ, the probability of moving into the 'Breeder' state (Table 3-3; Table 3-4). Older individuals were much more likely to breed in a given year than newly mature marmots (Fig. 3-1). Models with previous breeding state as a predictor of Ψ were moderately supported (Table 3-3), although age was a much better predictor (Table 3-4; Fig.

3-1). Older marmots that bred during the previous year were slightly more likely to breed in the current year than those that had not, although the difference between the two was negligible (Fig. 3-1).

When model-averaged estimates of breeding probabilities were used to predict the number of breeding females in a subset of the population during 2007-2009, the results were within 1-2 litters of the observed values in each year (Fig. 3-2). Year-to-year variation in the number of breeding females was also predicted accurately (Fig. 3-2).

Survival / cost of reproduction

Although there was moderate support for breeding state as a predictor of survival, its effect size was negligible (Table 3-3; Table 3-4; Fig. 3-3). Winter climate was a much stronger predictor of survival (Table 3-3; Table 3-4). Lower PDO and lagged PDO values (heavier snowpack and later snowmelt) were correlated with increased survival, which declined over the course of the study. The general pattern of survival in adult females was similar to that observed in the entire adult age-class (Chapter 2).

Non-breeding females showed faster rates of increase in the log ratio of body mass to zygomatic arch width over the course of the season than non-breeders. The difference in slopes was highly significant ($\Delta = -0.0021$, $p < 0.001$). This ratio, which serves as a rough index of body condition, also tended to be higher at the end of August for non-breeders than for breeders (Fig. 3-4).

Group fecundity

Model selection strongly favored social group size as a positive predictor of the number of juveniles produced per group. (Table 3-5). There was also strong support for a negative relationship between group fecundity and winter PDO, although the mixed effects models and negative binomial GLM's gave average effect sizes that differed by a factor of 2 ($e^{-.8} = 0.45$ vs. $e^{-.13} = 0.88$; Table 3-6). The 95 % confidence intervals for the beta coefficient corresponding to PDO's effects were large and overlapping with 0 in both cases, but this overlap was very small (Table 3-6). There were discrepancies in model-selection support for $\mathrm{PDO}_{\mathrm{lag}}$ and climate*group size interactions, which I interpreted to mean that support for these effects was ambiguous at best. Likelihood-ratio tests supported significant random effects of PDO (slope effect) and social group (intercept effect), implying that overall reproductive output and the effects of climate varied spatially.

Juveniles per female (average fecundity)

AIC weights strongly supported a negative relationship between average fecundity and winter PDO (Table 3-6). Although the 95 % confidence interval for the model-averaged PDO beta coefficient overlapped with zero, the bootstrapped distribution of this coefficient was heavily skewed towards negative values. Lagged winter PDO, group size, and group by climate interactions were not as well supported, and the confidence intervals for their beta coefficients all overlapped 0. Likelihood ratio tests indicated significant random effects of social group (intercept effect) on average fecundity, but no random slope effects were supported.

Litter size

The null model had the smallest AIC_C value in the litter size model set, which means that litter size was not well predicted by group size, winter climate, or a combination of the two. Litter size ranged from one to six individuals, although these extreme values were rare. The mean litter size was three (Table 3-6). When only data from 1999-2002 were considered, mother age and litter size were significantly positively related ($R^2 = 0.23$, $p = 0.002$). However, this pattern was not supported by the addition of data from 2007-2009. Average litter size did not vary significantly between social groups, but power was probably low given the unequal sample sizes ($F_{9,41} = 0.606$, $p = 0.78$; Fig. 3-5).

Discussion

Contrary to the predictions of the Evolved Constraint Hypothesis, hoary marmot females in the Yukon were not obligate biennial breeders. Instead, my results suggested that breeding in the previous year was correlated with increased probability of breeding in the current year. These findings contrast with the only other study of hoary marmot breeding patterns (Barash 1974) in which biennial breeding was first suggested. However, the former study was based on a sample of only 9 adult females, and took place during a single summer. In fact, the hypothesis of biennial breeding was derived primarily from Barash's (1974) observation of behavioral associations between adult female marmots, yearlings, and juveniles, and from the observation that approximately half of all females successfully weaned young in a given year.

Interestingly, the latter finding agrees with my results, in that the probability that a mature adult female (>3 yrs.) would breed was approximately 50% in all years (Fig. 3-1). Hoary marmot breeding patterns were also consistent between the two periods of my study. Because I did not have detailed information on reproductive status for the latter sample period (2007-2009), I could not include these years explicitly in my models. However, I was able to accurately predict the number of litters produced each year, which is a reasonable surrogate for the number of breeding females (Fig. 3-2) without including any information other than the number of adult females and their age-classes. The consistency of my results suggests that there is an intrinsic constraint on reproduction in hoary marmots, although the mechanism behind such a constraint is still unknown.

Importance of winter climate

Based on my results, the Environmental Constraint Hypothesis was not an adequate explanation for variation in hoary marmot breeding patterns. On the other hand, the low average probability of breeding could be due to winter conditions so consistently harsh that successful reproduction is uncertain regardless of environmental variation, female condition, or breeding history. In contrast to my breeding probability analysis, the results of my fecundity analyses were more ambiguous with regard to the influence of environment on other reproductive life history traits. Average fecundity (calculated across all adult females) was negatively related to PDO, but litter size was not. However, because of the small number of litters with known mothers, the probability of a type II error was probably quite high. Regardless, total social group reproductive output and juvenile survival were both reduced in years with warm winters and limited snowpack.

Cost of reproduction

The absence of survival costs associated with hoary marmot reproduction implies that the energetic costs associated with breeding and weaning young are not as important for marmot population dynamics as previously suggested (Barash 1980). I did not include an index of female body condition in my survival analyses because females were not all weighed or measured at the same point in the season. However, the seasonal activity patterns of breeding adult females in my study were consistent with those described by Barash (1980), which means they probably incurred similar energetic costs. In addition, breeders ended up at an energetic disadvantage by the end of the season (Fig. 3-4). Nevertheless, they were apparently able to cope with the stress of hibernation equally as well as non-breeders. Such abilities should be selected for in harsh, stochastic environments.

Survival patterns were consistent with the lack of evidence for biennial breeding, because without a high fitness cost of annual reproduction, there should not be strong selection for reproductive skipping. Breeding marmots tended to be in better condition than non-breeders at the beginning of the season (Fig. 3-4), so variation in individual female quality could have confounded my results. However, such differences in quality would presumably also have caused temporal variation in the average probability of breeding (see Fig. 3-1), unless the ratio of high to low quality individuals somehow remained constant over time despite large changes in population size (Fig. 3-6). Finally, my results were also consistent with conclusions from my previous analysis of hoary marmot survival patterns, which suggested that variability in winter conditions, especially snowpack, is more important than intrinsic factors (Chapter 2).

Reproductive suppression / age effects

Complete reproductive suppression can be said to occur when only one female is allowed to breed in a social group (Blumstein and Armitage 1999). This behavior is unlikely to be selected for unless the overwinter survival of juveniles is influenced by the presence of non-breeding subordinate adults. Under such circumstances, dominant females can obtain greater fitness by enhancing the survival of their own offspring than by allowing other females to breed (Allaine et al. 2000; Allaine and Theureiau 2004). My results (specifically the fact that the number of adult females per group was not a strong predictor of Ψ), and a previous study on the flexibility of hoary marmot mating systems (Kyle et al. 2007) both suggest that this pattern is rare among hoary marmots, which is consistent with the limited effect of subordinates on juvenile overwinter survival (Chapter 2). I also did not find strong evidence of partial reproductive suppression, defined as a reduction in subordinate fecundity due to harassment by dominant animals (Blumstein and Armitage 1999). The fact that average fecundity was not related to group size does not preclude partial reproductive suppression, because decreased subordinate fecundity could theoretically be offset by a dominant female producing more young. However, the data show that larger hoary marmot social groups produced more young per year. When social structure was modeled using the number of adult females as a covariate instead of total group size, the results were essentially the same.

Age affects breeding success to some degree in most if not all mammal species (Harvey and Zammuto 1985), so it is not surprising that age-class was an important variable in my models. However, the biological significance of this result is less clear. A positive relationship between age and breeding success could be the result of reproductive suppression if older, more experienced females are more likely to be dominant, as is the case in alpine marmots (Hackländer et al. 2003). On the other hand, social mechanisms are not required to explain a link between age and reproduction: younger females could simply be less effective at caring for their young, or less likely to reach parturition successfully. Because mating, birth, and weaning took place primarily underground at my site (Kyle et al. 2007), I cannot conclusively determine which explanation is correct.

Comparisons with other marmot species

Despite its potential importance, variation in breeding probability has received much less attention than fecundity or survival in demographic studies of marmot populations, and of mammals in general (Ozgul et al. 2007). At a coarse scale, average breeding probability is remarkably similar across the genus *Marmota*, and between populations of marmot species (Bryant 2005). This consistency provides additional support for the notion of an intrinsic constraint on reproductive success that is unrelated to social pressures or environment. However, breeding success is at least partially influenced by winter climate in yellow-bellied marmots, and potentially in Olympic marmots as well (Schwartz and Armitage 2004; Griffin et al. 2007). In addition, the marmot species with the lowest reported rate of breeding success, the golden marmot (*Marmota caudata*), lives in an environment that, while no colder than my study site, is extremely arid and unproductive (Blumstein and Arnold 1998). For alpine marmots, weather does not appear to affect breeding success, but body condition at the end of hibernation is important (Hacklander and Arnold 1999). Taken together, these data support the Ecological Constraint hypothesis hypothesis as a potential influence on breeding probability. Hoary marmots live in a harsher, more variable environment than most marmot species, and that variability clearly impacts some aspects of their life history (Chapter 2). Why, then, was hoary marmot breeding probability unrelated to winter climate?

Unfortunately, that question will have to remain unanswered for the time being. Spatial variation in habitat quality can affect reproduction (Ozgul et al. 2007), so the lack of data about differences between social group territories in the models could have obscured some underlying pattern. However, differences in food availability between individuals or territories do not seem to be strong influences on hoary marmots. In a feeding experiment at my study site, adult marmots that were fed rabbit chow *ad libidum* did not show significant differences in mass accumulation rates or fall body mass compared to control animals, and had equivalent overwinter survival rates (T.J. Karels et al., unpublished data). In addition, territory-specific estimates of primary productivity did not explain variation in survival (S. M. Morrison, T.J. Karels, and D.S. Hik, unpublished data).

A more promising potential explanation for my results comes from life history theory, which predicts that life history parameters with the greatest potential influence on population dynamics should be the least variable (Ozgul et al. 2007). Hoary marmots may therefore have evolved a consistent probability of breeding because breeding probability is potentially more important, demographically, than other aspects of their life history.

Breeding at a consistent rate every year may confer a long-term selective advantage on hoary marmots, but it is still a somewhat inefficient behavior given that both fecundity and juvenile survival vary as a function of climate. It also may result in maternal stress effects being passed on to their young (Sheriff et al. 2009), a hypothesis that I cannot test directly, but is consistent with the lagged PDO effects on juvenile survival described in Chapter 2. Ultimately, it may be impossible to pinpoint exactly how hoary marmot breeding patterns evolved, because a stochastic environment can potentially select for more than one optimum life history strategy (Orzack and Tuljapurkar 2001).

General conclusions / implications for marmot population dynamics

There is considerable interest in determining if alpine mammals in the Yukon exhibit cyclic population dynamics similar to the patterns observed in nearby boreal forest ecosystems. Although I do not have a long enough time series to formally test for population cycles, the total number of marmots in the study area did seem to oscillate over time (Fig. 3-6). This pattern cannot be solely attributed to climate-driven variation in survival, because survival rates declined steadily over the course of the study (Fig. 3-3). Whether the population was increasing or decreasing in a given year must therefore have depended on whether the relatively constant rate of breeding and variation in fecundity were sufficient to balance out annual mortality.

There has been speculation that marmots are able to compensate for the negative effects of years with reduced snowpack by increasing their reproductive output during the resulting longer, more productive growing seasons (Griffin et al. 2007). Based on the negative relationship between fecundity and PDO, a compensatory life-history tradeoff seems unlikely for hoary marmots, although such tradeoffs may be more important for marmots in less severe alpine environments (Griffin et al. 2007). In addition, my findings imply that small, newly formed social groups containing younger females have lower reproductive output, and may therefore be more likely to go extinct than older groups with more experienced breeders. Demographic mechanisms of Allee effects have also been identified in yellow-bellied and alpine marmot populations (Armitage and

Schwartz 2000; Stephens et al. 2002), and should probably be considered whenever effects of climate change on social animals are being studied.

Rather than depicting a life-history tradeoff, my results showed that reproductive parameters and survival were affected by winter climate in similar ways. They also suggested that hoary marmots are less conservative in their breeding habits than previously believed. Animals living in unpredictable environments often cannot afford to be overly cautious in terms of breeding, even if they have long maximum life-spans (Martin and Wiebe 2004). Hoary marmots in particular seem to have evolved mechanisms that obviate the need for such caution. Biennial breeding and other unusual life history patterns may often be facultative, rather than obligate behaviors (Dane 2002; Schwartz and Armitage 2004), except in the case of animals like albatrosses that exist at the extreme end of the K-selection spectrum (Jouventin and Dobson 2002). Climate change is expected to have severe consequences for many alpine animals (Brown 1971; McDonald and Brown 1992; Beever et al. 2003). Accurate characterizations of species' life histories are essential for predicting the nature and magnitude of those consequences.

Table 3-1. Abbreviations and descriptions of covariates used in analyses of female hoary marmot reproductive parameters.

Abbreviation	Definition and Description
PDO	Mean Pacific Decadal Oscillation from November to May in the winter during the most recent winter
PDO_{lag}	Mean Pacific Decadal Oscillation from November to May during the previous year
Age	Two age classes: Young (3 years old), and Old (>3 years)
Mother Age	Minimum mother age in years, for litter size analysis only
Group	Total number of non-juvenile marmots within social group
Ad. fems	Number of reproductively mature adult females in a social group
Time	Random annual variation
Brd	Factor variable. Yes = females that bred during the previous year, No = previous nonbreeders
1	No time variation (constant)
Young	Denotes a linear covariate applied only to female marmots 3 years of age.
Old	Covariates applied only to female marmots >3 years old.

Table 3-2. Results of Poisson overdispersion tests (Scrucca 2004) for three measures of hoary marmot fecundity, based on data from 10 hoary marmot social groups in the Ruby Range, Yukon Territory, 1999-2004 and 2007-2009. The corresponding linear model types used to model those variables are also shown. Error distributions were chosen based on test results. If significant overdispersion was present, both Poisson mixed effects models and negative binomial generalized linear models were used. If Poisson underdispersion was detected, Gaussian errors were used. Random effects were included based on likelihood-ratio tests using the most parameterized fixed-effect model in each model set (Bolker et al. 2009).

Response Variable	**Obs./Theor.Var**	**Statistic**	**p**	**Error Distribution**	**Random Effects**
Juveniles/Group	3.83	248.64	0.00	Poisson, Neg. Binomial	Social Group
Juveniles/Female	1.29	84.14	0.06	Poisson	Social Group, Social Group*PDO
Known Litter Size	0.57	23.33	0.99	Gaussian	None

Table 3-3. Model-selection results for multistate CMR analyses of adult female hoary marmot survival and breeding probability in the Ruby Range, Yukon Territory from 1999-2004. Parameters shown are survival probability (S), and the probability of breeding in a given year (Ψ). Detection probability (p) was modeled as a constant, and was estimated at 0.96 ± .02 (SE). Descriptions and abbreviations for all covariates are in Table 3-1. K is the number of estimated model parameters and ω is the model's AIC weight.

