

METAPOPULATION DYNAMICS OF YELLOW-BELLIED MARMOTS

By

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This thesis is dedicated to two geologists, Necdet and Aynur Ozgul, for their love and support in my endeavor to follow in their footsteps as a scientist.

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Many biological populations inhabit spatially heterogeneous landscapes, and the spatial heterogeneity often has important effects on population dynamics. However, very few empirical studies on long-lived vertebrates have thoroughly investigated the effect of spatial heterogeneity on population dynamics. Using 42 years of field data, I investigated the factors and processes that influenced the dynamics and persistence of a yellow-bellied marmot metapopulation in Colorado, USA.

Using a simple patch occupancy model, I investigated the relative influence of particular sites on metapopulation dynamics. A few colony sites were the major drivers of metapopulation dynamics, and regional persistence was highly sensitive to changes in the quality of these sites. Nonetheless, satellite sites also made a significant contribution to the long-term persistence of the metapopulation.

Using capture-mark-recapture (CMR) modeling approach, I investigated the spatiotemporal variation in demographic rates and its influences on local population dynamics. Survival and reproductive rates exhibited both spatial and temporal variation,

but the pattern of variation significantly differed among vital rates. Vital demographic rates that were the components of recruitment into the adult population (survival of young animals, litter size and breeding probability) exhibited a greater degree of variation over space and time than other vital rates, and were the main demographic factors driving the temporal fluctuations in population dynamics.

Using a stage-structured matrix model, I investigated the demographic causes of the spatial variation in local population dynamics. Variation in the survival of the young animals and that of reproductive adults made the largest contributions to the observed spatial variation in population growth rate. Using a vector-permutation matrix approach, I developed a matrix metapopulation model, and investigated the relative influence of local demographic rates and the dispersal rate on regional population dynamics.

Metapopulation dynamics mainly depended on a few colony sites, and the metapopulation growth rate was highly sensitive to changes in the demography of these high quality sites. The relative influence of dispersal on metapopulation growth rate was lower than that of the demographic rates. Most commonly used models of metapopulation dynamics emphasize the importance of regional processes, but do not explicitly consider the role of within-population demographic processes. However, my results underscore the need for the explicit consideration of the local demographic processes for understanding the dynamics and persistence of demographically and spatially structured populations.

CHAPTER 1 INTRODUCTION

Background

Several wildlife populations are influenced by multiple environmental factors that vary over space and time (Orzack and Tuljapurkar 1989, Tuljapurkar 1990, Post et al. 1997). It has become increasingly apparent that the spatial structure of populations often has important effects on population dynamics (Andrewartha and Birch 1954, Levins 1969, Hanski 1999), and investigating these effects may be critical to understanding the dynamics of these populations (Pulliam 1988, Kareiva 1990, Hanski and Simberloff 1997, Stacey et al. 1997, Tilman and Kareiva 1997, Akçakaya 2000b, Fagan et al. 2001). Ecologists and conservation biologists are increasingly relying on spatially-structured population models to address the influence of spatial heterogeneity on population dynamics (e.g., Lankester et al. 1991, Lahaye et al. 1994, Akçakaya and Sjørgen-Gulve 2000, Hokit et al. 2001). Although there are still gaps between theory and practice, several studies utilizing metapopulation (i.e., a set of local populations connected through dispersal) approaches have been moderately successful in explaining and predicting wildlife population dynamics in fragmented landscapes (e.g., Hanski et al. 1995, Moilanen et al. 1998).

The various methods of representing space, tracking populations and individuals, dealing with environmental variability, and describing dispersal have generated a variety of metapopulation models that differ in generality and realism (Kareiva 1990, Hanski 1999, Akçakaya and Sjørgen-Gulve 2000). Some of these models are data intensive, and

the lack of adequate data has precluded the application of more complex models. For many threatened species, data to parameterize complex models are often lacking, and simpler modeling approaches are the only option.

The presence-absence of a species at a particular site is the simplest form of data that can be collected during ecological field studies (Hanski 1994b). A class of metapopulation models that require only the presence-absence data are the patch occupancy models (reviewed in Hanski 1999). Despite the limitations of occupancy models, their simplicity and generality allow several important ecological questions to be addressed (Sjorgen-Gulve and Hanski 2000). Although adequate description of metapopulation dynamics might require more complex models, it is important to know what we can learn about the dynamics and persistence of a spatially structured population by analyzing these simple models. In certain situations, simple models may be as informative as more complex models and may yield similar results (Hokit et al. 2001, Lopez and Pfister 2001). However, there are very few comparisons of different modeling approaches applied to the same populations (but see Hokit et al. 2001).

Simple metapopulation models (e.g., patch occupancy models) emphasize the role of regional processes, such as dispersal and synchrony among local populations, but do not explicitly consider the role of local demographic processes, such as survival and reproductive rates, density dependence and temporal trends in these vital rates. However, local demographic processes can be important determinants of metapopulation dynamics (e.g., Burgman et al. 1993, Lahaye et al. 1994). Spatial variation in population dynamics is a consequence of local differences in demographic parameters (Caswell 2000, Oli and Armitage 2004, Bruna and Oli 2005). Also, the dispersal of individuals among local

populations is often dependent on demographic processes (Bowler and Benton 2005, Matthysen 2005). However, consideration of local demographic processes usually requires more data than is required by simple models (Akçakaya 2000a). As a result, very few studies of long-lived species have thoroughly investigated spatiotemporal variability in local demographic rates and its influence on population dynamics.

The relative significance of local and regional processes on population persistence is an important question from both theoretical and practical perspectives. A group of models, matrix metapopulation models (i.e., structured metapopulation models), attempts to incorporate local demographic processes and regional processes into modeling population dynamics across multiple sites (Akçakaya 2000a, Hunter and Caswell in press). These models form the basis of several published population viability analyses (PVA's, reviewed in Boyce 1992, Akçakaya 2000b, Beissinger and McCullough 2002). Recent developments in matrix metapopulation models have provided a framework for using the analytical approaches to matrix analysis (e.g., sensitivity and elasticity analyses) for metapopulation models (Hunter and Caswell in press). This approach provides an analytical framework for investigating the relative influence of local demography and dispersal on metapopulation dynamics. However, even simple matrix metapopulation models are data intensive and thus difficult to parameterize for most species; there are very few studies that provide sufficient data on all the demographic rates in multiple sites and the dispersal rates among sites. Therefore, little is known about the relative importance of local demographic processes on the dynamics of spatially structured populations, particularly for long-lived species.

Objectives

In this doctoral research, I investigated the factors and processes that influence the dynamics and persistence of a yellow-bellied marmot metapopulation in the upper East River Valley, Colorado. Long-term research by Dr. K. B. Armitage and his colleagues at the Rocky Mountain Biological Laboratory has yielded 41 years of demographic (trapping) data and 10 years of dispersal (radio-telemetry) data from several colonies (Van Vuren 1990, Armitage 1991, Schwartz et al. 1998, Armitage and Schwartz 2000). The long-term study of individually-identified animals in several discrete habitat patches provided adequate data for a rigorous examination of metapopulation dynamics using models with different degrees of sophistication. My specific objectives were (1) to investigate the relative influence of particular sites and site quality on metapopulation persistence, (2) to investigate the spatial heterogeneity in demographic rates and its influence on population dynamics, (3) to determine the relative influence of demographic rates and the dispersal rate on the metapopulation dynamics, and (4) to compare the utility of two metapopulation models with different degrees of complexity. This dissertation is organized into six chapters: a general introduction chapter (Chapter 1), four manuscript chapters (Chapters 2-5), and a general conclusion chapter (Chapter 6).

In Chapter 2, I parameterized and analyzed a stochastic patch occupancy model (Moilanen 2004), and investigated the relative influence of particular sites, site quality, network characteristics, and regional stochasticity on the persistence of the yellow-bellied marmot metapopulation.

In chapters 3 and 4, I investigated the spatiotemporal variation in local demographic processes and its influence on the local population dynamics. In Chapter 3, I investigated the spatiotemporal variation in age-specific survival rates using an age-

structured Cormack-Jolly-Seber model (Lebreton et al. 1992, Lebreton et al. 1993) and long-term capture-mark-recapture (CMR) data. In Chapter 4, I investigated the spatiotemporal variation in the components of reproduction; I analyzed stage-specific breeding probabilities using a multistate CMR model (Hestbeck et al. 1991, Brownie et al. 1993, Williams et al. 2001, Fujiwara and Caswell 2002) and age-specific litter sizes using a general linear model. In both chapters, I also tested a series of hypotheses concerning the effects of key environmental and social factors on the observed variation in each vital rate. Furthermore, using a Pradel's reverse-time CMR model (Pradel 1996, Nichols and Hines 2002), I modeled the realized population growth rate for each site and examined population dynamic consequences of the spatiotemporal variation in each vital rate.

Chapters 3 and 4 provide robust and detailed estimates of survival and reproductive rates for each local population. Using these estimates, I parameterized a stage structured matrix model for each site in Chapter 5, and investigated the demographic causes of spatial variation in local population dynamics of the yellow-bellied marmot. Next, using a vector permutation matrix approach (Hunter and Caswell in press) and the dispersal data, I developed a matrix metapopulation model that connected the local population dynamics via dispersal. Using this demographically and spatially structured model, I investigated the relative influence of local demographic rates and the dispersal rate on metapopulation dynamics.

Finally, Chapter 6 provides a general conclusion of the results presented in the previous chapters. This research aimed to provide a better understanding of the local and

regional processes that underlay the dynamics of the yellow-bellied marmot metapopulation, and to provide insights into the utility of different modeling approaches.