Model	**K**	**AIC_C**	**Δ AICc**	**ω**	**Deviance**
S PDO + PDO_{lag} **Ψ** Age	6	384.19	0	0.29	185.02
S PDO + PDO_{lag} **Ψ** Old: (Brd + N_{sub}), Young: N_{sub}	8	385.28	1.09	0.17	368.38
S PDO + PDO_{lag} **Ψ** Old: Brd	7	385.73	1.55	0.14	184.39
S PDO + PDO_{lag} + Brd **Ψ** Age	7	385.93	1.75	0.12	184.59
S PDO + PDO_{lag} + Brd **Ψ** Old: Brd + N_{sub}, Young: N_{sub}	9	387.09	2.9	0.07	367.96
S PDO + PDO_{lag} + Brd **Ψ** Old: Brd, Young: 1	8	387.51	3.33	0.06	183.96
S PDO + PDO_{lag} **Ψ** Old: Ad. Fems, Young: 1	6	387.91	3.73	0.05	375.4
S (PDO + PDO_{lag}) * Brd **Ψ** Age	9	388.71	4.53	0.03	182.93
S PDO + PDO_{lag} + Brd **Ψ** Old: Ad. Fems, Young: 1	7	389.66	5.47	0.02	374.96
S PDO + PDO_{lag} **Ψ** Old: N_{sub}, Young: 1	6	389.85	5.66	0.02	377.33
S (PDO + PDO_{lag}) * Brd **Ψ** Old: (Brd + N_{sub}) + Young: N_{sub}	11	389.97	5.79	0.02	366.3
S (PDO + PDO_{lag}) * Brd **Ψ** Old: Brd, Young: 1	10	390.36	6.17	0.01	182.32
S PDO + PDO_{lag} **Ψ** Old: Brd + PDO + PDO_{lag} + N_{sub}, Young: PDO + PDO_{lag} + N_{sub}	12	390.75	6.57	0.01	364.76

Table 3-4. Summed AIC weights (ω) for all parameters in a multi-state CMR analysis of adult female hoary marmots in the Ruby Range, Yukon, 1999-2004. Covariates of both survival (S) and breeding probability (ψ) are shown. Covariate descriptions are in Table 3-1.

Covariate	ω
S	
Stratum	0.33
Stratum*PDO	0.06
PDO	1.00
PDO_{lag}	1.00
ψ	
Stratum	0.47
Stratum*PDO	0.47
PDO	0.01
PDO_{lag}	0.01
Group	0.28
Ad. Fems	0.06
Age	0.71

Table 3-5. Model-selection results for linear models of hoary marmot reproductive parameters. K is the number of estimated model parameters and ω is the AIC weight. Response variables were the number of juvenile produce per social group and average fecundity (juveniles per female within social group). Due to highly significant overdispersion, juveniles per group were modeled using both negative binomial linear models and Poisson linear mixed models with social group as a random effect. Data were collected 1999-2004 and 2007-2009 from 10 social groups in the Ruby Range, Yukon Territory. The error distribution used and the type of model are shown in italics below the name of each response variable. GLMM's are Generalized Linear Mixed Models, and GLM's are Generalized Linear Models. Only models with Δ $AIC_C < 7$ are shown.

Model	**K**	**AIC_C**	**Δ AIC_C**	**ω**
Juveniles Per Group (*Poisson GLMM's*)				
Group*(PDO+PDO_{lag})	8	213.98	0	0.72
Group+PDO+PDO_{lag}	6	217.5	3.51	0.12
Group*PDO	6	217.82	3.83	0.11
Group+PDO	5	220.7	6.72	0.03
Juveniles Per Group (*Negative Binomial GLM's*)				
Group	3	315.63	0	0.22
Group+PDO	4	315.88	0.25	0.19
Group+PDO_{lag}	4	316.12	0.48	0.17
Group+PDO+PDO_{lag}	5	316.55	0.92	0.14
Group*PDO	5	317.91	2.28	0.07
Null	2	318.33	2.69	0.06
PDO	3	318.35	2.71	0.06
Group*PDO_{lag}	5	318.46	2.82	0.05
PDO_{lag}	3	320.45	4.82	0.02
PDO+PDO_{lag}	4	320.56	4.93	0.02
Group*(PDO+PDO_{lag})	7	320.87	5.24	0.02
Juveniles Per Female (*Poisson GLMM's*)				
PDO+PDOlag	4	185.04	0	0.38
Group*(PDO+PDO_{lag})	7	186.98	1.94	0.14
Group+PDO+PDO_{lag}	5	187.23	2.19	0.13
Group*PDO	5	187.32	2.28	0.12
PDO	3	187.66	2.62	0.1
Group+PDO	4	188.34	3.3	0.07
PDO_{lag}	3	189.87	4.83	0.03

Table 3-6. Model-averaged beta coefficients (β) , bootstrapped unconditional standard errors (SE), 95% confidence interval lower and upper limits (LCL and UCL), and summed AIC weights (ω) of parameters for models of group fecundity, individual fecundity (juveniles/adult female), and litter size of hoary marmots in the Ruby Range, Yukon Territory. SEs and 95% confidence limits were bootstrapped with 1000 replications. Except for litter size, analyses were based on data from 1999-2004 and 2007-2009, while analyses of known litter sizes were based on data from 1999-2002 and 2007-2009. Due to highly significant overdispersion, juveniles per group were modeled using both negative binomial linear models and Poisson mixed models with social group as a random effect. Juveniles per female were modeled using Poisson mixed models with social group random effects. Litter size data were approximately normally distributed, and were modeled as such.

Model	**Model-averaged β**	**SE**	**LCL**	**UCL**	**ω**
Juveniles Per Group					
(*Poisson GLMM's*)					
PDO	-0.80	0.71	-2.59	0.00	1.00
PDO_{lag}	0.28	0.38	-0.58	1.00	0.86
Group	0.10	0.06	0.00	0.21	1.00
Group*PDO	0.06	0.08	-0.02	0.28	0.83
Group*PDO_{lag}	-0.01	0.05	-0.09	0.12	0.73
Juveniles Per Group					
(*Negative Binomial GLM's*)					
PDO	-0.13	0.36	-1.35	0.02	0.73
PDO_{lag}	0.09	0.20	-0.16	0.55	0.41
Group	0.06	0.04	0.00	0.13	0.85
Group*PDO	0.00	0.03	-0.01	0.12	0.08
Group*PDO_{lag}	0.00	0.02	-0.02	0.06	0.07
Juveniles per female					
(*Poisson GLM's*)					
PDO	-0.26	0.49	-1.61	0.17	0.99
PDO_{lag}	0.20	0.37	-0.49	1.05	0.69
Group	0.00	0.04	-0.07	0.09	0.48
Group*PDO	0.01	0.05	-0.06	0.16	0.26
Group*PDO_{lag}	0.00	0.05	-0.12	0.10	0.15
Liter Size					
(*Gaussian GLM's*)					
Intercept	3.00	0.19	2.64	3.38	1.00

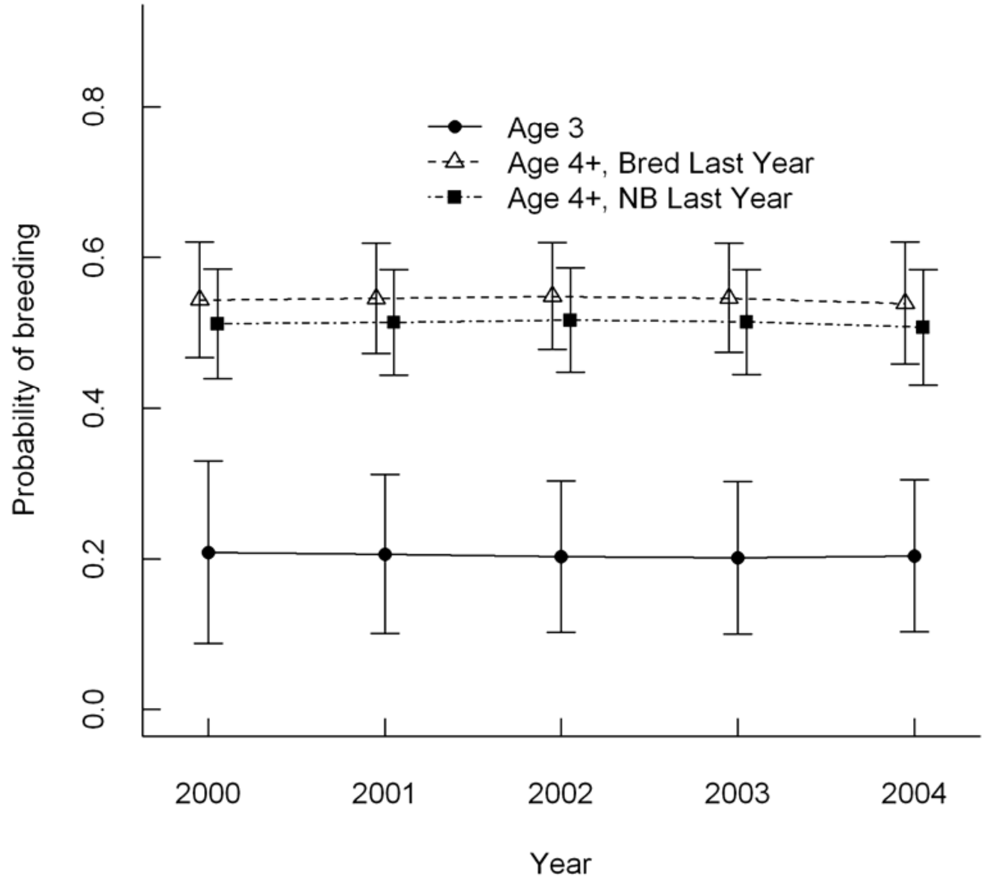

Figure 3-1: Model-averaged probability of breeding as a function of age, previous breeding state, and time. Results are based on 6 years of trapping data (1999-2004) for adult female hoary marmots in the Ruby Range, Yukon. Values are model-averaged annual parameter estimates ± 1 SE.

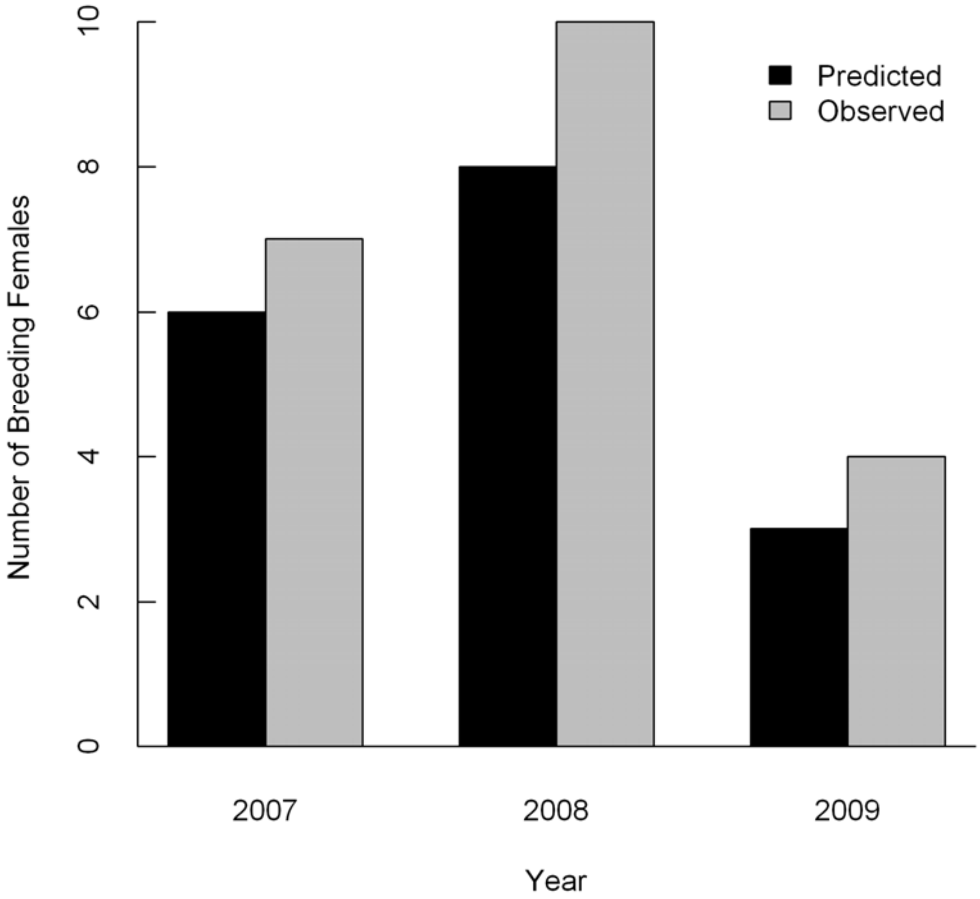

Figure 3-2: Observed and predicted number of breeding females summed across four hoary marmot social groups from the Ruby Range, Yukon, 2007-2009. Predictions were based on model-averaged breeding probability estimates derived from the same study site in 1999-2004, assuming one litter per breeding female per season. Predictions were rounded to the nearest whole number.

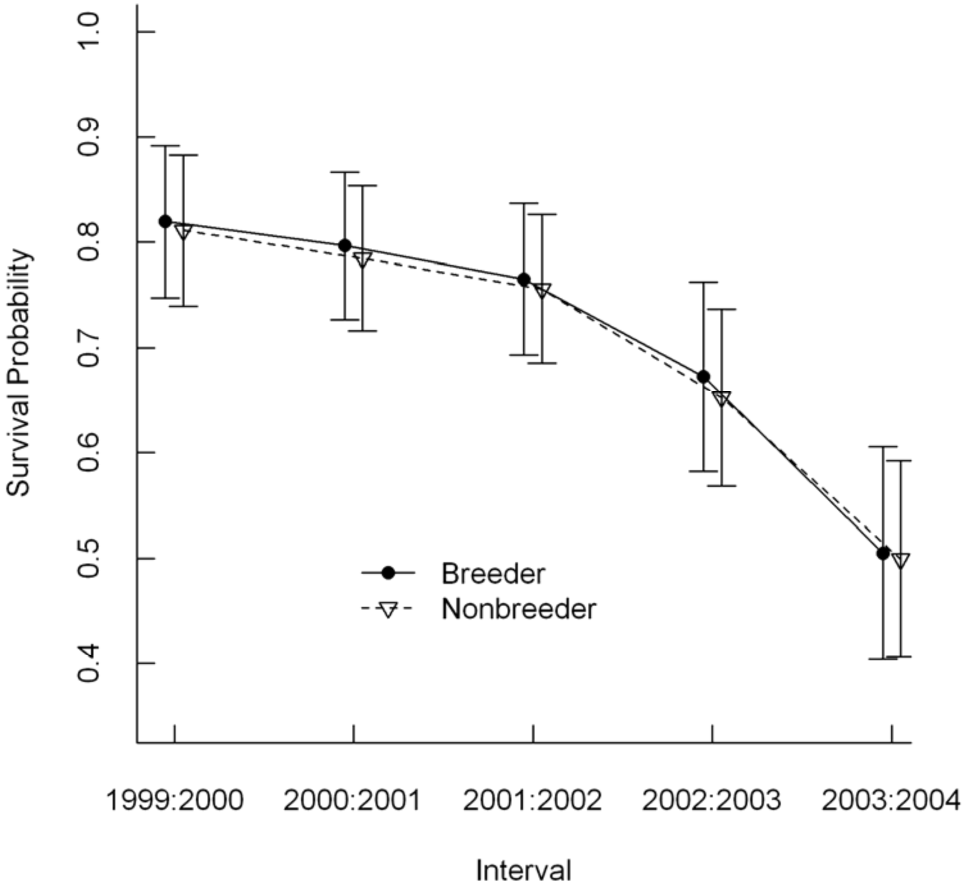

Figure 3-3: Overwinter survival for adult female hoary marmots in the Ruby Range, Yukon, between 1999 and 2004. Survival rates for breeding and non-breeding individuals are shown. Values are model-averaged parameter estimates ± 1 SE.