The Study System

The yellow-bellied marmot (*Marmota flaviventris*) is a large, diurnal, burrow-dwelling rodent, widely distributed in the mountainous region of the western United States (Frase and Hoffmann 1980). This research was based on data collected by K. B. Armitage and his colleagues during a long-term study of marmots in the Upper East River Valley (2900 m above sea level, 38° 57' N - 106° 59' W), near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado (Armitage 1991, Schwartz et al. 1998). Distribution of marmots in the East River Valley is patchy and closely associated with the local mosaic of meadow and forest vegetation. Marmots typically occupy meadows associated with talus and large boulders, where they build their burrow systems (Svendsen 1974). These distinct habitat patches vary in size ranging from satellite sites as small as 0.01 ha, to colony sites as large as 7.2 ha. Small and lower quality patches (satellite sites) are typically occupied by a single adult female, her litter, and sometimes an adult male. Large and higher quality patches (colony sites) are occupied by one or more matriline, each typically consisting of one male, two or more closely related adult females, yearlings (1-year old), and young (Armitage 1991, 1998).

A marmot's circannual cycle has two phases, the active period (approximately 5 months) and hibernation (approx. 7 months), that entail, sequentially, emergence from the burrow, reproduction, growth, preparation for hibernation, immergence into burrow, and hibernation (Armitage 1991). The circannual cycle is a major constraint on individual growth and population dynamics, because the short active season limits reproduction to a single annual litter and delays reproductive maturity until two years of age. This is

probably the major factor leading to sociality in marmots (Armitage 1981). Marmots produce a litter of 1 to 8 young that appear above ground around late June. Most young marmots remain and hibernate at their natal site. Most of the dispersal takes place among yearlings; almost all of the yearling males and half of the yearling females disperse beyond their natal site (Schwartz et al. 1998).

Population re-establishment can occur when daughters are recruited into their natal colonies or an immigrant occupies an empty burrow. Immigration occurs when deceased residents are not replaced by recruits from within the colony. Matrilineal groups can exclude potential immigrants, thus securing the site for their progeny (Armitage 2003c). Thus, the nature of population turnover is strongly influenced by the social system. The major cost of living in a matrilineal group is reproductive suppression; the dominant, reproductive females tend to suppress the reproduction in subordinate females (Armitage 1989, 2003c, Oli and Armitage 2003).

Survival and reproduction seem to be affected by the length of the active season, which varies from year to year (Armitage and Downhower 1974). The main agent of winter mortality is unsuccessful hibernation, and the main agent of summer mortality is predation (Van Vuren 1990). The number of males does not substantially affect the fecundity rates. Yearling males are chased away by the adult male; hence their dispersal is inevitable. Social tolerance of adults seems to be critical in female dispersal; females disperse earlier when rates of aggression are high and remain longer when they are low. Yearlings may assess the probability of future reproductive success and decide to remain or disperse (Armitage 1991). Detailed biology of yellow-bellied marmots in Gothic, Colorado, is described in detail by Armitage (1991, 2002). Although a great deal is

known about their biology and social system, the relative role of local and regional processes in determining the dynamics and persistence of the yellow-bellied marmot metapopulation is unknown.

CHAPTER 2
EFFECTS OF PATCH QUALITY AND NETWORK STRUCTURE ON PATCH
OCCUPANCY DYNAMICS OF A YELLOW-BELLIED MARMOT
METAPOPOPULATION

The presence/absence of a species at a particular site is the simplest form of data that can be collected during ecological field studies. We used 13 years (1990-2002) of survey data to parameterize a stochastic patch occupancy model for a metapopulation of the yellow-bellied marmot in Colorado, and investigated the significance of particular patches and the influence of site quality, network characteristics, and regional stochasticity on the metapopulation persistence. Persistence of the yellow-bellied marmot metapopulation was strongly dependent on the high quality colony sites, and persistence probability was highly sensitive to small changes in the quality of these sites. A relatively small number of colony sites was ultimately responsible for the regional persistence. However, lower quality satellite sites also made a significant contribution to long-term metapopulation persistence, especially when regional stochasticity was high. The northern network of the marmot metapopulation was more stable compared to the southern network, and the persistence of the southern network depended heavily on the northern network. Although complex models of metapopulation dynamics may provide a more accurate description of metapopulation dynamics, such models are data-intensive. Our study, one of the very few applications of stochastic patch occupancy models to a mammalian species, suggests that stochastic patch occupancy models can provide important insights into metapopulation dynamics using data that are easy to collect.

Introduction

Many biological populations occupy spatially heterogeneous environments, and there is a growing realization that spatially-mediated processes (e.g., dispersal, habitat connectivity) are vital for the regional persistence of populations. Ecologists are increasingly relying on metapopulation theory to understand the influence of spatial heterogeneity on dynamics and persistence of biological populations (e.g., Lankester et al. 1991, Lahaye et al. 1994, Akçakaya and Atwood 1997, Hokit et al. 2001).

The presence/absence of a species at a particular site is the simplest form of data that can be collected during ecological field studies (Hanski 1994b). A class of metapopulation models that capitalizes on such data is the stochastic patch occupancy models (SPOMs). The theory of SPOMs has been well developed, and these models have received much practical application (Moilanen and Hanski 1998, Hanski 1999, Moilanen 1999, Moilanen and Cabeza 2002). SPOMs assume that suitable habitat occurs in discrete patches surrounded by unsuitable matrix and that occupancy of each patch is determined by local colonization and extinction events. These turnover events are assumed to depend on factors such as patch area (a proxy for local population size), spatial arrangement of patches, dispersal ability of the species, and spatially correlated environmental stochasticity (regional stochasticity). These assumptions are reasonable for many biological populations inhabiting highly fragmented landscapes, where only a small portion of the landscape often provides suitable habitat (Hanski and Ovaskainen 2003).

An important question that can be addressed using SPOMs is: what is the relative significance of particular patches or networks (patch groups) for patch occupancy dynamics? Intuitively, low quality patches that are poorly connected to other patches will have lesser influence on metapopulation dynamics than high quality patches that are well

connected. However, low quality patches may, under certain conditions, significantly influence regional dynamics (Brown 1969, Gill et al. 2001). If there is no significant contribution of the low quality patches, metapopulation dynamics may depend only on the high quality patches, and the interactions between high and low quality patches may resemble source-sink (Pulliam 1988, Pulliam and Danielson 1991) or mainland-island dynamics (Schoener 1991). The importance of a particular patch (or network) can be investigated by comparing simulated patch occupancy dynamics with and without that patch (or network). Previous studies have observed that persistence of a particular patch network may depend on the presence of other networks (e.g., Moilanen et al. 1998).

SPOMs have mostly been used to model the metapopulation dynamics of large invertebrates or small vertebrates. The preference for small-bodied habitat specialists is dictated by the criteria of regional persistence as a classical metapopulation: high rate of population increase, short generation time, and high habitat specificity (Murphy et al. 1990, Hanski 1999). However, some mammal populations that occupy discrete habitat patches also exhibit characteristics of metapopulations, and SPOMs can be applied to such populations as well (e.g., Moilanen et al. 1998).

A mammal species that meets the assumptions of the SPOMs is the yellow-bellied marmot, *Marmota flaviventris* (Audubon & Bachman 1841). Yellow-bellied marmots occupy discrete habitat patches that vary in quality (Svendsen 1974), and populations can go locally extinct and be recolonized by individuals from surrounding patches (Svendsen 1974, Armitage 2003b). Although there is a gradient from low quality to high quality sites, marmot habitats can be grouped into two major quality types: (1) colony (high quality), and (2) satellite (low quality) sites. The persistence of the metapopulation is

believed to be dependent mainly on the colony sites, but the relative influence of colony and satellite sites on the marmot metapopulation dynamics is unknown.

In this study, we used long term (1990-2002) patch occupancy data and a SPOM to investigate metapopulation dynamics of yellow-bellied marmots in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Colorado (hereafter referred to as Colorado). Specifically, we investigated the relative influence of particular sites, site quality, network characteristics, and regional stochasticity on the persistence of the yellow-bellied marmot metapopulation.

Materials and Methods

Study Area and Species

The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent, widely distributed in the mountainous region of the western United States (Frase and Hoffmann 1980). Marmots typically occupy meadows with talus and large boulders, under which they dig their burrow systems (Svendsen 1974). The distribution of marmots in Colorado is patchy (Fig. 2-1) and is closely associated with the local mosaic of meadow and forest vegetation. The distinct habitat patches vary in size, ranging from 0.01 ha to 7.2 ha (K. B. Armitage, unpublished data). However, the density of marmots varied remarkably among sites, and local patch area does not necessarily represent the local population size (Armitage and Schwartz 2000). We use the term "site quality" to describe the combined effect of multiple environmental factors (including patch area) on local population size. Satellite sites (lower quality patches) are typically occupied by a single adult female, her litter, and sometimes an adult male. Colony sites (higher quality patches) are occupied by one or more matriline, each typically consisting of one male, two or more closely related adult females, yearlings (1 year old), and young (Armitage 1991, 1998).

Typically, all yearling males and about half of the yearling females disperse (Van Vuren 1990, Schwartz et al. 1998). Recolonization occurs when an immigrant occupies an empty habitat patch. Matrilineal groups can exclude potential immigrants unless all individuals die and the habitat patch is empty, thus reducing the chance of a 'true' rescue effect (Armitage 1991, 2003b). Local extinction occurs when a matriline dies out or deserts a site. However, local turnover events can be concealed by the immediate occupation of an empty site by immigrants, thus creating an 'apparent' rescue effect. The detailed biology of yellow-bellied marmots in Colorado is described by Armitage (1991, 2002).

Although the number of patches in the yellow-bellied marmot metapopulation in Colorado is smaller than that observed in some studies, our study system meets the four conditions of regional persistence as a metapopulation (Murphy et al. 1990, Hanski et al. 1995). First, marmots live in spatially discrete habitat patches. Their burrow systems are typically located in open meadow patches with rocky outcrops (Svendsen 1974). Philopatric marmots rarely go >50 m away from burrows because of the predation risk. Second, all local populations face the risk of local extinction in the absence of a rescue effect. The average population size of the largest colony is approximately 20 animals, and local extinction is possible due to predation, disease, environmental and demographic stochasticity or catastrophes. Third, the probability of survival during dispersal decreases with the distance moved (Van Vuren 1990). Therefore, low survival of the long-distance dispersers can result in a distance-dependent dispersal. Finally, the local population dynamics are sufficiently asynchronous (Armitage and Downhower 1974, Armitage 1977, 2003b, Oli and Armitage 2004). Asynchrony in local population dynamics

increases the probability that an extinct local population is reestablished, or a declining population is rescued by dispersers from other local populations (Hanski et al. 1995). Therefore, the yellow-bellied marmot system provides one of the few examples of naturally occurring mammalian metapopulations to which SPOMs can be applied (e.g., Bryant 1998, Moilanen et al. 1998, Stephens et al. 2002).

Model Structure

We used Program SPOMSIM (Moilanen 2004) to parameterize and simulate a SPOM for the yellow-bellied marmot metapopulation. SPOMSIM is a computational modeling tool designed for the parameterization and analysis of SPOMs. In SPOMSIM, subfunctions can be chosen for describing the dispersal kernel, connectivity function, colonization probability, extinction probability, and rescue effect (Moilanen 2004).

The shape of the dispersal kernel is important only when the metapopulation consists of several small networks that are far from each other, which was not the case in our system. Therefore, we used the simple negative exponential function for describing the dispersal kernel:

$$D(d_{ij}, \alpha) = \exp(-\alpha d_{ij}) \quad (1)$$

where d_{ij} is the distance between patches i and j , and α is the distribution parameter of the dispersal distances ($1/\alpha =$ average dispersal distance).

For the connectivity function, we used the subfunction that includes the effect of local patch area (patch quality in this study) on connectivity:

$$S_i(t) = A_i^c \sum_{j \neq i} O_j(t) D A_j^b \quad (2)$$

where $O_j(t)$ is the occupancy status of each patch at time t , D is the dispersal kernel (Eq.

1), and A_i is the quality of patch i . Parameter b scales emigration, and parameter c scales immigration as a function of patch quality (Moilanen and Nieminen 2002).

Moilanen (2004) recommends that the choice of the colonization function be based on the biology of the studied species. Because marmot colonies typically contain only few individuals, we used the subfunction that includes the Allee effect in colonization (Hanski 1994b):

$$C_i(t) = \frac{[S_i(t)]^2}{[S_i(t)]^2 + y^2} \quad (3)$$

where $S_i(t)$ is the connectivity of patch i at time t (Eq. 2), and y is a model parameter.

For the extinction function, we used two alternative subfunctions, one that was used in the incidence function model (IFM) and the other in spatially realistic Levin's model (SRLM):

$$E_i = \frac{\mu}{A_i^x} \quad (\text{IFM}) \quad (4)$$

$$E_i = 1 - \exp\left(\frac{-\mu}{A_i^x}\right) \quad (\text{SRLM}) \quad (5)$$

where μ is the extinction probability of a patch of unit size, and parameter x scales the extinction risk as a function of patch area (for a discussion see Foley 1997).

The rescue effect can be included in the SPOM, and it essentially decreases the extinction probabilities of well-connected patches. We used the generalized version of the rescue effect function to determine the strength of the rescue effect:

$$E_i(t) = \min\{1, (1 - C_i(t))^R E_i\} \quad (6)$$

where parameter R determines the strength of the rescue effect.

Different models with alternative combinations of connectivity and extinction functions were parameterized and the most parsimonious model was identified using Akaike's Information Criterion corrected for small samples, AIC_c (Burnham and Anderson 2002, Grimm et al. 2004).

Parameter Estimation

SPOMs can be parameterized with survey data from a single year; however, data from several years provide more robust estimates of parameters (Moilanen 1999). A long-term study in Colorado has provided occupancy data for most sites; however, some sites were not surveyed every year (Armitage 1991, Schwartz et al. 1998). We used data from 21 known sites surveyed between 1990 and 2002 to parameterize the SPOMs, as this period provided the most complete occupancy information (Fig. 2-2).

In SPOMs, patch area is often used to indicate local population size. This indicator is based on the assumption that as the patch area increases, local population size increases, hence the local extinction risk decreases. Patch area is preferred by many authors, because estimating area is generally easier than estimating local population size or other measures of patch quality. However, the density of marmots varied remarkably among sites. We used the average number of adult females per site (conditional on occupied years) as a measure of patch quality, because it was a more accurate measure of local population size than was patch area.

Where possible, independent estimation of model parameters is preferable in order to reduce the number of parameters to be estimated from site occupancy data (Hanski 1999). Parameter α of the dispersal kernel was estimated using independent dispersal data, while the remaining model parameters (b , c , y , μ , x , and R) were estimated from the

site occupancy data using the Markov Chain Monte Carlo method (Moilanen 1999). Analysis of local population dynamics during the last 40 years did not reveal any significant trend in population sizes (Schwartz et al. 1998, Schwartz and Armitage 2003, Oli and Armitage 2004). Therefore, it was reasonable to assume that the yellow-bellied marmot metapopulation was at a stochastic quasi-equilibrium.

Model Simulation

Metapopulation dynamics were simulated using the most parsimonious model which was selected based on AIC_c as described above. Each scenario was simulated 1000 times for 100 years. Model predictions included changes in average proportion of occupied patches and proportion of simulated replicates that survived throughout 100 years, and average metapopulation lifetime (Hanski 1994b, Moilanen et al. 1998).

Influence of site quality and network structure. We classified each habitat patch either as a colony site or a satellite site based on the average number of adult females. Nine sites that had > 1 adult female on average were designated as colony sites, and 12 sites that had < 1 adult female on average as satellite sites.

Using the most parsimonious model, we simulated three alternative scenarios: (1) colony sites excluded, (2) satellite sites excluded, (3) original configuration. Predictions of alternative models on metapopulation persistence were compared to assess the relative influence of colony and satellite sites on the overall metapopulation dynamics (e.g., Hanski 1994a).

The Colorado yellow-bellied marmot metapopulation can be divided into two networks, the northern and the southern network, which are separated by areas of unsuitable habitat. The most parsimonious model was used to simulate three alternative scenarios: (1) northern network, (2) southern network, and (3) entire network. The

predictions of alternative models on metapopulation persistence were compared to assess the significance of compartmentalization among sites (e.g., Moilanen et al. 1998).

Significance of regional stochasticity. Spatial correlation in environmental stochasticity (regional stochasticity) can heavily influence metapopulation persistence (Hanski and Ovaskainen 2003). Regional stochasticity is included in SPOMSIM based on log-normal variation in patch area, which creates a yearly synchronous variation in both extinction and colonization rates (Moilanen 2004). The standard deviation (σ) of this variation quantifies the level of synchrony. The level of regional stochasticity could not be directly estimated; therefore, we used two levels of regional stochasticity ($\sigma = 0.1$ & 0.2) and analyzed the sensitivity of model predictions to regional stochasticity.

Adequacy of the SPOM

We used the robust design occupancy modeling approach (MacKenzie et al. 2002, MacKenzie et al. 2003) to investigate the adequacy of the SPOM used for simulations of the yellow-bellied marmot system. The robust design occupancy model uses occupancy data and provides a framework for estimating the rate at which occupied sites go extinct (ε) and the rate at which unoccupied sites are recolonized (γ). We used program MARK V 4.0 (White and Burnham 1999) to implement the robust design occupancy model with parameters ψ (proportion of sites occupied), ε (probability of an occupied site becoming unoccupied), γ (probability of an unoccupied site becoming occupied), and ρ (detection probability on a visit to the site) (MacKenzie et al. 2002, MacKenzie et al. 2003). Robust design occupancy models implemented in program MARK provides more flexibility in modeling recolonization and extinction probabilities, and allows comparison of several alternative model structures that are not included in SPOMSIM.

Program MARK can be used to estimate time-specific rates of extinction and colonization, and time-varying individual covariates can be used to incorporate site-specific information into the model. We estimated the site- and time-specific extinction and colonization rates for 21 sites for 13 years using the most parsimonious SPOM. We used these estimates as time-varying site covariates for estimating ε and γ parameters using MARK. Years for which the occupancy status was unknown were treated as missing values. Because we did not have >1 sample occasion per year, we assumed that there were no false zeros (indicating that the site was not occupied) in our occupancy history, and set our detection probability parameter (ρ) to 1.0. Considering the conspicuousness of the presence of marmots at a given site and the high intensity of observation efforts, we believe that this is a reasonable assumption.