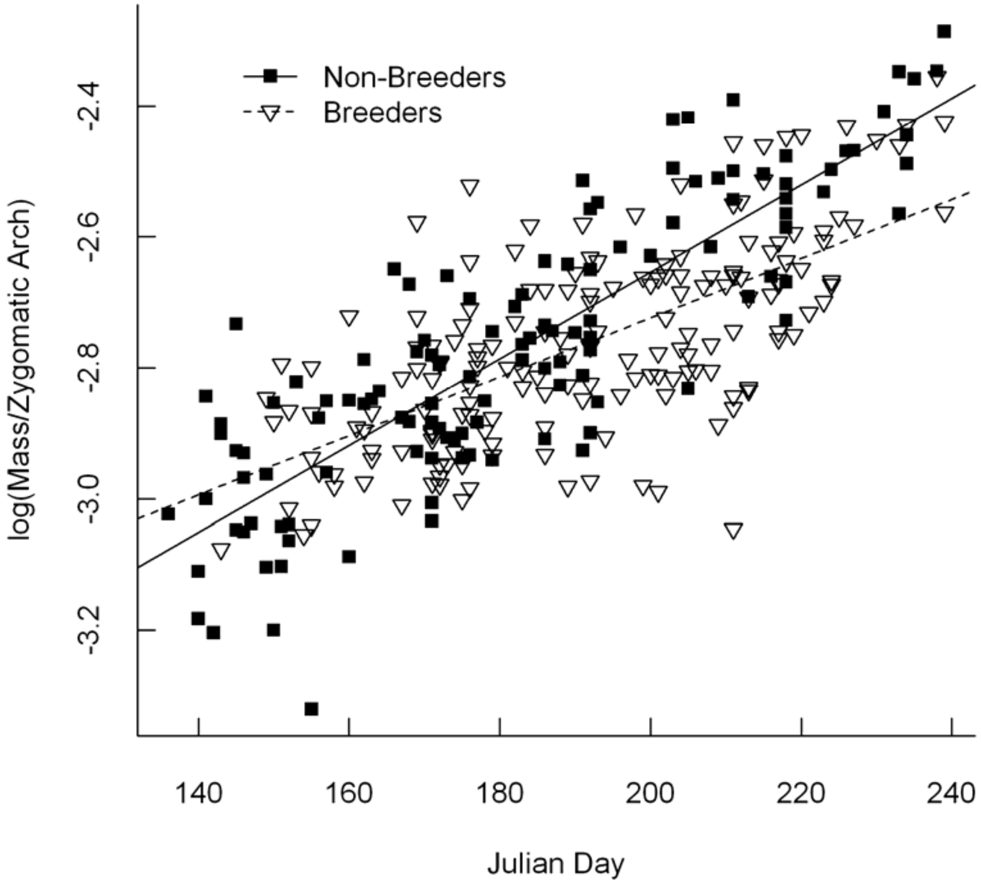

Figure 3-4: Change in log-transformed body condition index (mass / zygomatic arch width) over time for non-breeding and breeding female hoary marmots in the Ruby Range, Yukon. Data from 1999-2004 are shown pooled across years. The best fit lines for linear regressions are shown.

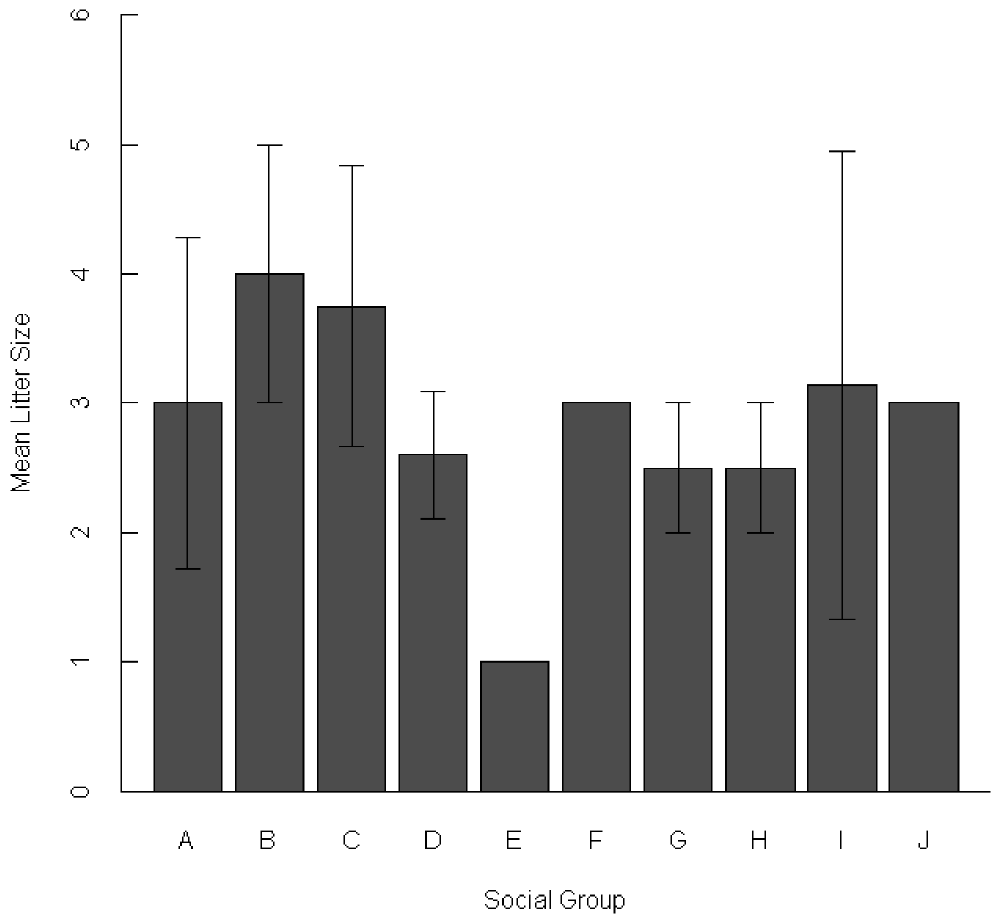

Figure 3-5. Mean litter size (± 1 SE) for all hoary marmot social groups in the study area in the Ruby Range, Yukon, between 1999-2009. Mean litter size did not vary significantly between groups ($F_{41,9}$ = 0.606, p = 0.78).

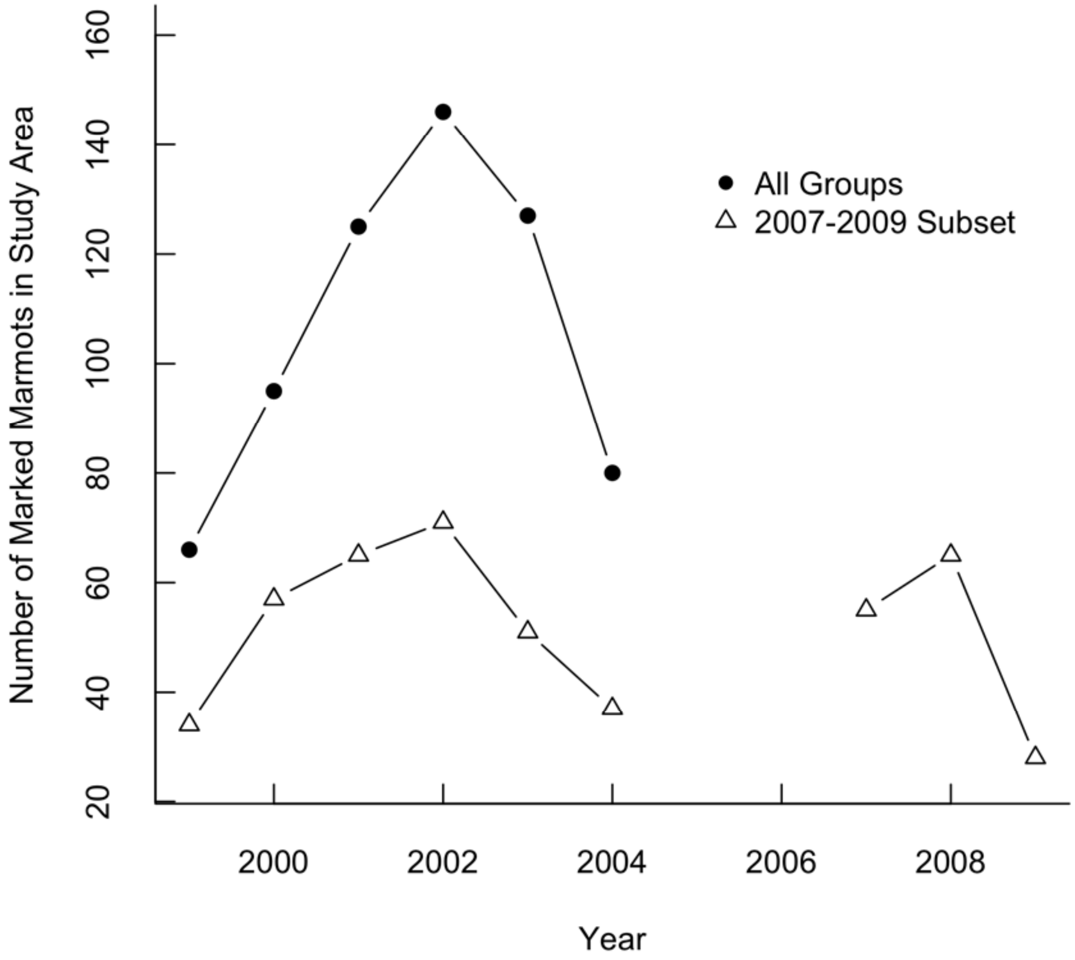

Figure 3-6: Population size of a hoary marmot colony in the southwest Yukon during the years 1999-2004 and 2007-2009. In 1999-2004, ten social groups living in a single valley were censused. In 2007-2009, a subset of four groups, spaced amongst all aspects in the valley, were studied. The number of marmots in the whole valley and the subset are shown for 1999-2004, while only the subset is shown in 2007-2009.

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Chapter 4. Integrating survival and reproduction to explain variation in climate-sensitivity of alpine mammal populations

Introduction

There is a great deal of interest in studying the demographic effects of weather and environment on animal populations to predict the ecological consequences of climate change. Most related research on vertebrates has tended to focus on a single species at a time (Ainley 2002; Beever et al. 2003; Schwartz and Armitage 2004). These species are often identified as 'indicator species' for the regions they inhabit, based on criteria chosen to ensure that they are representative of the larger animal community. However, the effectiveness of indicator species is rarely tested, and in fact, two species can react to changing weather or climate patterns in completely different ways, even if they are closely related or ecologically similar (Chapter 2). Meta-analyses have begun to reveal widespread relationships between climate change and species ranges as well as with specific life history traits (Walther et al. 2002; Parmesan and Yohe 2003; Post et al. 2009). However, unless we understand why some species are more sensitive to weather variation and average climate than others, the results of climate change research cannot be effectively generalized from one species to the next.

Weather and other external forces act on population dynamics by affecting demographic parameters (i.e. life history traits like age-specific survival and fecundity). However, a change in any one of these parameters does not necessarily influence the population growth rate, because some parameters have more influence than others (Caswell 2001). The relative importance of a given parameter, such as juvenile survival, can vary over space and time (Nichols et al. 2000; Morrison and Hik 2007), and should also depend on the life history strategy of a species. Furthermore, life history strategies themselves may also differ from one population or environment to the next (Bears et al. 2009). As a result, the demographic consequences of climate change cannot be studied or predicted without considering the role of life history.

The contributions of individual life history traits to population growth can be decomposed in a number of ways. Typically, this task is accomplished via Life Table Response Experiments (LTREs) using matrix population models, which are subject to several key assumptions that are often violated in wild populations. In particular, the assumptions of demographic and environmental stasis are rarely met. Stochastic LTREs designed for analyzing transient population dynamics have recently been developed, but these methods require data collected across a wide spatial and temporal scale, and may not always be practical (Caswell 2010; Davison et al. 2010). An alternative approach is to estimate both the population growth rate and the relative contributions of demographic parameters to that rate directly from mark-recapture data (Nichols et al. 2000; Nichols and Hines 2002). These estimates are derived and interpreted somewhat differently than the results of a standard LTRE. However, both approaches are considered retrospective analyses, and both ostensibly meet the same objective (Cooch et al. 2001). Despite calls for more study into their differences (Cooch et al. 2001), a direct comparison has not been conducted (but see Sandercock and Beissenger 2002 and Lima et al. 2003 for other comparisons of matrix models and reverse-time modeling).

In this chapter I used both LTREs and reverse-time modeling (Nichols et al. 2000) to compare the population dynamics of collared pikas and hoary marmots, two mammalian herbivores living in an alpine environment characterized by a harsh, variable winter climate. Both in the Yukon and elsewhere, pikas and marmots often live almost literally on top of each other, making their burrows in the same alpine boulder piles, and foraging for similar species in adjacent meadows (V.P. Patil personal observation; Barash 1973). Although the potential for inter-specific competition exists, the two appear to spatially segregate their foraging activities (Karels et al. 2004; Morrison et al. 2004), and direct agonistic interactions have rarely been observed (K. O'Donovan unpublished data). Predation is also rarely observed for either species, possibly because both collared pikas and hoary marmots are obligately associated with large talus piles, and both alarm call extensively when predators are nearby (Holmes 1984; Trefry and Hik 2009). However, the survival rates of both species have been linked to abiotic conditions, particularly the quality and depth of snowpack and the timing of spring snowmelt (Chapter 2; Morrison and Hik 2007). Interestingly, the two species respond to variation in winter climate in very different ways. Pika survival is positively related to the length of the previous growing season, while juvenile marmot survival appears to increase during cold, snowy winters, probably as a result of their need for snowpack as insulation

(Chapter 2; Morrison and Hik 2007). In addition, at a long-term study site in the Yukon, the two species appear to fluctuate in abundance independently of each other (D.S. Hik, unpublished data)

I had four main objectives in this study: first, to conduct the first comparison of LTREs and mark-recapture methods for decomposing demographic contributions to λ using empirical data to assess the implications of choosing one method over the other; second, to identify the demographic parameters that had the most influence on pika and marmot population growth rates; third, to determine why populations of collared pikas and hoary marmots in a shared environment followed different trajectories, and to identify the role of life history in shaping those differences; and finally, to quantify the influence of climate-mediated variation in survival on the population dynamics of collared pikas and hoary marmots.

I hypothesized that the basic life history strategy of each species would determine which demographic parameters made the greatest contribution to population growth. Collared pikas have relatively short lives (3-5 years) and low annual survival rates (<0.5; Morrison and Hik 2007), which means that if a pika fails to reproduce in a given year, it may not get another chance. Variation in fecundity should therefore have made a greater contribution to pika population growth than survival. Hoary marmots, on the other hand, can live for 10 years or more in the wild, have relatively constant breeding probability, and take several years to reach reproductive maturity (Chapter 2). The ability of an individual marmot to contribute to the population should therefore have been more strongly influenced by variation in survival, especially in the younger age-classes, than by fecundity. These predictions, combined with the fact that winter climate is strongly linked with survival for both species, led me to expect that climate would have a greater cumulative influence on the population growth of hoary marmots than on collared pikas.