We used AIC_c for model comparison, and for the identification of the most parsimonious model in the candidate model set. Candidate models differed in the way parameters ε and γ were modeled. We used four alternative model structures for modelling extinction rate, ε . First, we modelled ε as a constant rate $\{\varepsilon(\cdot)\}$. Second, we modelled ε as a time-specific rate and let it vary among years $\{\varepsilon(t)\}$. Third, we let ε vary among sites and used site quality as a constant site covariate $\{\varepsilon(Q)\}$. Finally, we used the extinction rate estimated from SPOM as a time-varying site covariate $\{\varepsilon(E)\}$. We also used four alternative model structures for modelling recolonization rate, γ . Similar to ε , we initially modelled γ as a constant $\{\gamma(\cdot)\}$ and a time-specific $\{\gamma(t)\}$ rate. Then, we let γ vary among sites and through time, and used the colonization $\{\gamma(C)\}$ and connectivity $\{\gamma(S)\}$ parameters estimated from SPOM as time-varying site covariates. We expect the models in which the time-varying site covariates (estimated from SPOM)

were used as predictors of extinction and recolonization rates to be more parsimonious than the time-specific or constant recolonization and extinction rate models.

Results

Parameter Estimation

We used independent dispersal data from 90 radio-instrumented marmots (Van Vuren 1990) to estimate the dispersal kernel parameter, α . The average dispersal distance was 2.087 km, and α was estimated as the inverse of the average dispersal distance ($\alpha = 1/(2.087) = 0.479$). To evaluate the robustness of our estimate, we set α as a free parameter in SPOMSIM, and estimated it from patch occupancy data. This method gave an estimate of 0.337, which was slightly smaller than our independent estimate. These estimates indicated fairly high dispersal ability, which was consistent with previous field observations (Van Vuren 1990). We performed simulations using both values of α , and found that the qualitative conclusions remained unchanged. Here, the independent estimate of α (0.479) was used for parameterizing the dispersal subfunction and simulation of alternative scenarios. The remaining model parameters were estimated using the 13 year occupancy data (Fig. 2-2) and the Markov Chain Monte Carlo estimation technique provided in SPOMSIM.

We used AIC_c weights to select the best model from a set of 8 candidate models (Table 2-1). The most parsimonious model (model #5 in Table 2-1) included the following subfunctions:

- Negative exponential function (Eq. 1) for describing the dispersal kernel (α fixed at 0.479).
- Connectivity function that included the effect of local patch quality (Eq. 2).
- Colonization function with the Allee effect in colonization (Eq. 3).

- Extinction function from the original IFM (Eq. 4).
- Rescue effect with parameter R (strength of the rescue effect) fixed at 1.0 (Eq. 6).

The differences in AIC_c values between the best model (model # 5) and other alternative models were more than 2 except in two cases: model # 1 (original IFM) and model # 7 (Table 2-1). The model structure of the best model (model # 5) differed from that of original IFM (model # 1) in that model # 5 included the effect of local patch quality on connectivity by including the model component A_i^c (in Eq. 2). Despite the small differences in AIC_c values, we used model with the smallest AIC_c value (model # 5) for simulating metapopulation dynamics. Parameter values of the most parsimonious model are given in Table 2-2.

Scaling of extinction risk with patch quality, parameter x , was in the higher end of the typical range ($0.5 < x < 1.5$: Moilanen 2004), indicating that local extinction probability decreased rather quickly with increasing population size. The intrinsic extinction probabilities for the smallest (0.3 adult females on average), average (1.3 adult females) and largest (3.8 adult females) patches were 0.78, 0.08 and 0.02, respectively. Incidentally, value of x estimated for the yellow-bellied marmots was very close to the one estimated for the American pika, *Ochotona princeps* (Moilanen et al. 1998).

Scaling of emigration with patch quality was weak ($b < 0.2$), indicating that quality of a patch did not substantially influence the emigration rate. Scaling of immigration with patch quality was in the typical range ($c < 0.5$), indicating that local patch quality had a significant influence on the immigration rates (Moilanen 2004).

Model Simulation

The patch occupancy dynamics of the yellow-bellied marmot metapopulation was simulated using the most parsimonious model (model #5 in Table 2-1) with the parameter

estimates given in Table 2-2. For all simulations, the average proportion of occupied patches and the proportion of surviving simulation replicates were reported for two different levels of regional stochasticity ($\sigma = 0.1$ and $\sigma = 0.2$).

As expected, simulations of the entire network showed equilibrium dynamics at the lower regional stochasticity, and higher regional stochasticity did not have a significant effect on long-term metapopulation persistence (Fig. 2-3A). To understand the influence of site quality on metapopulation persistence, we simulated sites of each quality type separately. The average proportion of occupied patches in nine colony sites showed a rapid decline followed by a long period of stability, in the absence of satellite sites (Fig. 2-3B). Despite their lower quality, satellite sites seemed to contribute to the overall metapopulation persistence. When regional stochasticity was low, 12% of the simulated replicates went extinct within 100 years, whereas 20% went extinct when regional stochasticity was high. In the absence of the satellite sites, average persistence time of the metapopulation decreased from infinity to 2481 years.

Absence of colony sites significantly altered the overall metapopulation persistence. Even at the lower level of regional stochasticity, the proportion of occupied patches declined very rapidly to zero within 30 years. None of the simulated replicates survived past 40 years in the absence of the colony sites (Fig. 2-3C). Average persistence time of the metapopulation that included only 12 satellite sites was only 10 years.

To evaluate the sensitivity of patch occupancy dynamics to changes in the quality of colony sites, we gradually reduced the quality of each colony site, and simulated patch occupancy dynamics using the new values. Our simulations showed that a 20% decline in quality of colony sites significantly affected regional persistence. The proportion of

occupied patches declined to 60% at the end of 100 years at the lower regional stochasticity, whereas, it declined to 46% at the higher regional stochasticity (Fig. 2-4A). At lower regional stochasticity, 96% of the simulated replicates persisted at the end of 100 years, whereas, at higher regional stochasticity, only 80% persisted (Fig. 2-4A). This 20% reduction in the quality of colony sites resulted in a decrease in average metapopulation life time from infinity to 3254 years.

These results indicated that persistence of the yellow-bellied marmot metapopulation in Colorado heavily depended on the quality of a few colony sites. To analyze the influence of these high quality sites on metapopulation persistence, we repeated the simulations by excluding one, two, three, and four of the highest quality sites (Fig. 2-1). Simulations with the low level of regional stochasticity showed that the metapopulation persistence was relatively unaffected by the absence of the two best quality sites (Fig. 2-4B,C). However, in the absence of the best three sites, site occupancy gradually declined to 42%, and 15% of the simulated replicates went extinct within 100 years (Fig. 2-4B,C). In the absence of the best four sites, the metapopulation was no longer persistent; the proportion of occupied patches rapidly declined, and only 45% of the simulated replicates persisted for 100 years (Fig. 2-4B,C).

We used connectivity-based clustering analysis available in SPOMSIM to test for the existence of hierarchical network structure of the metapopulation in terms of connectivity between networks (Moilanen 2004). This analysis revealed the existence of two networks: upper-valley (northern) and lower-valley (southern) networks (Fig. 2-1), which was also consistent with our biological understanding of the marmot system. Thus, we examined the differences in the dynamics of these two networks. The metapopulation

in the northern network was more stable than the southern network. The proportion of occupied patches in the northern network did not decline during 100 years of simulations either under low or high regional stochasticity levels (Fig. 2-5A). On the other hand, the southern network was very unstable, and the proportion of occupied patches frequently declined to zero (Fig. 2-5B). Very few of the simulated replicates survived till the end of 100 years (Fig. 2-5B).

We repeated our simulations using values sampled from the 95% confidence interval of parameter estimates, and each replicate was run with the new set of parameter values. Our previous results remained unchanged, indicating that our results were fairly robust to small changes in the parameter values.

Adequacy of the SPOM

To investigate the adequacy of SPOM for the yellow-bellied marmot system, we compared a set of candidate models using the robust design occupancy modeling approach (Tables 2-3 and 2-4). In general, including time-specific, but not site-specific, variation in colonization and extinction rates resulted in poor model likelihoods (Table 2-4). Models with constant colonization and extinction rates had higher likelihoods compared to time-specific models that ignored site-specific differences. Model likelihoods were significantly improved when time- and site-specific extinction probabilities estimated using the SPOM were included as covariates. The models that included connectivity or colonization parameters as covariates did not significantly differ from constant colonization rate models (first three models in Table 2-4). Nonetheless, two models with SPOM-predicted colonization rates were among the best models. These findings indicated the adequacy of the SPOM for modeling the dynamics of the yellow-bellied marmot metapopulation.

Discussion

Our study suggests that (1) persistence of the yellow-bellied marmot metapopulation strongly depends on the colony sites. (2) Overall metapopulation persistence was highly sensitive to small changes in number and quality of colony sites. (3) Lower quality sites contributed to the long-term persistence of the yellow-bellied marmot metapopulation, especially when the regional stochasticity was high. (4) The northern network was more stable compared to the southern network, and the persistence of the southern network strongly depended on the northern network.

Previous studies indicated that colony sites generally are more persistent than satellite sites mainly because of the fact that colony sites are occupied by matrilineages that may persist for many generations (Armitage and Downhower 1974, Armitage and Schwartz 2000, Armitage 2003b). Increased matriline sizes improve the persistence of the local population by affecting survival and net reproductive rate (Armitage and Schwartz 2000, Armitage 2003b). Consistent with these observations, our results suggest that colony sites are the major drivers of the yellow-bellied marmot metapopulation dynamics, and that the quality of these sites was especially important; a small decline in site quality resulted in a significant decline in metapopulation persistence. Also, a small number of colony sites might be ultimately responsible for the metapopulation persistence. The dependence of metapopulation persistence on a small number of high quality sites has been suggested to be a general rule in long-lived species (Harrison 1991, Schoener 1991), and has been observed in American pika, *Ochotona princeps* (Moilanen *et al.* 1998), a species that shares similar life-history characteristics. These results emphasize the importance of local site quality, and of environmental factors that may influence local site quality, for metapopulation persistence.