Methods

Both study species, the study site, and basic capture methods for hoary marmots are described in Chapter 1. All hoary marmot social groups in the 4 km^2 study area were trapped between 1999-2004, while a subset of four groups distributed amongst the South, East, and West aspects of the valley were trapped in 2007-2009. Most pikas in the study area with active haypiles were trapped each year from 1998-2009, using native vegetation as bait. Pika trapping methods are described in detail elsewhere (Franken and Hik 2004; Morrison and Hik 2007). Pikas are diurnal, highly visible, and philopatric to their territories from one year to the next, so the absence of a pika from a territory where it was active was taken as strong evidence of that pika's death.

Matrix model structure and parameterization

I constructed age-structured Leslie projection matrices to describe the asymptotic population dynamics of both pika and marmot populations (Caswell 2001; Keyfitz and Caswell 2005). One matrix was built for each over-winter interval encompassed by the data for each species. These matrices were based on a post-birth census, as breeding occurs at the beginning of the field season for both species and is typically not observed. Matrices were based on female demographic data, although both male and female data were used to parameterize the survival estimates of non-adult marmot age classes due to small female sample sizes in some years. Previous analyses (Chapter 2) did not suggest any measurable differences in survival between juvenile male and female marmots, and there is no *a priori* reason to expect such differences (no sexual dimorphism and no sex-bias in dispersal until mortality) (Barash 1989). Pikas were modeled using two age classes, while marmots were assigned four: juveniles, yearlings, two-year-olds, and sexually mature adults. Models included age-specific survival probabilities (P_i), fecundity (M_i), and fertility (F_i), where i indicates the age-class. Matrix structure and the corresponding life-cycle diagrams for hoary marmots (a) and collared pikas (b) are shown in Fig. 4-1.

Survival parameters were estimated by modeling survival as a function of year, age-class, and sex in program MARK (White and Burnham 1999), using the RMark extension in R (Laake and Rexstad 2007; R Developement Team 2009). Detection probability was modeled as a constant, and was estimated as being close to 1 for both species (0.96 ± 0.02 for marmots, 0.90 ± 0.04 for pikas). Cormack Jolly Seber (CJS) survival models were used for estimating pika survival, and for marmot survival between 1999 and 2004 (Lebreton et al. 1992).

For the latter subset of marmot data (2007-2009), survival was modeled in a robust design framework, with capture and recapture probability allowed to vary between years (Kendall and Pollock 1992). This approach was chosen because marmot trapping effort was not consistent between years, and the trapping period in 2009 was considerably shorter than in the other two years, meaning that 2009 detection probability could not be reliably extrapolated from previous estimates. To improve marmot detection probability estimates in 2009, sampling was broken into 4 trapping sessions. Effort, time spent trapping, time of day, and weather conditions were kept as constant as possible between trapping sessions. For 2007-2008, marmot sampling was broken into two distinct trapping periods. The first period extended from snowmelt to the third week of July, when all juveniles had been born, and the second extended until the end of August. This division was chosen to ensure that essentially all individuals were present and available for capture in both periods (Nichols et al. 2000).

For both species, some juveniles could not be associated with a specific mother. In addition, not all juveniles could be sexed confidently. I therefore estimated average fecundity as the number of female juveniles plus half the number of unknown-sex juveniles divided by the number of reproductively mature females (Equation 1).

Equation 1. Formula for estimating average age-specific fecundity of hoary marmots and collared pikas.

$$M_i = \frac{\#\,\text{fjuvs} + \left(\frac{\#\,\text{unknownjuvs}}{2}\right)}{\#\,\text{f adults}}$$

Fertility calculations for pikas differed slightly from those for marmots (Equation 2). Pika fertility was calculated as the product of the survival probability from age i to age i+1 and the average fecundity for age i+1 (Equation 2a). Marmot fertilities were the product of the probability of survival from age i to age i+1, the probability of breeding for age i+1 (from chapter 3), and the fecundity term for age i+1 (Equation 2b). Because I did not have estimates of marmot breeding probability for 2007-2009, I used the average probability from 1999-2004 for all years.

Equation 2. Formulas used to calculate age-specific fertility estimates for collared pikas and hoary marmots.

a. Pika fertility

$$F_i = P_i \times M_{i+1}$$

b. Marmot fertility

$$F_i = P_i \times \Psi_{i+1} \times M_{i+1}$$

i = age class

Only the oldest age class was reproductively mature in both species (age 1 for pikas, and age 3 for marmots), but both matrices include fecundity terms for the next-oldest age class because of the post-birth design (Fig. 4-1; Caswell 2001). Matrices were constructed for each overwinter period in the two datasets, for total of 11 pika matrices (1998-1999 through 2008-2009) and 7 marmot matrices (1999-2000 to 2003-2004, 2007-2008, and 2008-2009).

Matrix Model Analyses

Methods for matrix model analysis were the same for both pikas and marmots. Once a set of matrices was constructed, the first step was to calculate the projected asymptotic population growth rate (λ_{asym}). This was derived as the dominant eigenvalue of each projection matrix (Caswell 2001). I then determined the proportional contributions that each demographic parameter (P_i, M_i, F_i) made to λ_{asym} using a random design LTRE (Caswell 2001). In an LTRE, the relative importance of a particular parameter is evaluated as the product of the partial derivative of λ_{asym} with respect to that parameter (also referred to as its sensitivity) and the covariance of that parameter with all other parameters (Equation 3). Standard errors and confidence intervals for parameter contributions and λ_{asym} were estimated by bootstrapping with 1000 replications (Caswell 2001).

Equation 3. The formula for variance in λ_{asym}. a_{ij} and a_{kl} represent the matrix entries corresponding to the i or k row and j or l column of a Leslie matrix, over all possible values of i,j,k, and l.

$$V(\lambda) = \sum_{ij} \sum_{kl} cov\left(a_{ij}, a_{kl}\right) \times \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}}$$

For a population to grow at its projected asymptotic growth rate, several assumptions must be met. First, the population is assumed to be in stable-age distribution, meaning that all age-classes are growing at the same rate. Second, all demographic rates are assumed to be deterministic and constant, an assumption that is rarely met in wild populations living in harsh, variable environments. λ_{asym} is therefore not expected to reflect short-term or transient population dynamics (Sandercock and Beissinger 2002). However, even if conditions are not constant, it may still be useful as an instantaneous gauge of current demographic conditions, or of the potential lifetime fitness of an individual living in a certain environment (Caswell 2001). Caswell (2001) used the analogy of a vehicle's speedometer (which provides valuable information despite its inability to predict how far the car will actually travel in an hour). Nevertheless, λ_{asym} may perform poorly if some or all of the underlying assumptions are strongly violated, or if the models used to derive it do not adequately capture the biology of the organism (Sandercock and Beissinger 2002).

Reverse-time modeling

As an alternative to $\lambda_{asym,}$, I estimated a second measure of population growth rate (λ) directly from my mark-recapture data. This approach relies on the concept of reverse-time modeling (Lebreton et al. 1992; Pradel 1996). Essentially, if survival can be estimated by determining the probability that an individual present in a given year will be present and alive the next year, then recruitment can be estimated by modeling the probability that an individual alive and present now was also alive and in the study population the year before (Nichols 2000). The actual population growth rate from one year to the next can then be determined as a function of survival and recruitment, even if the population has not been completely censused (Pradel 1996). Estimation of λ in this way also allows for detection probability to be formally incorporated, and provides a straightforward means of calculating parameter standard errors and confidence intervals. These estimates will be referred to as λ_{real} to differentiate them from λ_{asym} values derived from population matrices, following Sandercock and Beissinger (2002).

I also calculated contributions made by demographic parameters to λ_{real} based on the seniority parameters (γ) in reverse-time mark-recapture models (Nichols et al. 2000). This technique has been described as an alternative approach to the kinds of questions that LTREs were designed to address (Cooch et al. 2001), but the two methods have not been directly compared using empirical data. A seniority parameter describes the probability that an individual present in the population at time i was also present at time i-1, while accounting for detection probability. In other words, it is essentially the reverse-time equivalent of survival in a standard CJS model (which is the probability that an individual alive at time i will also be alive and present at i+1). In models with no age-structure, γ_i reflects the proportional contribution of surviving individuals to the population at time i, while $1-\gamma_i$ is the combined proportional contribution of recruitment and immigration (individuals that were captured for the first time at i) (Nichols et al. 2000).

I estimated λ_{real} for both pikas and marmots in all years where data was available. I modeled γ in a multi-state framework for both species, with juvenile and non-juvenile age-classes as different 'states'. The adult age-class was therefore associated with two γ parameters, γ_{AJ} (the contribution of juvenile survival to adults) and γ_{AA} (the contribution of adult survival to adults). $1- (\gamma_{AJ}+ \gamma_{AA}) = \gamma_{Imm}$ is therefore an estimate of apparent immigration, or the contribution that newly captured individuals made to the current adult population. This term should closely reflect the true importance of immigration if capture probability is equal between marked and unmarked animals, and if the proportion of individuals in the population that have been captured at least once is close to 1 (Nichols et al. 2000). The three γ parameters described above will always sum to one. Finally, I also estimated the proportional contribution of reproductive parameters (breeding probability and fecundity) at each time i as the estimated proportion of juveniles in the population at i+1 (Equation 4). These modeling methods, and the underlying theory, are described in detail in Nichols et al. (2000) and Nichols and Hines (2002).

Equation 4. Formula for estimating the proportional contribution of fecundity, breeding probability, and other reproductive parameters to λ_{real} for any time interval from time i to time i+1. N is the number of individuals in an age class, and superscripts represent the age-class (J for juveniles, A for adults).

$$\text{Proportional contribution of reproductive parameters to } \lambda = \frac{N_{i+1}^{J}}{N_{i+1}^{J} + N_{i+1}^{A}}$$

This approach has a potential limitation, because the four parameters described above only represent contributions to λ_{real} for the adult population. However if the population is in stable-age distribution, λ_{real} is the same for all age classes (Nichols et al. 2000). As an additional comparison, I also calculated time-specific γ values for pikas and marmots using basic Pradel models with no age-structure (Pradel 1996). These basic γ terms represent the proportion of the population in year i that was alive in year i-1. A value greater than 0.5 therefore indicates that survival (across all age-classes), was more important than recruitment and immigration combined (Nichols et al. 2000).

Using two age-classes allowed for direct comparison between γ terms and LTRE contributions for pikas, but made this comparison less straightforward for marmots. However, as in Chapter 2, I was particularly interested in the importance of juvenile marmot survival relative to other age-classes. The two age-class distinction was also the most parsimonious means of separating individuals that entered the population through birth versus those that entered through apparent immigration. Finally, λ_{real} and γ can only be calculated for specific age-classes, and this classification seemed the simplest way to evaluate those parameters for the bulk of the population. To assess the relevance of γ_{AJ}, γ_{AA}, and 1- (γ_{AJ}+ γ_{AA}), I calculated λ_{real} for all age classes and for adults only, which allowed me to see if the population truly was in stable age distribution. I also calculated γ for both pikas and marmots using models with no age-structure. This term can be interpreted as the proportional contribution of survival (by all age classes) to population growth.

Multi-state models can be used to estimate the probability of movement from any state to any other state. However, because the two 'states' in my models represented ages, some of these transitions were biologically impossible (Nichols et al. 2000). Impossible parameters like the probability of a juvenile 'surviving' backwards into a previous time period and the transition probabilities for juvenile to adult and juvenile to juvenile were fixed at 0. Maximum-likelihood estimates of variance were not available for all parameters, so I bootstrapped all models with 1000 replications to determine standard errors and confidence intervals.

Retrospective and prospective demographic analyses

The four parameters described above can be interpreted in a similar manner as Leslie matrix elasticity terms (Nichols et al. 2000), and in fact, the two quantities are similar in some cases (Lima et al. 2003; Ozgul et al. 2007b). However, they have several important differences in theory and interpretation. First, like λ_{asym}, matrix elasticities are asymptotic, and describe the potential dynamics of a system if it were to continue on its current trajectory indefinitely. An elasticity term for a parameter evaluates the proportional effects of future changes in that parameter, regardless of whether such changes are biologically plausible (Caswell 2008). Seniority parameters, on the other hand, are 'retrospective' values, meaning that they are derived directly from data, and reflect observed variation in the relative contributions of parameters to population dynamics over a specific time interval. Although it has been suggested that they can be used in a similar manner to prospective elasticities (Nichols and Hines 2002), as a retrospective tool for population analyses seniority parameters have more in common with LTRE contributions (Cooch et al. 2001; Caswell 2008). Both methods decompose observed variation in a population growth rates into contributions from individual vital rates.

λ Modeling

The final step in my analyses was to model λ_{real} directly using winter climate as a linear constraint. The objective was to determine whether the effects of climate on survival and reproduction in hoary marmots (Chapter 2; Chapter 3) and on survival in collared pikas (Morrison and Hik 2007) were strong enough to translate into variation in population growth rate. This analysis was intended to help validate the results of the reverse-time models, and to evaluate the relative effectiveness of reverse-time modeling and matrix models in predicting pika and marmot population dynamics. Although LTREs consider variation in λ_{asym} rather than λ_{real} , they are still expected to be informative about the drivers of population dynamics over short time scales.

Results

Projected and realized growth rates

Realized and projected λ were positively correlated for both species (Fig. 4-2; marmots: r = 0.86, p = 0.01; pikas: r = 0.8, p = 0.02). However, marmot λ_{asym} varied more than λ_{real} from year to year, while the reverse was true for pikas (Fig. 4-2). The marmot population showed a positive realized growth rate (λ_{real}) in 4 of 7 time intervals, while the pika population increased in 7 of 11 time intervals, indicating that neither population was following a stable trajectory (Fig. 4-2). On the other hand, the projected growth rate (λ_{asym}) of the pika population was negative in 9 out of 11 time intervals. The marmot population was projected to increase in 3 out of 7 time intervals for which projection matrices were derived. For marmots, λ_{asym} values were more stable than λ_{real}, and remained close to one throughout the study. In the pika population, λ_{real} had a range similar to that of λ_{asym} (0.48-1.51 versus 0.27-1.81), but λ_{asym} was lower in 10 out of 11 time periods (mean difference = 0.3). During the 9 years when both species were being studied, pika and marmot population growth rates were not significantly correlated ($\lambda_{real:}$ r = -0.52, p = 0.23, λ_{asym}: r = -0.18, p = 0.72).

Comparison of λ_{real} between the adult age-class and the total population

λ_{real} estimates for adults and for all ages were similar and significantly correlated in the hoary marmot population (r = 0.8, p = 0.03; Fig. 4-3), suggesting that it was in an approximately stable age-distribution. The two measures of population growth were not significantly correlated in the pika population (r = 0.3, p = 0.52; Fig. 4-3). The results for pikas showed prominent peaks in both adult and total population growth rate, but these peaks occurred at different times (Fig. 4-3). Although age-classes grew at different rates in the pika population, both pikas and marmots conformed reasonably well with the expected stable-age distribution associated with each matrix model (Table 4-1). For marmots, the highest estimated rates of λ_{real} for either age-class occurred during the first overwinter interval in the study. However, a smaller proportion of the population may have been captured during the first year when trapping protocols were still being developed. No such peak was observed for pikas, but the first 3 years of available pika trapping data (1995-1997) were not used. In general, λ_{real} could be estimated with much greater precision for marmots than for pikas (Fig. 4-3).

LTRE results

Marmots

The relative contribution of demographic parameters to λ_{asym} varied annually (Fig. 4-4). Juvenile survival was the single greatest contributor to variation in λ_{asym} in 3 out of 7 years (Fig. 4-4). However, two-year-old survival, adult survival, and fecundity terms made important contributions in several years (Fig. 4-4). On average, two-year-old survival had the greatest impact on λ_{asym} (Table 4-2). However, the high rank of two-year-old survival was strongly influenced by a single time interval (2003-2004) when both λ_{asym} and estimated survival rates for older age-classes were unusually low (Fig. 4-4). When the LTRE was re-run without that time period, juvenile survival appeared 4 times as important as any other model parameter (Table 2). Juvenile survival made the greatest contribution in 3 out of 4 intervals when the population was projected to increase, but contributed very little to steep decline in λ_{asym} during 2003-2004 (Fig. 4-4).

As with most matrix models, some demographic rates like adult survival were incorporated into more than one model parameter. These lower-level demographic parameters' importance can be evaluated as the sum of all contributions from model parameters that include them (Caswell 2001). For example, the true contribution of adult survival (contribution (P_3) + contribution (F_3)) was 0.22 + 0.13 = 0.35 based on all the data, and 0.079+0.131 = 0.21when 2004 was excluded. Adult survival and two-year-old survival made approximately equal contributions to λ_{asym} when all data were analyzed (P_A contribution = 0.35, P_2 contribution = 0.35), while the lower level fecundity parameter (M_A) was somewhat less important (contribution = 0.20). When 2004 was excluded, fecundity had the second-highest lower-level parameter contribution (0.17), but that was almost four times smaller than the contribution made by juvenile survival.

<u>Pikas</u>

The results of the pika LTRE did not identify any one parameter as being consistently the most important (Fig. 4-4). Bootstrap standard errors indicate that there were no significant differences between the contributions of individual parameters (Table 4-2). However, fertility terms tended to be more important than survival (Table 4-2). Fertility terms made the greatest contributions during both years when λ_{asym} exceeded 1 (Fig. 4-4). The mean lower-level contributions of demographic rates were as follows: fecundity (.75) > juvenile survival (0.59) > adult survival (0.41).

Reverse-time modeling

Marmots

Based on the proportional contributions of adult survival (γ_{AA}), juvenile survival (γ_{AJ}), apparent immigration ($1- \gamma_{AA} - \gamma_{AJ}$) and fecundity (Equation 4) to adult population growth, adult survival was the single most important parameter in all but the first time period (1999-2000) (Fig. 4-5). Juvenile survival was 2-3 times less important than adult survival in most years (Fig. 4-5). Apparent immigration contributed little to the adult population, except in 1999-2000 (Fig. 4-5). Fecundities and juvenile survival made similar contributions in most years. Overall, the proportional contribution of parameters to λ_{real} varied annually. Mean contributions were: adult survival (0.69) > fecundity (0.23) > juvenile survival (0.19) > apparent immigration (0.11). The ranking of individual γ parameters from the multi-state reverse-time models was not clearly related to whether λ_{real} was increasing, decreasing or stable (Fig. 4-5). When γ was estimated for the total population, ignoring age-structure, it was greater than 0.5 in all years, indicating that most individuals in the population were survivors from previous years rather than juveniles or new immigrants (Table 5). The average values of this basic γ was 0.67 (SE = 0.05). There was a strong negative relationship between γ and λ_{real} (r = -0.91, p = 0.004).

Pikas

As with the LTRE results, the reverse-time models indicated that fecundity had a greater impact than either juvenile or adult survival in most years (Fig. 4-5). However, apparent immigration accounted for almost half of the adult population growth rate on average (mean contribution of γ_{Imm} to λ_{real} = 0.43). Apparent immigration was more important than either juvenile or adult survival in 9 out of 11 years, and was the single most important demographic parameter in 4 of those years (Fig. 4-5). The size of the contribution made by apparent immigration was also positively correlated with λ_{real} for both adults and the total population, although this correlation was only significant for the total population (adults: r = 0.53, p = 0.09, all ages: r = 0.71, p = 0.01). However, it was not correlated with mean winter PDO from the most recent winter, or with winter PDO lagged by one year (PDO: r = 0.18, p = 0.59; PDO_{lag}: r = 0.008, p = 0.98). Juvenile survival ranked the lowest among the four parameters, with an average γ_{AJ} value of 0.20. When γ was estimated for the total population, ignoring age-structure, it was less than 0.5 in 9 of 11 years (Table 4-3). The average value of γ over the entire study was 0.36 (SE = 0.06). There was a trend for λ_{real} (estimated for the whole population) to decrease as γ increased, but it was not significant at the 0.05 level ($r = -0.57$, $p = 0.06$).

Validating previously described relationships between winter climate and survival

Previous analyses of hoary marmot survival rates (see Chapter 2) had not incorporated the most recent 3 years of data (2007-2009). During this period, juvenile survival was positively related with the mean winter Pacific Decadal Oscillation value (PDO), in contrast to the negative correlation between survival and PDO between 1999 and 2004 (Fig. 4-6; Chapter 2). However, winter PDO values in 2007-2009 were lower than in any year between 1999-2004. Using the linear relationship between juvenile survival and PDO during 1999-2004, predicted survival rates for both the winter of 2007-2008 and 2008-2009 exceeded 1.00. For pikas, adult survival was positively related to lagged winter PDO (Fig. 4-6; $R^2 = 0.37$, $p = 0.02$). Neither juvenile or adult collared pika survival was correlated with non-lagged PDO.

Models of climate effects on λ

For both pikas and marmots, models in which λ_{real} varied as a function of time and sex were compared with models containing PDO and/or lagged PDO (PDO_{lag}) as covariates. Within the marmot model set, the model containing both PDO and PDO_{lag} had the most support and was ~3 times better at explaining variation in λ_{real} than the model with random time variation (Table 4-3). The beta coefficients PDO and PDO_{lag} were both negative (β-PDO = -0.24, SE = 0.04; β-

PDO_{lag} = -0.22, SE = 0.05). For pikas, models containing PDO or PDO_{lag} had essentially no support. There was moderate support for sex-specific differences in λ_{real}, but the best model, which included time variation but no sex effects, was twice as well supported as the best model that included sex (Table 4-3).

Discussion

Comparing methods for retrospective population analyses

Marmots

As predicted, both modeling methods identified survival as being more influential on λ than reproduction. The marmot LTRE strongly pointed to the importance of juvenile survival, as this parameter was identified as making a larger contribution to projected λ than any other (Fig. 4-4). Juvenile hoary marmots have the smallest energy reserves of any age-class, which is probably why they appear more sensitive to winter conditions than older marmots (Barash 1976). Also, the probability of juvenile overwinter survival can vary widely from year to year (1999-2009 values ranged from 0.10 to 0.96), which means that this age-class could easily represent a bottleneck to recruitment into the breeding adult population (Chapter 2). The LTRE therefore implied that climate-mediated variation in juvenile survival had a substantial influence on the growth rate of the hoary marmot population. There was also some indication that juvenile survival, and therefore winter climate, tended to be more important when the population was increasing most rapidly, whereas the survival of older age-classes played a more substantial role when the projected population growth rate was well below one. These results were consistent with studies of yellow-bellied marmot population dynamics, which found that variation in juvenile survival played a major role in the population dynamics of that species (Ozgul et al. 2007a), but that the demographic parameters responsible for population growth and decline were not necessarily the same (Oli and Armitage 2004).

Although the reverse-time modeling results also identified survival parameters as being important, they indicated that the proportional effect of a change in juvenile survival on λ_{real} for the adult population was much smaller than the effect of changing adult survival. This discrepancy between γ_{AJ} and the LTRE contribution of juvenile survival cannot be attributed to differences between prospective and retrospective contributions to population growth, because both approaches used in this paper were retrospective (Cooch et al. 2001). Differences could be partly the result of my decision to group all non-juvenile age-classes together. However, given that the LTRE contributions of juvenile survival were three to four times larger than those for any other parameters in some years, model-structure alone is an insufficient explanation. Another potential source of differences was the fact that γ_{AJ} reflects contributions to the adult age-class only, but because the population appeared to be in stable-age distribution in most years, seniority parameters like γ_{AJ} were reasonable indices of contributions to the total population. However, the γ terms derived using reverse-time modeling are closely analogous to prospective elasticities, in that they only describe the independent contributions of individual parameters to the current population (Nichols et al.

2000). LTRE contributions, on the other hand, incorporate covariance between parameters, which are rarely independent of each other (Caswell 2001). Seniority parameters do explicitly incorporate the relative abundance of individuals in each age class, while the LTRE approach assumes conformity to a theoretical stable age distribution (Nichols and Hines 2002; Cooch et al. 2001). The adult age-class accounted for close to half the marmot population in most years (Table 4-3), which is likely part of the reason that adult survival generally made the greatest proportional contribution to λ_{real}.

When modeled directly, the correlation between λ_{real} and winter PDO (Table 4-4) was similar to that observed for adult survival (Chapter 2; Chapter 3), but stronger, which implies that climate-mediated changes in juvenile survival were having a substantial effect. This pattern was more consistent with the results from the LTRE than with the γ estimates, but the results from both methods were generally consistent with expectations based on hoary marmot life history.

Pikas

For the collared pika population, there was agreement between the LTRE and the reverse-time models in terms of the relative importance of survival and reproduction. However, the large contribution of apparent immigration to the adult pika population in most years suggests that my matrix models of pika dynamics, which assumed population closure, were unrealistic. Although it is possible to incorporate immigration into matrix models and LTREs, doing so requires modeling the immigration rate as a proportional function of the current population size (Cooch et al. 2001). There was no *a priori* reason to make such an assumption about collared pika immigration in the Ruby Range. This omission was most likely the reason that λ_{asym} was consistently lower than λ_{real} (Fig. 4-3). Projected and realized population dynamics are not expected to be identical, but there is also no expectation that one should be biased with respect to the other as long as the underlying matrix model is properly constructed (Nichols and Hines 2002). In general, if a population is unlikely to be closed, the reverse-time approach to identifying influences on population growth is likely to be superior (Nichols and Hines 2002).

Multiple lines of evidence suggest that the apparent immigration parameter reflected actual immigration in this study. First, pika detection probability was close to 1 (Morrison and Hik 2007) and the proportion of individuals with active haypiles that escaped capture was generally low (D.S. Hik, unpublished data). Therefore, apparent immigration was unlikely to reflect individuals that were already present in the study area. Second, animals first captured as adults were genetically dissimilar to those captured as juveniles inside the study area (J. Zgurski, unpublished data). As a result, it seems reasonable to conclude that the influx of new pikas each year was responsible for maintaining a dynamic equilibrium of pika abundance over time (geometric mean $\lambda_{real} = 1.00$).

General comparison

Had I chosen only to model pika dynamics using Leslie matrices that ignored immigration, I would have reached an unnecessarily dire conclusion about the population’s likely fate. Although immigration could be incorporated into matrix models as a per-capita function of population size (Cooch et al. 2001), I would not have recognized the need for such models or been able to parameterize them without first using the reverse-time approach. Given the potential for such gross mischaracterizations of population dynamics, the obvious question becomes: When are LTREs likely to be the preferred method for studying variation in population growth? The most obvious answer is that the choice depends on whether transient or asymptotic dynamics are of more interest. In highly variable environments an asymptotic growth rate is expected to be less useful than a realized one (Sandercock and Beissinger 2002). However, my results suggest that asymptotic population growth rate estimates can describe annual variation in population growth in both closed and open populations, for animals with varying life histories, and despite the presence of environmental stochasticity. Basic matrix models have been shown to be adequate for describing equilibrium dynamics of marmot populations before, but those authors concluded that transient dynamics were more difficult to model, and required a more sophisticated, individual-based approach (Stephens et al. 2002). Realized and projected population growth rates of wild animal populations have only been directly compared in one other study, which concluded that the two were not significantly different but also not closely correlated (Sandercock and Beissenger 2002).

In my study, the strong correlation between λ_{asym} and λ_{real} may be due to high detection probabilities and precision in my demographic parameter estimates. In addition, both the pika and marmot populations appeared to conform well to the stable-age distributions predicted by their respective matrix models, which helped to ensure the robustness of those models. Another possibility, which would be consistent with Stephens et al. (2002), is that annual weather variation was minor enough that the local environment was essentially in a state of dynamic equilibrium, and transient dynamics were relatively unimportant. However, this explanation seems unlikely given the amount of annual variability in winter snowpack and in the timing of spring snowmelt at my study site (Chapter 1; Chapter 2). The high correlation between λ_{asym} and λ_{real} was particularly surprising for the collared pika population, given the importance of immigration for that species. Unfortunately, I do not have an adequate explanation for that result, so it is difficult to say whether matrix models without immigration terms would be similarly effective at describing the dynamics of other open animal populations.

In situations where realized and projected population growth rates are closely correlated, the choice between LTREs and reverse-time modeling may be philosophical. For example, whether juvenile or adult survival could be said to make the greater contribution to hoary marmot population dynamics in some years depends on whether one is interested more in the proportional abundance of animals derived from different parts of the life cycle (which is described by γ terms), or in the degree of covariance between demographic parameters, each other, and λ (which is incorporated into LTRE analyses). Further direct comparisons of these approaches, using both empirical and simulated data, could help to clarify which metric of contributions to population growth is more useful.

Implications for pika and marmot population dynamics

My findings supported my overall hypothesis that life history differences would help to explain differences in the population dynamics of collared pikas and hoary marmots. This study therefore reinforces the importance of considering a species' entire life cycle when investigating the demographic consequences of environmental change. Many studies of wildlife populations, including pika and marmot species, focus exclusively on survival, while causes of variation in reproduction are not examined as intensively (Ozgul et al. 2007b). However, reproductive parameters like fecundity and age at first reproduction can make substantial contributions to population dynamics (Dobson and Oli 2001; Oli and Dobson 2003). More widespread use of reverse-time mark-recapture methods would help to alleviate this imbalance, because these methods provide a relatively simple framework for estimating and modeling recruitment directly from mark-recapture data (Nichols et al. 2000; Pradel 1996).

Dispersal behavior also appeared important in explaining why pikas and marmots had different population dynamics. Most male hoary marmots disperse by the time they are 4 or 5 years old (T.J. Karels, unpublished data), but the impact of dispersal on population dynamics has not been previously studied for this species. Permanent dispersal from one known social group to another was uncommon over the course of this study, implying that most dispersers move at least several kilometers away from their natal territories. Given that γ_{Imm} parameters represented the upper limit of the true contribution of immigration to population dynamics, successful long-distance dispersal events may be rare. Successful dispersal events are common in both yellow-bellied and alpine marmot populations (Van Vuren and Armitage 1994; Stephens et al. 2002) and yellow-bellied marmots are apparently capable of dispersing more than 10-15 kilometers (Floyd et al. 2005). However, dispersal success depends at least partially on the availability of vacant territories (Stephens et al. 2002), whereas marmot social group territories in the Ruby Range are quite large (up to 500-600 m in diameter), and established territories cover almost all of the suitable habitat in the study area. Immigration and emigration rates can differ between populations based on habitat characteristics and population density (Pulliam 1988) so the study population of marmots could simply have been a dispersal source rather than a sink.

Based on the proportional importance of immigration and local recruitment, it is tempting to characterize the marmot population I studied as a source, while the pika population could be seen as a sink (Pulliam 1988). However, because high levels of immigration can suppress local fecundity or increase local mortality, the characterization of the pika population as a sink is not necessarily warranted (Watkinson and Sutherland 1995). In the presence of immigration, both the pika and the marmot population appeared to be relatively stable on average (mean $\lambda_{real} = 1.02$ for marmots, 1.00 for pikas). However, without large-scale surveys of collared pika occupancy in the surrounding habitat it is difficult to determine whether the study population of collared pikas represents a sink or is simply part of a larger, spatially structured population (e.g. Franken and Hik 2004). Such surveys would also facilitate comparison with the

American pika, a closely related species that appears to display typical metpopulation dyanamics (Moilanen et al. 1998; but see Clinchy et al. 2002 for an alternative explanation), and whose distribution already appears to be shrinking due to climate change (Beever et al. 2003, 2010).