Local population sizes of yellow-bellied marmots can fluctuate remarkably over time (Armitage and Downhower 1974, Schwartz et al. 1998, Oli and Armitage 2004). These fluctuations can occur at a local scale due to factors such as predation (Van Vuren 2001, Armitage 2004), or at the regional scale due to regional fluctuations in environmental conditions (Armitage 1994, 2003b). Regional factors influencing local population dynamics are explicitly considered in the stochastic patch occupancy modeling approach; however, local population dynamics are assumed to be insignificant and generally overlooked (Hanski 1999). Given that the yellow-bellied marmot metapopulation persistence is highly sensitive to changes in the quality of a few colony sites, a complete understanding of marmot metapopulation dynamics likely requires consideration of factors and processes that influence the dynamics of local populations. Overall, however, SPOM provided a reasonable description of the dynamics of the marmot metapopulation.

Although the colony sites rarely went extinct during our study period, there remains a possibility that factors such as predation, disease, and demographic stochasticity can cause local extinctions of colony sites in the long-term. Despite the high importance of colony sites for regional persistence, our results suggest that lower quality satellite sites may also contribute markedly to the long-term persistence of the yellow-bellied marmot metapopulation. The risk of metapopulation extinction increases in the absence of the satellite sites, especially when the fluctuations in site qualities are regionally synchronous. Although satellite sites are much lower in quality than colony sites, they create a buffer effect (Brown 1969, Gill et al. 2001) by increasing connectivity among colony sites and providing temporary sources of recolonization when surrounding colony

sites locally go extinct. Observed importance of lower quality sites for the regional dynamics suggests that the yellow-bellied marmot system is not a perfect mainland-island system as suggested for other long-lived species (Harrison 1991, Schoener 1991), and it shows characteristics of a metapopulation in which the extinction–recolonization dynamics play an important role. Ignoring the relative role of satellite sites and considering only dynamics of colony sites can lead to underestimation of metapopulation extinction probability.

Patch occupancy dynamics in two networks indicated that the northern network was more stable and likely to persist longer than the southern network. Moreover, in the absence of the northern network the southern network was unlikely to persist. The observed difference between the persistence of the two networks was largely due to the difference in the number of higher quality sites; the northern network included 6 colony sites, whereas the southern network included only 3 colony sites. This observation is consistent with our results that the number and quality of colony sites were the most important factors affecting regional persistence of the yellow-bellied marmot metapopulation. These findings emphasize the importance of a few sites that act as a connection between the two networks for metapopulation persistence.

Moilanen and Nieminen (2002) found that including the effect of local patch area in SPOMs significantly improved the connectivity measure. In our study, the model that included the effect of local patch quality in the connectivity measure had a slightly better likelihood compared to alternative models including the original IFM, which ignored the effect of local patch quality on connectivity (Hanski 1994b). To investigate the differences between the predictions of the SPOM used in this study and IFM, we repeated

the simulations with the parameterized IFM. Simulation results were qualitatively very similar to those of our original SPOM, but IFM predicted a higher contribution of satellite sites to metapopulation persistence. In the absence of satellite sites, IFM predicted substantially lower persistence of colony sites compared to those predicted by the SPOM used in this study. Including local patch quality in the estimation of the connectivity parameter increased the connectivity of higher quality sites, hence the overall persistence of the colony sites as well as of the entire metapopulation.

We assumed that the yellow-bellied marmot metapopulation was a discrete metapopulation with no connections to populations outside the study area. However, this assumption is unlikely to be correct. Based on 10 years of radiotelemetry study (Van Vuren 1990) and 41 years of intensive survey (Armitage 1991, Schwartz et al. 1998), we are confident that all major marmot sites inside or within close proximity of our study area are included in our analyses. However, immigration into and emigration out of the study metapopulation did occur (Van Vuren 1990). Ignoring the connectivity of the yellow-bellied marmot metapopulation to outside of the study area can result in an overestimation of colonization ability, hence in an overestimation of regional persistence (Moilanen 2002). It is also important to note that we assumed a detection probability of 1.0 during our analyses; however, it may be an unrealistic assumption for some of the remote satellite sites that have been surveyed less frequently. False zeros in these sites can result in slight overestimation of the intrinsic extinction rates, dispersal distances and colonization ability (Moilanen 2002). Therefore, our measures of persistence are not conservative, and should be interpreted with caution.

Finally, we utilized the robust design occupancy modeling approach to test the adequacy of the SPOM used for simulations of the yellow-bellied marmot system. We found that colonization and extinction events varied among sites; thus, an important assumption of the classical metapopulation model (Levins 1969) was not appropriate for the yellow-bellied marmot metapopulation. Considering site-specific connectivity measures and extinction probabilities estimated using the SPOM significantly improved the likelihood of the resulting model. Therefore, we believe that the SPOM adequately described the site occupancy dynamics of the yellow-bellied marmot metapopulation. Our study is one of the first studies to use the robust design occupancy modeling approach to test the adequacy of a SPOM. We suggest that this approach could be utilized rather easily in other studies as well.

Behavioral interactions among individuals can influence population dynamics of social organisms (Grimm et al. 2003). The yellow-bellied marmot is a socially complex species (Blumstein and Armitage 1999, Armitage and Schwartz 2000), and an accurate description of the dynamics of marmot metapopulations may thus necessitate models that can incorporate behavioral interactions among individuals. However, models that allow explicit consideration of behavioral interactions (e.g., individual-based models) are structurally complex and data-intensive. Although models that consider behavioral interactions should be preferred when data are available to parameterize such models, it is important to know what we can learn about dynamics and persistence of a population by analyzing models with simple data requirements. For many species, data to parameterize more complex models are usually lacking and simple models like SPOMs or robust design patch occupancy models are the only option. Ovaskainen and Hanski's (2004)

findings that SPOMs adequately mimic the behavior of more complex models are encouraging to those who lack detailed demographic and behavioral data to parameterize individual-based models. Patch occupancy models are frequently applied to modeling metapopulation dynamics of many invertebrates (e.g., Kuussaari et al. 1996, Wahlberg et al. 1996, Appelt and Poethke 1997, Biedermann 2000, Kindvall 2000), but the application of such models to avian or mammalian metapopulations are clearly underrepresented (see Moilanen *et al.*, 1998 for an exception). This study provides one of the very few applications of SPOMs as well as robust design occupancy models to study the dynamics and persistence of mammalian metapopulations.

In conclusion, this study demonstrated that the dynamics of yellow-bellied marmot metapopulation mainly depended on a few colony sites, and the regional persistence was highly sensitive to changes in the quality of these sites. Nonetheless, satellite sites made an important contribution to the long-term persistence of the yellow-bellied marmot metapopulation. Given the high sensitivity of metapopulation persistence to local population size, future studies of the yellow-bellied marmot metapopulation should also consider local population dynamics. Nonetheless, our analyses based on simple site occupancy data provided an adequate description and several useful insights regarding the dynamics and persistence of the yellow-bellied marmot metapopulation.

Table 2-1. Models and subfunction definitions used in SPOMSIM, and Akaike's Information Criterion values corrected for small sample size (AIC_c), number of parameters (#par) and model likelihoods. Connectivity function parameter *c* was fixed at "0" for the models without the effect of local patch, and it was set as a "free" parameter for the models with the effect of local patch. "IFM" is extinction probability function used in the original incidence function model, and "SELM" is the one used in the spatially explicit Levin's model. Subfunction for the rescue effect was modeled with *R* (strength of the rescue effect) fixed at "1", and *R* set as a "free" parameter during parameter estimation.

Model	<i>c</i>	Extinction probability	<i>R</i>	AIC _c	ΔAIC _c	# par	Model likelihood
1	0	IFM	1	161.4	0.8	5	0.670
2	0	IFM	Free	162.8	2.2	6	0.333
3	0	SELM	1	162.7	2.1	5	0.350
4	0	SELM	Free	164.7	4.1	6	0.129
5	Free	IFM	1	160.6	0.0	6	1.000
6	Free	IFM	Free	162.6	2.0	7	0.368
7	Free	SELM	1	161.4	0.8	6	0.670
8	Free	SELM	Free	163.5	2.9	7	0.235

Table 2-2. Markov Chain Monte Carlo estimates of the parameters for the best stochastic patch occupancy model (model #5 in Table 2-1). The 95% confidence intervals for the parameters that are independently estimated are given as “fixed”. The α is the dispersal function parameter, b and c are the connectivity function parameters, y is the colonization function parameter, u and x are the extinction function parameters, and R is the rescue effect function parameter.

Model parameters	Estimates	95% CI
a	0.479	fixed
b	0.056	0.000 – 0.283
c	0.351	0.088 – 0.398
y	6.579	6.579 – 8.570
u	0.127	0.094 – 0.128
x	1.465	1.445 – 1.859
R	1	fixed

Table 2-3. Definition of robust design occupancy models used for modeling colonization (γ) and extinction (ε) probabilities.