Validation of survival models

Previous studies found that both pika and marmot survival were linearly related to winter weather conditions as indexed by the PDO (Morrison and Hik 2007, Chapter 2). Because this chapter incorporates several years of data that were not available for those analyses, I was able to examine whether relationships between pika and marmot survival and winter climate persisted over time. When all 12 years of data were considered, adult collared pika survival was still significantly positively related to winter PDO with a lag of one year, the same pattern observed by Morrison and Hik (2007). However, the relationship was somewhat weaker than they concluded, and at least one notable outlier was present. The relationship between winter PDO and hoary marmot survival changed much more dramatically, from a negative correlation to a positive one (Fig. 4-2). However, this result was not necessarily inconsistent with my previous findings (see Chapter 2). Mean winter PDO values for both 2007-2008 and 2008-2009 were more negative than at any time between 1999 and 2004 (the first period of observations). Also, a PDO value of -0.85 in the winter of 2000-2001 (the most negative value in the dataset prior to 2007) corresponded to a 0.96 probability of juvenile marmot survival. Extrapolating from the observed relationship between PDO and survival from 1999 to 2004 to include the more recent years would have resulted in nonsensical predicted survival probabilities exceeding 1.00. Consequently, the true relationship had to either become non-linear or disappear completely.

My new findings suggest that the former is the case, although two data-points are clearly insufficient to confirm this trend. Increased snowpack results in both greater winter insulation and later spring snowmelt. Although the evidence from 1999-2004 suggested that the former was more important for marmots, a tipping point may have been crossed during the last few winters in the study. This hypothesis is consistent with considerable published evidence for relationships between winter PDO, winter weather, and animal demography in the Yukon and elsewhere (Mantua et al. 1997; Moore et al. 2002; Morrison and Hik 2007; Hegel et al. 2009). Non-linear relationships between climate indices, weather variables, and animal population dynamics have only been documented in a few instances, but have important implications for projecting the ecological effects of climate change (Mysterud et al. 2001).

Implications for alpine animals in the Yukon

Climate change is projected to increase high-elevation snowpack in the Yukon (Hegel et al. 2009). My results indicate that in the short term, such a trend would benefit hoary marmots living in high-alpine sites while collared pikas would be either relatively unaffected or negatively impacted. Because climate may affect alpine animals in the Yukon nonlinearly, such an increase could eventually have detrimental effects on both species by decreasing the length of the growing season. In addition, collared pikas are quite sensitive to heat, just like their southern relatives (Smith 1974; Beever et al. 2010), so the positive relationship between collared pika survival and temperature as indexed by PDO that was documented by Morrison and Hik (2007) is unlikely to persist beyond a certain point. However, while the effects of directional long-term climate change are difficult to predict, correlations between PDO and local weather variables more repeatable (Mantua et al. 1997). It may therefore be possible to predict periods when hoary marmot population growth rates should be higher or lower than the long-term average, although a longer time-series would be needed for validation. Of course, both population dynamics and the factors that influence them can vary spatially and as a function of elevation for small mammals (e.g. Gillis et al. 2005), so my findings should be interpreted cautiously with regard to pika and marmot populations in substantially different environments (at or near treeline, for example).

If dispersal remains an important part of pika demography in the southwest Yukon, then indirect effects of climate change could be as important as temperature and precipitation patterns, and could result in further divergence of pika and marmot responses to climate. Of particular concern is a large projected rise in treeline (Danby and Hik 2007), which means that alpine habitat patches will probably become smaller and more isolated. Whether forested habitat poses a significant dispersal barrier to either collared pikas or hoary marmots is currently unknown. Collared pikas are capable of dispersing large distances (>10 km) over forbidding landscapes like the glaciers of the St. Elias icefields, and some marmot species are capable of covering even longer distances through inhospitable desert terrain (Floyd et al. 2005), but forests could pose an equal challenge through the combination of reduced visibility and increased predation risk. I cannot determine exactly how important changes in the immigration rate of either species might be in the future based on the results in this chapter, because retrospective analyses are generally considered inappropriate for answering such questions (Caswell 2008). However, variation in immigration rates is probably more important for collared pikas than for hoary marmots, at least in habitats similar to my study area. I therefore anticipate that future reductions in connectivity, by whatever mechanism, would be more likely to threaten pika populations.

Although hoary marmots were more sensitive to winter conditions than pikas, that sensitivity did not correspond with greater annual variability in λ_{real}. Instead, as already discussed, their geometric mean realized growth rates suggested that both populations were on track to remain relatively stable. λ_{asym} was also generally higher for marmots than for pikas, although both populations were projected to decline over time. In other words, long-term population dynamics and demographic sensitivity to climate are not necessarily related, even in environments where the climate is harsh and highly variable.

Identifying mechanistic links between climate, weather, and specific demographic parameters (Chapter 2, Chapter 3), is clearly an important step in identifying the risk posed by climate change to wildlife. However, as this study illustrates, life history must be considered as potential link between climate and demography. Although the demographic importance of life history can be decomposed for both projected and realized population growth rates, so far few researchers have examined λ_{asym} and λ_{real} simultaneously. When there is no *a priori* reasons for selecting one metric over the other, direct comparisons can yield a more complete picture of population dynamics than either one alone, and using multiple methods of population analyses simultaneously can draw attention to violated assumptions and inadequacies in model structure. Regardless of the method, retrospective analyses cannot be used to predict the consequences of future changes in a specific life history parameter (Caswell 2008). They can, however, illuminate the mechanisms that drive population dynamics. Those mechanisms cannot be ignored when studying the ecological importance of climate, or when trying to project the effects of climate change from one species to the next. Even ecologically similar species that share the same habitat can be influenced by very different environmental and demographic forces.

Table 4-1. The actual and projected distribution of hoary marmots (a) and collared pikas (b) amongst age-classes. Data for both species are from populations in the Ruby Range, Yukon. Projected distributions are based on Leslie matrix models that assume a stable-age distribution (the proportional abundance of age-classes that would allow all segments of the population to change at the same rate).

a. Hoary marmots

	Projected				Actual			
Year	**Age 0**	**Age 1**	**Age 2**	**Age A**	**Age 0**	**Age 1**	**Age 2**	**Age A**
2000	0.15	0.14	0.14	0.58	0.07	0.33	0.13	0.48
2001	0.2	0.17	0.16	0.47	0.11	0.06	0.33	0.5
2002	0.24	0.2	0.16	0.4	0.32	0.08	0.05	0.55
2003	0.27	0.11	0.1	0.52	0.2	0.25	0.05	0.51
2004	0.24	0.21	0.22	0.33	0.17	0.17	0.22	0.44
2008	0.31	0.2	0.14	0.36	0.34	0.22	0.07	0.37
2009	0.38	0.05	0.05	0.52	0.16	0.06	0.29	0.48
Mean	0.26	0.15	0.13	0.48	0.2	0.17	0.16	0.48

b. Collared pikas

	Projected		Actual	
Year	**Age J**	**Age A**	**Age J**	**Age A**
1998	0.35	0.65	0.35	0.65
1999	0.53	0.48	0.5	0.5
2000	0.29	0.71	0.33	0.67
2001	0.67	0.33	0.73	0.27
2002	0.5	0.5	0.54	0.46
2003	0.73	0.27	0.47	0.53
2004	0.7	0.3	0.69	0.31
2005	0.51	0.49	0.48	0.52
2006	0.39	0.61	0.32	0.68
2007	0.45	0.55	0.41	0.59
2008	0.24	0.76	0.19	0.81
2009	0.37	0.63	0.36	0.64
Mean	0.47	0.53	0.44	0.56

Table 4-2. Results of Life Table Response Experiments (LTREs) conducted for hoary marmot and collared pika populations in the Ruby Range, Yukon. The hoary marmot LTRE was parameterized with data collected between 1999 and 2004, and between 2007 and 2009. The collared pika LTRE includes data collected between 1998 and 2009. Values represent the proportional contributions of age-specific survival and fecundity parameters to variation in the projected population growth rate (λ_{asym}), averaged over time. SE represents 1 standard error, which was estimated by bootstrapping. The hoary marmot LTRE was run with and without the matrix representing the interval from 2003 to 2004, because trapping effort in 2004 was lower than in other years, and the reliability of parameter estimates from that period was questionable.

Hoary marmots

		w/o 2004	
	Parameter	**LTRE contribution**	**SE**
	Juv. Surv. (P_0)	0.64	0.16
	Yearl. Surv. (P_1)	0.02	0.09
	Two-yr. Surv. (P_2)	0.09	0.11
	Adult Surv. (P_A)	0.08	0.06
	Two-yr. Fert. (F_2)	0.04	0.04
	Adult Fert. (F_A)	0.13	0.15

		with 2004	
	Parameter	**LTRE contribution**	**SE**
	Juv. Surv (P_0)	0.18	0.06
	Yearl. Surv. (P_1)	0.13	0.05
	Two-yr. Surv. (P_2)	0.28	0.05
	Adult Surv. (P_A)	0.22	0.03
	Two-yr. Fert. (F_2)	0.07	0.02
	Adult Fert. (F_A)	0.13	0.07

Collared Pikas

	Parameter	**LTRE contribution**	**SE**
	Juv. Surv. (P_J)	0.18	0.06
	Adult Surv. (P_A)	0.07	0.07
	Juv. Fert. (F_J)	0.41	0.14
	Adult Fert. (F_A)	0.34	0.13

Table 4-3. Seniority parameters (γ) for hoary marmots and collared pika populations in the Ruby Range, Yukon. Seniority parameters were estimated from reverse-time mark-recapture models in which all age-classes were pooled. Maximum-likelihood estimates, standard errors (SE), and lower (LCL) & upper (UCL) bounds of 95 % confidence intervals are shown.

Hoary marmots

	Estimate	**SE**	**LCL**	**UCL**
1999	0.55	0.06	0.43	0.66
2000	0.66	0.05	0.56	0.76
2001	0.60	0.05	0.51	0.68
2002	0.69	0.05	0.59	0.77
2003	0.74	0.05	0.62	0.83
2007	0.58	0.06	0.45	0.69
2008	0.86	0.06	0.71	0.94
Mean	0.67	0.05	0.55	0.76

Collared pikas

	Estimate	**SE**	**LCL**	**UCL**
1998	0.31	0.06	0.21	0.43
1999	0.34	0.09	0.19	0.52
2000	0.17	0.06	0.09	0.31
2001	0.33	0.07	0.21	0.47
2002	0.40	0.09	0.25	0.57
2003	0.38	0.08	0.25	0.54
2004	0.19	0.05	0.11	0.30
2005	0.55	0.07	0.42	0.68
2006	0.41	0.06	0.30	0.53
2007	0.56	0.07	0.42	0.70
2008	0.34	0.06	0.23	0.47
Mean	0.36	0.07	0.24	0.50

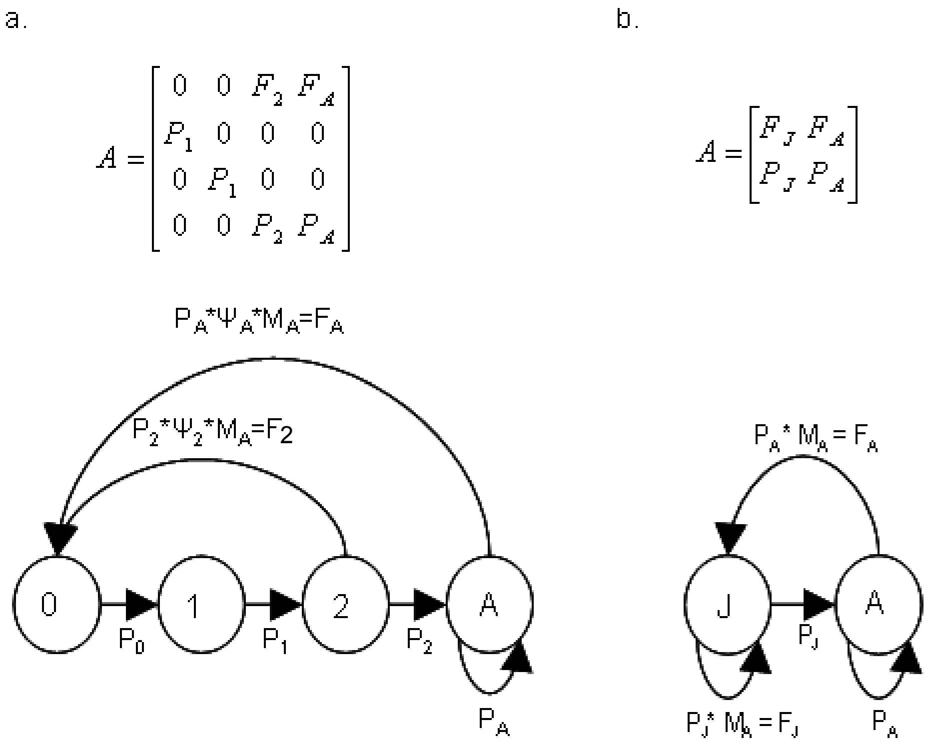
Table 4-4. Model selection results for models of variation in realized population growth rate (λ_{real}), for hoary marmots and collared pikas in the Ruby Range, Yukon. Models are based on data collected between 1999 and 2004, and between 2007 and 2009 for hoary marmots, and on data from 1998 through 2009 for collared pikas. Model terms were PDO (mean winter Pacific Decadal Oscillation value), PDO_{lag} (winter PDO lagged by one year), TIME (random annual variation), SEX (males versus females), and 1 (no annual variation). 'K' is the number of parameters in a model, and ω is the AIC_C weight.

Hoary marmots

Model	**K**	**AIC_C**	**Δ AIC_C**	**ω**	**Deviance**
$PDO+PDO_{lag}$	9	1354.93	0	0.66	85.2
TIME	11	1356.86	1.94	0.25	82.97
SEX * ($PDO+PDO_{lag}$)	12	1359.24	4.32	0.08	83.25
SEX * TIME	16	1363.47	8.55	0.01	79.01
PDO	8	1370.86	15.93	0	103.21
PDO_{lag}	8	1379.2	24.27	0	111.55
1	7	1401.7	46.78	0	136.12

Collared pikas

Model	**K**	**AICc**	**Δ AICc**	**ω**	**Deviance**
TIME	29	4266.93	0	0.64	211.26
SEX + TIME	30	4268.47	1.54	0.3	210.66
SEX * TIME	43	4271.68	4.75	0.06	185.48
PDO_{lag}	17	4278.58	11.65	0	248.28
SEX + PDO_{lag}	18	4280.07	13.14	0	247.68
PDO	17	4281.04	14.11	0	250.75
SEX * PDO_{lag}	19	4281.29	14.36	0	246.82
1	16	4282.21	15.28	0	253.99
SEX	17	4283.7	16.77	0	253.4



$$A = \begin{bmatrix} 0 & 0 & F_2 & F_A \\ P_1 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & P_A \end{bmatrix}$$

$$A = \begin{bmatrix} F_J & F_A \\ P_J & P_A \end{bmatrix}$$

Figure 4-1. Projection matrices and corresponding life cycle diagrams for age-structured matrix models of hoary marmot and collared pika population dynamics. Hoary marmots were modeled using four age classes (0, 1, 2, and A), and collared pikas were modeled using 2 classes (J and A). P_i, M_i, Ψ_i, and F_i terms represent age-specific survival, fecundity, breeding probability, and fertility for each of i age-classes.

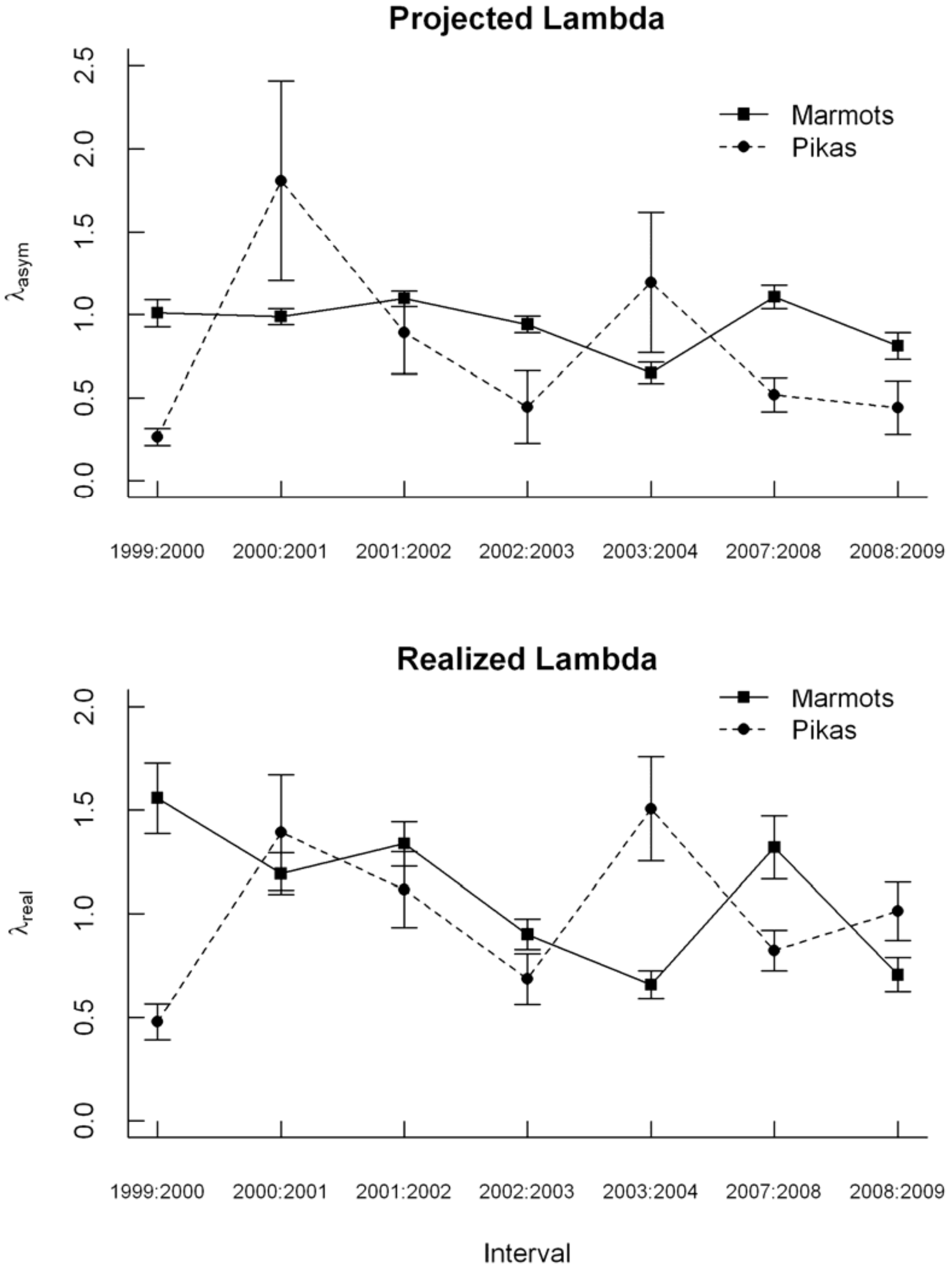


Figure 4-2. Projected population growth rate (λ_{asym}) and realized population growth rate (λ_{real}) for hoary marmot and collared pika populations in the Ruby Range, Yukon, from 1999-2004 and 2007-2009. λ_{asym} values were derived from Leslie matrices, while λ_{real} was estimated using reverse-time mark-recapture models. Error bars represent 1 standard error. λ_{asym} standard errors were boostrapped, while λ_{real} standard errors were estimated using maximum-likelihood.

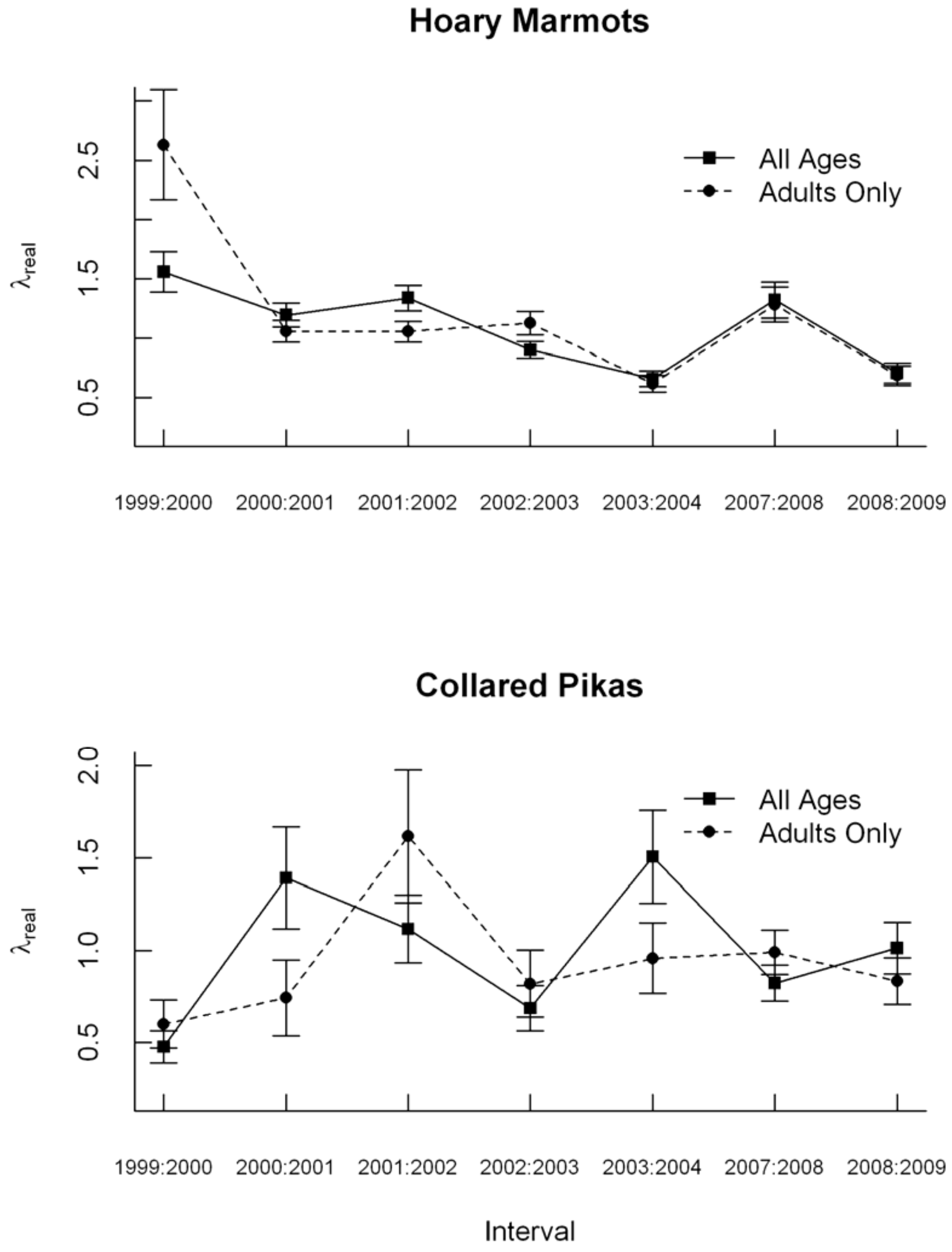


Figure 4-3. Comparison of the realized population growth rate (λ_{real}) for all ages and for the adult age-class only, based on mark-recapture studies of collared pikas and hoary marmots in the Ruby Range, Yukon. Collared pika data are from 1999 through 2009, and hoary marmot data are from 1999 to 2004 and from 2007-2009. λ_{real} values were estimate using reverse-time mark-recapture models. Error bars represent 1 standard error.

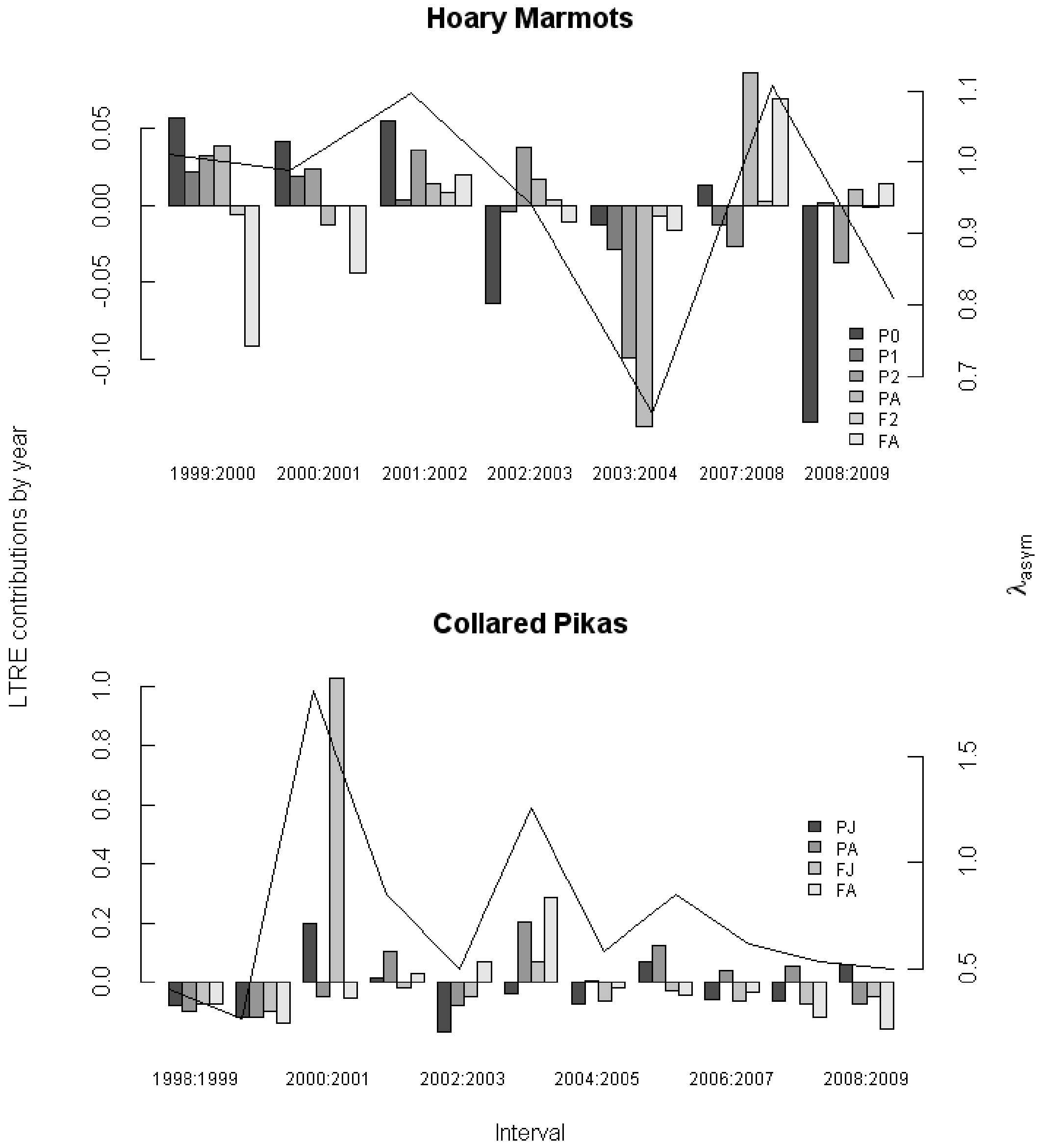


Figure 4-4. Results from Life Table Response Experiments based on long-term mark-recapture studies of hoary marmots and collared pikas in the Ruby Range, Yukon. The hoary marmot LTRE was based on population data from 1999-2004 and 2007-2009. The collared pika LTRE was based on data from 1998-2009. Each cluster of bars represents the proportional contributions made by age-specific demographic parameters to variation in projected population growth (λ_{asym}) during a specific overwinter interval. Contributions are plotted against the left y-axis. The hoary marmot models included six parameters (Juvenile survival = P_0, yearling survival = P_1, two-year-old survival = P_2, adult survival = P_A, two-year-old fertility = F_2, and adult fertility = F_A). The collared pika models included four parameters (Juvenile survival = P_J, adult survival = P_A, juvenile fertility = F_J and adult fertility = F_A The straight line shows the projected population growth rate (λ_{asym}) for each interval, which is plotted against the right y-axis.

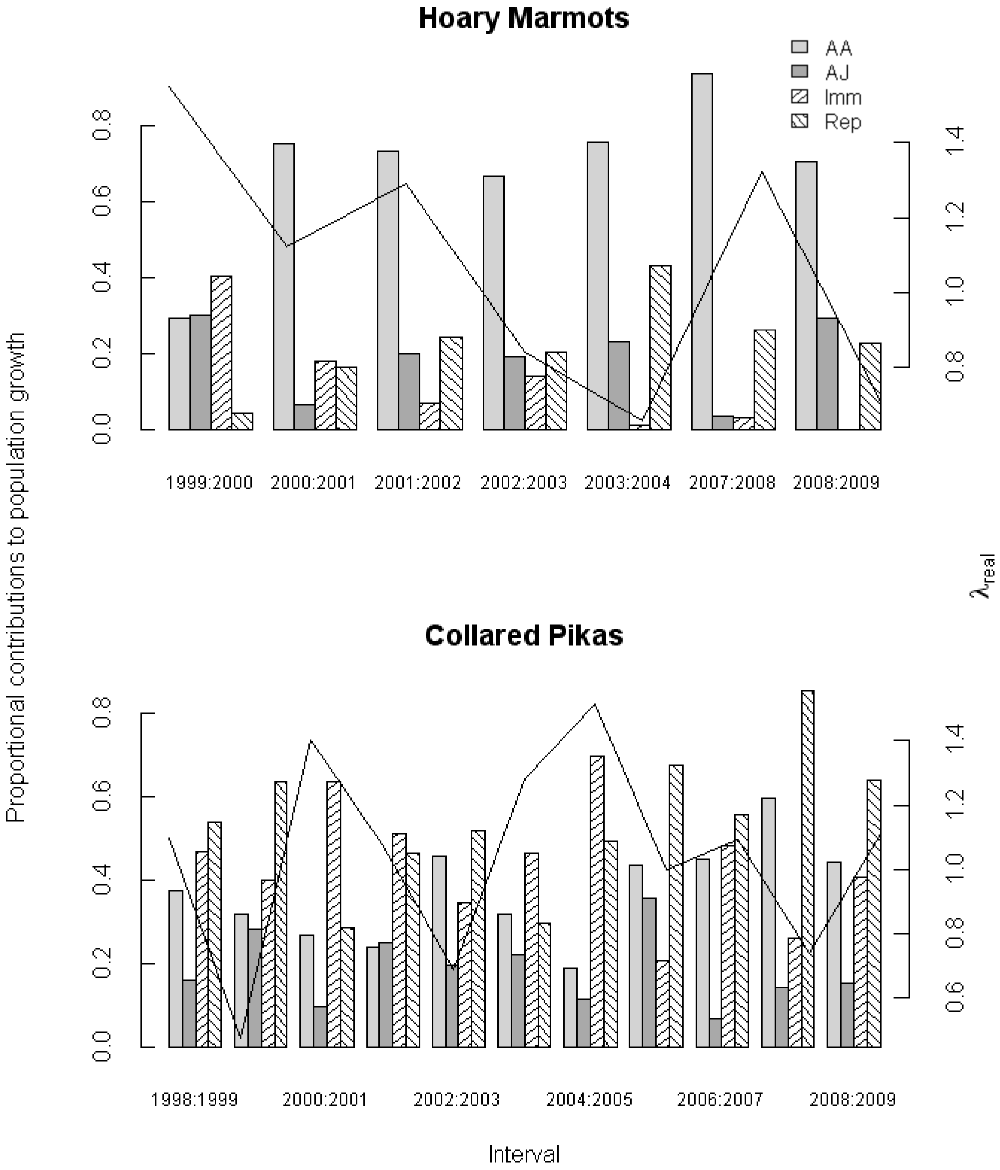


Figure 4-5. Proportional contributions of demographic parameters (Adult survival = AA, juvenile survival = AJ, apparent immigration = Imm, and reproductive parameters (breeding probability & fecundity) = Rep) to the realized population growth rate (λ_{real}) of the adult age class, in hoary marmot and collared pika populations from the Ruby Range, Yukon. The height of each bar (plotted against the left y-axis) represents the proportional effect of a unit change in that parameter on λ_{real}. Contributions were estimated using reverse-time modeling and methods described in Nichols et al. (2000). The solid line represents λ_{real} (for all age-classes combined), which is plotted against the right y-axis.