Notation	Biological significance
$\varepsilon(\cdot)$	constant extinction rate
$\varepsilon(t)$	time-specific extinction rate
$\varepsilon(Q)$	extinction rate with <i>site quality</i> as a constant site covariate
$\varepsilon(E)$	extinction rate with <i>extinction</i> * as a time-varying site covariate
$\gamma(\cdot)$	constant colonization rate
$\gamma(t)$	time-specific colonization rate
$\gamma(C)$	colonization rate with <i>colonization</i> * as a time-varying site covariate
$\gamma(S)$	colonization rate with <i>connectivity</i> * as a time-varying site covariate

* Estimated using the parameterized stochastic patch occupancy model.

Table 2-4. Number of parameters (#Par), Akaike's Information Criterion corrected for small sample size (AIC_c), deviances, and model likelihoods for the robust design occupancy models fitted to the yellow-bellied marmot data. Parameters ε and γ are the extinction and colonization rates, respectively. Initial occupancy rate (Ψ) was estimated as a constant rate, and detection probability (ρ) was set to 1 in all models. For model definitions see Table 2-3.

Model	# Par	AIC_c	Deviance	ΔAIC_c	Model likelihood
$\varepsilon(E) \gamma(S)$	5	158.4	143.7	0	1.00
$\varepsilon(E) \gamma(\cdot)$	4	158.9	148.1	0.5	0.75
$\varepsilon(E) \gamma(C)$	5	159.2	144.5	0.8	0.67
$\varepsilon(Q) \gamma(S)$	5	164.7	150.1	6.3	0.04
$\varepsilon(Q) \gamma(\cdot)$	4	165.2	154.4	6.8	0.03
$\varepsilon(Q) \gamma(C)$	5	165.4	150.8	7	0.03
$\varepsilon(\cdot) \gamma(S)$	4	176.2	165.3	17.8	0
$\varepsilon(\cdot) \gamma(C)$	4	177.1	166.2	18.7	0
$\varepsilon(\cdot) \gamma(\cdot)$	3	178.1	170.5	19.7	0
$\varepsilon(\cdot) \gamma(t)$	14	282.3	149.3	123.9	0
$\varepsilon(t) \gamma(\cdot)$	14	284.6	151.6	126.2	0

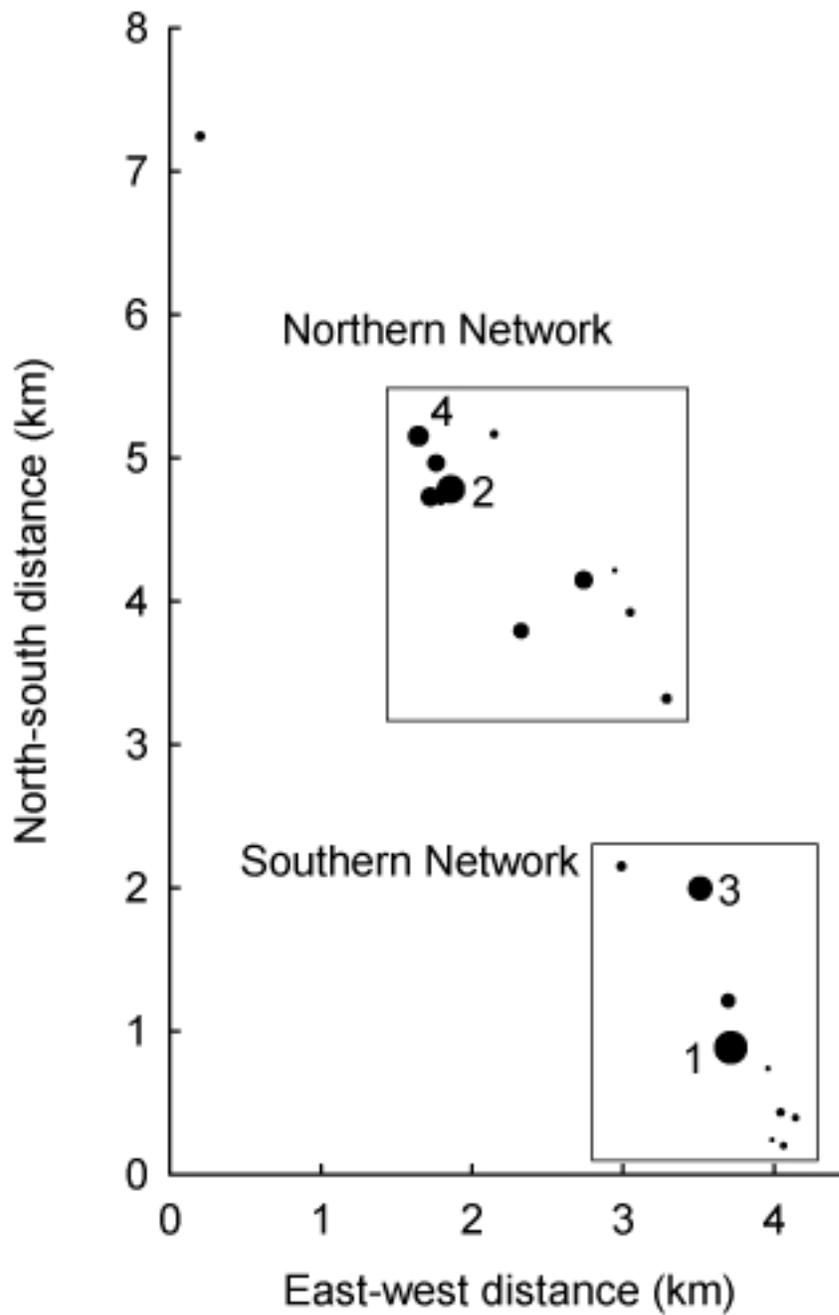


Figure 2-1. The structure of the yellow-bellied marmot metapopulation in Colorado. Diameters of circles are proportional to the estimated quality of each site. Four highest quality sites are indicated with numbers. The figure also shows the division of the metapopulation into northern and southern networks.

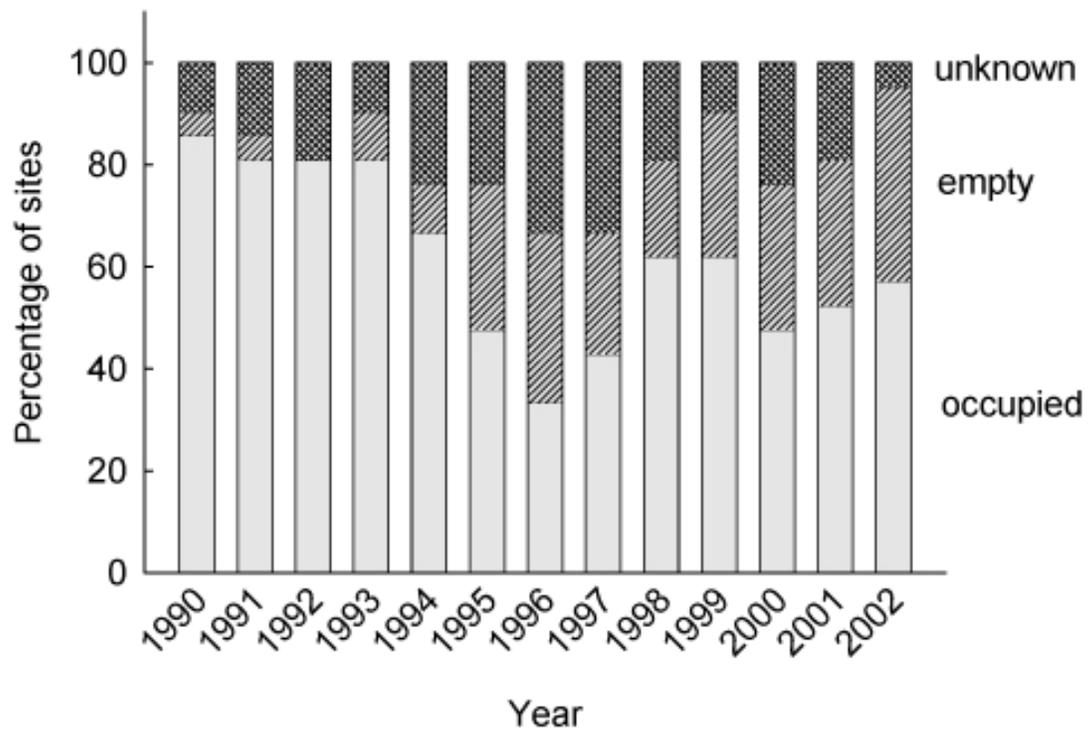


Figure 2-2. Yearly proportions of occupied patches, empty patches, and patches with unknown occupancy status, for the period between 1990 and 2002.