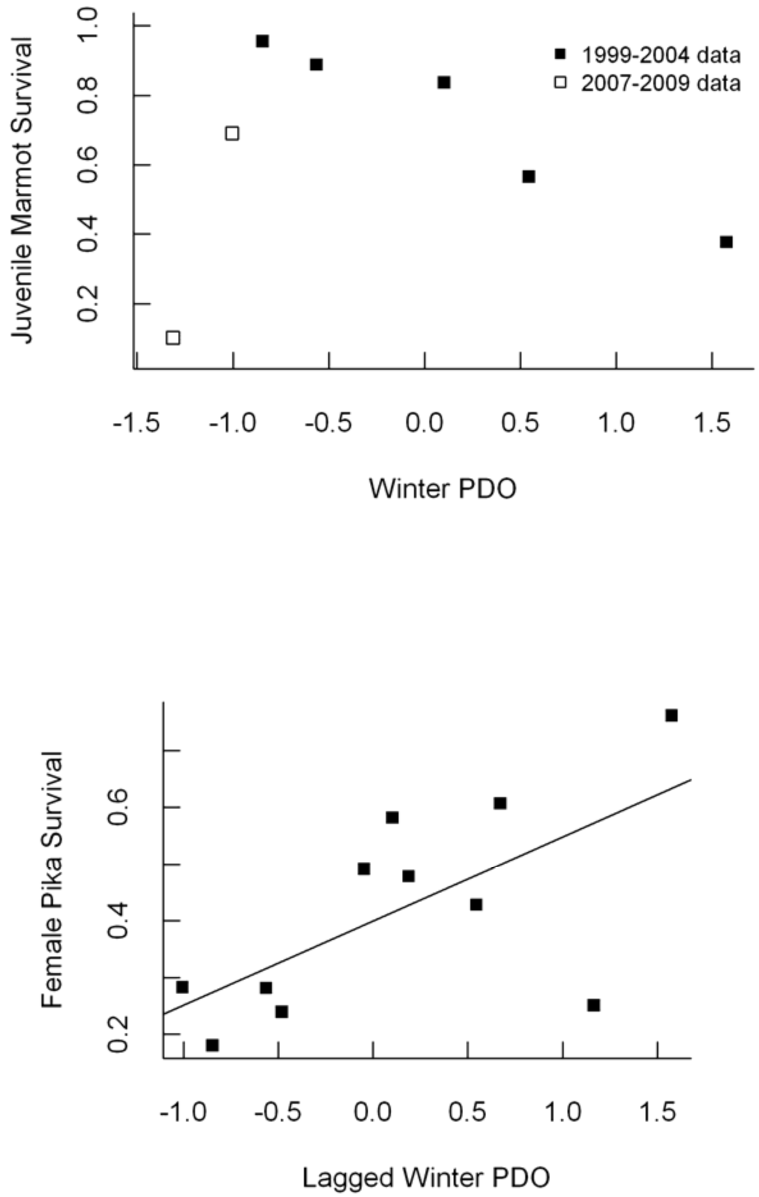


Figure 4-6. Relationships between survival parameters and the mean winter Pacific Decadal Oscillation (PDO) for hoary marmots and collared pikas in the Ruby Range, Yukon. The top panel shows winter PDO from the most recent winter plotted against the probability of juvenile hoary marmot overwinter survival. The bottom panel shows winter PDO lagged by one year plotted against adult female collared pika survival. Hoary marmot juvenile survival estimates are based on data collected between 1999 and 2004, and between 2007 and 2009. Collared pika estimates are based on data from 1998 to 2009. The solid line in the bottom panel represents the significant positive linear relationship between lagged winter PDO and ($R^2 = 0.37$, $p = 0.02$).

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Chapter 5: Conclusions

My primary objective in this thesis was to investigate the effects of winter climate, social structure, and life history on hoary marmot population dynamics. My results are summarized below, and depicted graphically in Fig. 5-1. Winter climate was strongly related to juvenile survival, weakly linked with adult survival and fecundity, and did not appear to influence breeding probability (Chapter 2; Chapter 3). I found little evidence for social influences on demography (Chapter 2; Chapter 3). Age was an important determinant of survival (Chapter 2) and breeding probability (Chapter 3), but could not be used to predict variation in fecundity. Finally, variation in population growth rates was largely determined by juvenile and adult survival, while reproductive parameters and immigration made smaller contributions in most years (Chapter 4).

Synthesis

Taken as a whole, my research suggests that winter climate had a dominant influence on hoary marmot demography, with a much greater impact than any intrinsic factors related to social group size or composition. In that respect, my thesis adds to the growing body of literature that explicity links winter climate with animal population dynamics in the Yukon, and that document the value of the Pacific Decadal Oscillation (PDO) as a biologically meaningful index of climate variability in northwestern North America (Mantua et al. 1997; Mantua and Hare 2002; Morrison and Hik 2007; Hegel et al. 2009). However, in contrast to other alpine mammals in the Yukon, hoary marmots were negatively affected by winters with high PDO values, which corresponded with shallow snow-pack and early spring snowmelt (Moore et al. 2002; Morrison and Hik 2007; Hegel et al. 2009). This result was best explained as the result of a tradeoff between the value of snow as winter insulation and the costs associated with late snowmelt and shortened growing season (Chapter 2). For marmots hibernating in an environment where the mean winter temperature is approximately -20°C (D.S. Hik, unpublished data), having adequate insulation is likely to be of primary importance.

Social dynamics could have potentially influenced all aspects of the hoary marmot life cycle via the dual mechanisms of social thermoregulation and reproductive suppression (Arnold 1988; Blumstein and Armitage 1998; Armitage 1999; Boyles et al. 2008). Surprisingly, social structure appeared to have little influence on either survival (Chapter 2) or reproduction (Chapter 3). Social effects on both survival and fecundity are evident in other marmot species, particularly the alpine marmot (*Marmota marmota*) (Farand et al. 2002; Hackländer et al. 2003; Allaine and Theuriau 2004). However, as discussed at length in Chapter 2, the benefits of social thermoregulation in hoary marmot social groups may simply have been overwhelmed by the severity of winter conditions in the Yukon. Because the presence of non-breeding subordinate adults in the hibernacula had very limited benefits in terms of juvenile survival, reproductive suppression would probably have had little adaptive value. That may be why I failed to find evidence that suppression had occurred (Chapter 3).

Climate clearly did not affect all age-classes or life history parameters of hoary marmots equally. Some of these differences, like the fact that juvenile survival was considerably more sensitive to winter conditions than adult survival (Chapter 2), were expected and consistent with predictions based on hibernation energetics (Blumstein and Armitage 1998). The results from my investigation of reproductive parameters were more surprising. In particular, variation in breeding probability could not be explained by climate, social pressures, or previous breeding state, although there was a sound theoretical basis for expecting all those factors to be important (Chapter 3). Breeding probability was substantially reduced in younger females, however, which suggests that newly established social groups composed of young individuals may be more sensitive to climate-mediated changes in survival and fecundity than other groups.

Although the relative influence of life history parameters on population dynamics was not clearly linked with their relative sensitivity to winter climate, the population growth rate was still well correlated with winter PDO values (Chapter 4). This correlation could not have been predicted based on patterns of survival or fecundity alone, because climate can sometimes influence different life history parameters in conflicting ways (Forchhammer et al. 1998). It is therefore essential to consider an animal's entire life cycle when studying the demographic effects of climate change. Changing winter conditions did not appear to cause a tradeoff between survival and reproduction in my study population (Chapter 2; Chapter 3), but studying any one life history trait in isolation would still have given me an incomplete and potentially misleading understanding of how hoary marmots are affected by their environment (Chapter 4).

Suggestions for future research

The notion that social influences on demography are only important within a certain environmental range has not been widely accepted in the literature on marmot biology. However, research on wild marmot populations has been heavily biased towards only two of the 14 extant species. As described in Chapter 3, information on the other species is sometimes based on scant data, outdated methods, or outright conjecture. My research on an abundant but poorly-known marmot species is only a small step towards closing that knowledge gap. More widespread comparative studies across the genus could greatly improve our understanding of the importance of social structure to animals living in harsh environments.

The hoary marmot is also an excellent candidate for studies of demographic responses to climate change along a large latitudinal gradient. It is abundant in mountain habitats throughout northwestern North America, with a range that spans approximately 13 degrees of latitude (Gunderson et al. 2009). Even a simple monitoring program to document things like the timing of spring emergence (Inouye et al. 2000), patch occupancy (Beever et al. 2003), or approximate population size (Karels et al. 2004) at sites across that range could provide a wealth of information about the relative importance of average winter climate versus inter-annual climate variability. Detailed studies of hoary marmot populations at multiple latitudes could also be a powerful tool for testing hypotheses about how the relative importance of social structure is affected by mean winter conditions. There are numerous national and local parks scattered throughout the hoary marmot's range that could be coordinated for such an effort.

Unfortunately, until now hoary marmots have been incredibly understudied, even compared to other alpine mammals. Based on a search in Google Scholar (conducted 4 May 2010), the hoary marmot had been the subject of only 10 peer-reviewed journal articles papers prior to research at my study site. Eight of those were published over 25 years ago, and none explicitly examined population growth rates. This ignorance appears to reflect a more general lack of commitment by ecologists and managers to monitor and investigate alpine ecosystems. Given their potential value as tools for understanding the ecology of climate change, a renewed focus on these environments, and the species that inhabit them, seems warranted.

Implications for climate change ecology / take home messages

My investigation of hoary marmot population dynamics demonstrates the importance of 'ecological context' in population biology and climate change ecology (Agrawal et al. 2007). When studying the effects of climate change on alpine animals, it is essential to consider more than the rate and magnitude of change. The way an animal experiences its environment is also likely to be important. For example, while a group of hibernating marmots may depend on a thick insulating blanket of snow for their survival, food-hoarding pikas living nearby will suffer if that snow takes too long to melt and delays the onset of the growing season (Morrison et al. 2009). The average environment to which a particular species is adapted (Chapter 2), as well as its life history (Chapter 4), can also help determine how that species will be affected.

Thanks to field experiments like the international tundra experiment (ITEX), we now know a great deal about how plant communities respond to warming, both in arctic and alpine systems and elsewhere (Henry and Molau 2003). However, climate can influence animal populations directly, in ways that are not mediated by bottom-up processes (Chapter 2). Unfortunately, it is often impossible to manipulate climate or its relevant components on a scale that is biologically meaningful to most vertebrates, even small mammals like marmots. Despite their limitations, long-term population studies may often be the best available tool for understanding how animals respond and adapt to a changing environment.

Although the hoary marmot is a useful model organism for studying the effects of climate change, it and other potential 'indicator species' should not be studied in isolation. As demonstrated explicitly in Chapter 4, and qualitatively in Chapters 2 and 3, both the effect of climate on specific demographic parameters and the importance of those parameters can differ from one species to the next, even if they are closely related, ecologically similar, and/or sympatric. The contrast between marmot and pika population dynamics in Chapter 4 is a useful illustration of how problematic such predictions can be. Both pika and marmot species have been proposed as potential indicators of alpine animal responses to climate change (Beever et al. 2003; Schwartz and Armitage 2004), yet collared pikas and hoary marmots cannot be reliably used even to predict the effects of climate variability on each other (Chapter 4). However, comparative studies of pikas, marmots, and other climate-sensitive animal species have great potential as tools for understanding how climate and other extrinsic factors affect population dynamics.

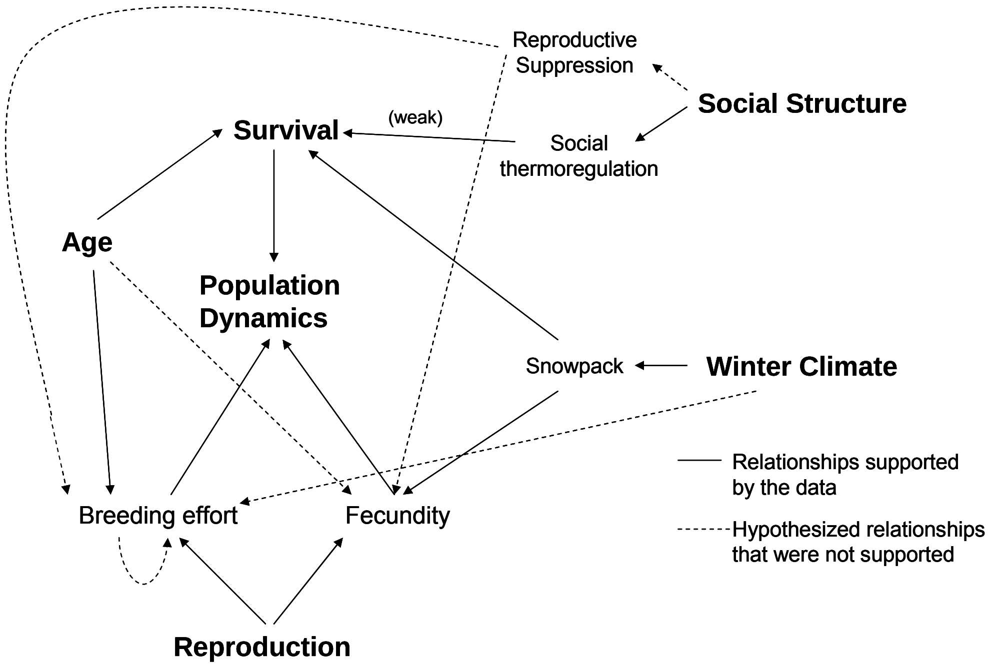

Figure 5-1: Summary diagram of results from Chapters 2, 3, and 4 describing the relationships between winter climate, social structure, life history parameters, and population dynamics of hoary marmots in the southwest Yukon. Solid lines show expected relationships that were supported by the data, while dotted lines show relationships that had a theoretical basis, but little or no empirical support.

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