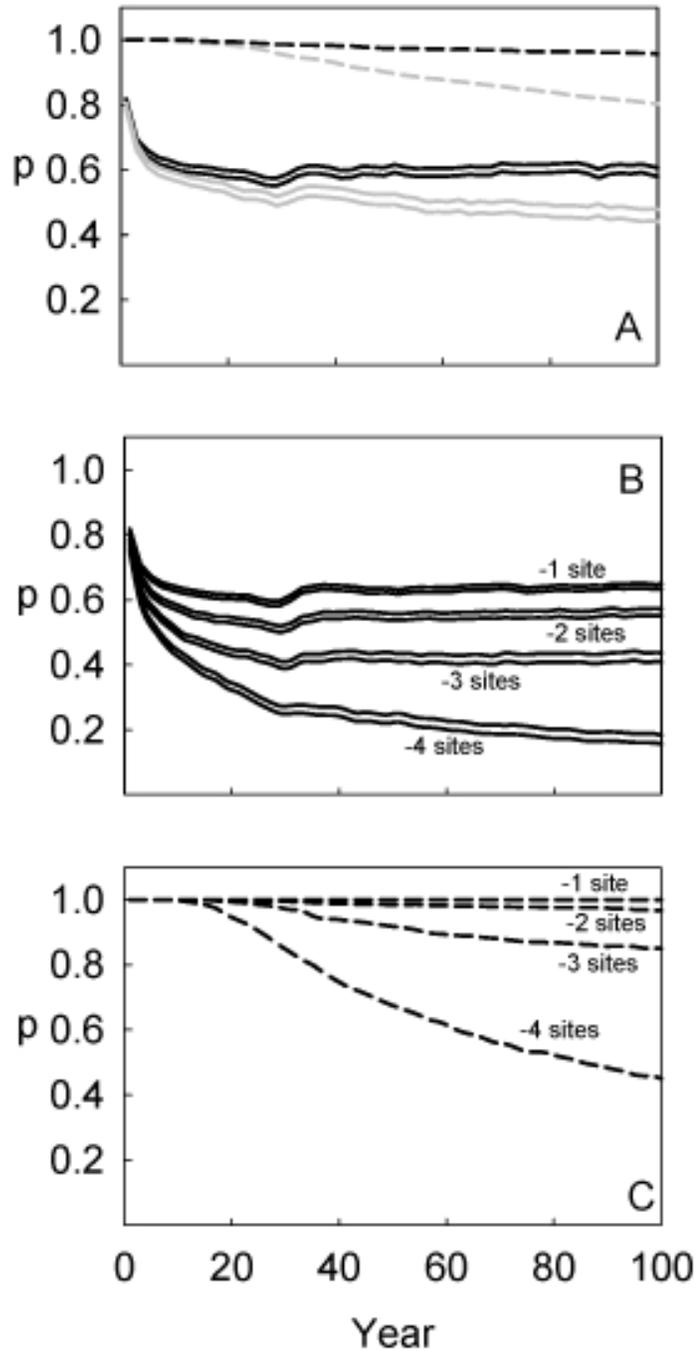


Figure 2-3. Predicted patch occupancy in 1000 replicate simulations of the yellow-bellied marmot metapopulation using the parameterized stochastic patch occupancy model. Confidence intervals (95%) for the proportion of occupied patches in all sites (A), colony sites only (B), and satellite sites only (C) are given as solid lines. Proportion of surviving replicates for all sites (A), in only colony sites (B), and in only satellite sites (C) are given as dashed lines. Simulation results with regional stochasticity set at $\sigma = 0.1$ are shown as black lines, and for $\sigma = 0.2$ are shown as gray lines.

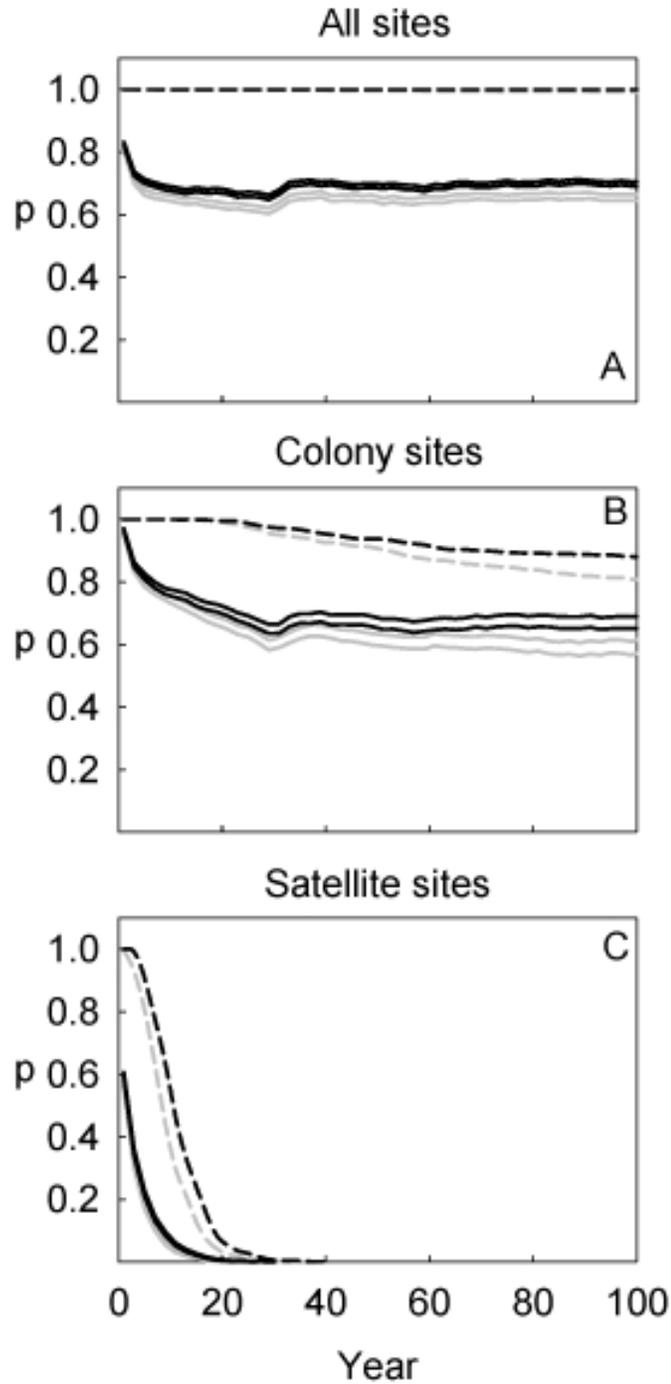


Figure 2-4. Predicted patch occupancy in 1000 replicate simulations (A) when the quality of colony sites was reduced by 20%, and (B, C) when 1, 2, 3, and 4 highest quality colony sites were excluded from the network. These sites are indicated in Fig. 2-1. Confidence intervals (95%) for the proportion of occupied patches are given as solid lines. Proportion of surviving replicates are given as dashed lines. Simulation results with regional stochasticity set at $\sigma = 0.1$ are shown as black lines, and for $\sigma = 0.2$ are shown as gray lines.

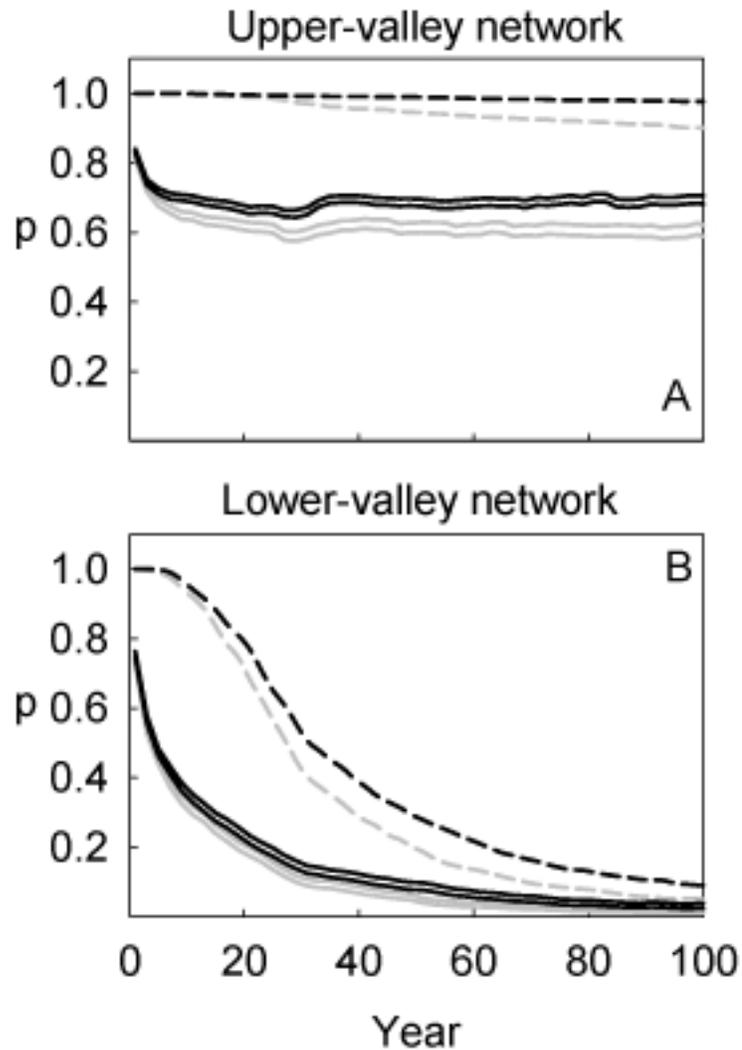


Figure 2-5. Predicted patch occupancy in 1000 replicate simulations for the northern and southern networks. Confidence intervals (95%) for the proportion of occupied patches in the northern (A) and the southern (B) network are given as solid lines. Proportion of surviving replicates in the northern (A) and the southern (B) network are given as dashed lines. Simulation results with regional stochasticity set at $\sigma = 0.1$ are shown as black lines, and for $\sigma = 0.2$ are shown as gray lines.

CHAPTER 3
SPATIOTEMPORAL VARIATION IN AGE-SPECIFIC SURVIVAL RATES OF THE
YELLOW-BELLIED MARMOT

Spatiotemporal variation in age-specific survival rates can profoundly influence population dynamics, but few studies of vertebrates have thoroughly investigated both spatial and temporal variability in age-specific survival rates. We used 28 years (1976 - 2003) of capture-mark-recapture (CMR) data from 17 locations to parameterize an age-structured Cormack-Jolly-Seber model, and investigated spatial and temporal variation in age-specific annual survival rates of yellow-bellied marmots (*Marmota flaviventris*). Survival rates varied both spatially and temporally, with survival of younger animals exhibiting the highest degree of variation. Juvenile survival rates (mean \pm SE) varied from 0.52 ± 0.05 to 0.78 ± 0.10 among sites and from 0.15 ± 0.14 to 0.89 ± 0.06 over time. Adult survival rates varied from 0.62 ± 0.09 to 0.80 ± 0.03 among sites, but did not vary significantly over time. We used reverse-time CMR models to estimate the realized population growth rate (λ), and to investigate the influence of the observed variation in age-specific survival rates on λ . The realized growth rate of the population closely covaried with, and was significantly influenced by, spatiotemporal variation in juvenile survival rate. High variability in juvenile survival rates over space and time clearly influenced the dynamics of our study population, and is also likely to be an important determinant of the spatiotemporal variation in the population dynamics of other mammals with similar life history characteristics.

Introduction

Populations inhabiting spatially heterogeneous landscapes are influenced by multiple environmental factors that vary over space and time (Orzack and Tuljapurkar 1989, Tuljapurkar 1990, Post et al. 1997). Such spatiotemporal variation in environmental factors can cause differences in vital demographic rates, and these differences can significantly influence the dynamics, regulation, and persistence of populations (Kareiva 1990, Pulliam and Danielson 1991, Tilman and Kareiva 1997).

Survival is a crucial demographic parameter influencing population growth rate, and thus the population dynamics, of many populations (Stearns 1992, Pfister 1998, Heppell et al. 2000, Sæther and Bakke 2000, Oli and Dobson 2003), and it can be influenced by spatiotemporal variation in factors such as weather, habitat quality, disease, competition and predation (e.g., Jorgenson et al. 1997, Coulson et al. 1999, Coulson et al. 2000, Farand et al. 2002). Although several studies have examined the causes and population dynamic consequences of temporal variation in survival (e.g., Francis 1995, Sæther 1997, Coulson et al. 2000, Blums et al. 2002, Oli and Armitage 2004), less attention has been paid to the influence of spatial heterogeneity on this important demographic parameter. Nonetheless, a significant spatial variation in survival has been reported for a number of species. For example, Coulson et al. (1999) observed spatial differences in survival rates among local populations of Soay sheep (*Ovis aries*). Waser et al. (1995) attributed spatial differences in survival of dwarf mongooses (*Helogale parvula*) to variation in habitat quality. Several studies on ground squirrels have reported elevational variation in the demographic parameters (Bronson 1979, Zammuto and Millar 1985, Dobson and Oli 2001, Gillis et al. 2005). However, the population dynamic consequences of such variation have rarely been addressed.

Survival rates of many long-lived species vary by age; individuals of different ages often respond differentially to changes in environmental factors. In general, survival rates of young animals are generally lower than those of adults, and also are expected to be more variable over space and time (e.g., Fowler and Smith 1981, Douglas and Leslie 1986, Clutton-Brock et al. 1987, Gaillard et al. 1998, Portier et al. 1998, Doherty et al. 2004). Older individuals are typically less severely affected by spatiotemporal changes, and their survival rates are expected to be less variable. Elucidating the interactive effects of extrinsic and intrinsic factors (e.g., age, stage) on survival rates is important for a thorough understanding of the dynamics, regulation, and persistence of populations. However, simultaneous examinations of both spatial and temporal variation in extrinsic factors, and their influence on age-specific survival rates, have been rare (but see Ringsby et al. 1999, Sæther et al. 1999, Graham and Lambin 2002). This is due primarily to the difficulty in collecting demographic data over large spatial and temporal scales. Consequently, spatiotemporal variations in age-specific survival rates of long-lived species remain poorly understood.

We used data from a long-term study of the yellow-bellied marmot (*Marmota flaviventris*) to investigate the spatiotemporal variation in age-specific survival rates. Using an age-structured Cormack-Jolly-Seber (CJS) model, we analyzed 28 years of capture-mark-recapture (CMR) data from 17 discrete habitat patches within our study site. We estimated age-specific survival rates, and examined both spatial and temporal variation in these rates. We also tested a series of hypotheses concerning the effects of key environmental factors on the observed variation in survival rates. Finally, using a Pradel's reverse-time CMR model, we estimated the realized population growth rate, and

investigated the influence of the observed variation in age-specific survival rates on the realized population growth rate, and hence on the dynamics of the yellow-bellied marmot population.

Materials and Methods

Study Area and Species

The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent, occupying montane regions of the western North America (Frase and Hoffmann 1980, Armitage 2003a). Our study area is located in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38° 57' N, 106° 59' W). The marmots in our study area occupy 17 discrete habitat patches (Fig. 3-1). The elevation of marmot sites varies from 2700 to 3100 m above sea level. Habitat characteristics vary within and between sites from rolling grassy meadows to steeper talus slopes (Svendsen 1974). These distinct habitat patches vary in size and quality, ranging from satellite sites as small as 0.01 ha, to colony sites as large as 7.2 ha. Colony sites are occupied by one or more matriline, each typically consisting of one or more adult females, yearlings, and juveniles with an adult male defending one or more matriline, whereas, satellite sites are typically occupied by a single adult female, her litter, and sometimes an adult male (Armitage 1991, 1998). The biology of yellow-bellied marmots in Colorado is described in detail by Armitage (1991, 2003a).

Field Methods and Data

From 1962 to 2003, yellow-bellied marmots were live-trapped and individually marked using numbered ear tags (details in Armitage 1991). Animal identification number, sex, mass and reproductive condition were recorded for each animal. Trapping concurrently occurred in 17 sites known to be occupied by marmots.

Four variables were used as site-specific covariates in the CMR analyses: (1) elevation (m), (2) aspect (slope direction: 1 = southwest, 0 = northeast), (3) slope (degrees), and (4) the average number of adult females per site. The Upper East River Valley stretches in a southeast-northwest direction, gaining elevation towards the northwest. Marmot sites on the west side of the East River Valley have steeper slopes facing northeast (38° - 98°), whereas sites on the east side are located on gradually inclined meadows generally facing southwest (183° - 280°).

Seven time-specific climatic variables were used as temporal covariates in the CMR analyses: (1) length of the growing season (number of days between first bare ground and the first killing frost), (2) annual precipitation (cm), and (3) monthly mean summer (May–August) temperature ($^{\circ}\text{C}$) were obtained from Crested Butte Weather Station (National Oceanic and Atmospheric Administration), approximately 10 km south of the study area, whereas (4) duration of permanent snow cover (days), (5) annual amount of snow fall (cm), (6) Julian date of first permanent snow pack, and (7) Julian date of first bare ground were obtained from Rocky Mountain Biological Laboratory, Gothic. Mean monthly temperature during the active season (May–August) ranged from $9.7 - 11.9^{\circ}\text{C}$, and annual precipitation ranged from $38.6 - 86.6$ cm. For a detailed description of time-specific climatic factors, see Schwartz & Armitage (2005).

Capture-Mark-Recapture (CMR) Analysis

Although our study spanned 42 years (1962-2003), we analyzed data from the last 28 years (1976-2003), because this period provided the most comprehensive CMR data for the entire region. We used data from 860 resident females; all of these females were captured and marked as pups and their ages were known exactly. Sixty-nine known dispersers that moved among sites (identified based on trapping data) were excluded from

the analyses. Seventeen sites were grouped into eight categories on the basis of site quality and location (Fig. 3-1). Four major colony sites were considered separately: (1) Picnic, (2) River (two adjacent sites were grouped into one), (3) Marmot Meadow and (4) Gothic. Satellite sites were typically occupied by few individuals. We assumed that survival rates of marmots occupying adjacent satellite sites that share similar habitat characteristics (e.g., size, aspect, elevation) were similar. Therefore, satellite sites were grouped with respect to their location: (5) north satellites, (6) west satellites, (7) east satellites and (8) south satellites.

We implemented the CMR models using Program MARK (White and Burnham 1999). We used an age-structured CJS model (Lebreton et al. 1992, Lebreton et al. 1993) to estimate and model age-specific apparent survival (ϕ) and recapture rates (ρ), and to investigate the spatial and temporal variation in these rates. We used Program UCARE V2.02 (Choquet et al. 2003) to test the goodness-of-fit of the CJS model. We used Akaike's Information Criterion, corrected for small sample size, (AIC_c) for model comparison, and for the identification of the most parsimonious model from a candidate model set (Burnham and Anderson 2002). Model comparison was based on the differences in AIC_c values, ΔAIC_c . We used AIC_c weight as a measure of relative support for each model. The underlying process standard deviation (σ) of the estimated parameters over space (or time) was used as an estimate of the spatial (or temporal) variation. The σ was estimated using the variance components procedure implemented in Program MARK, which is an extension of the procedure described in Burnham et al. (1987).

The CMR analyses proceeded in a stepwise fashion. In preliminary analyses, we tested for site and time effects on overall survival rates. We then proceeded to determine the appropriate age structure for our study population. Previous demographic studies of yellow-bellied marmots have used 2 or more age classes (Schwartz et al. 1998, Oli and Armitage 2004). Thus, we parameterized and compared the following models with alternative age structures: no age structure, two age classes (juveniles: 0-1 yr; adults: >1 yr), three age classes (juveniles: 0-1 yr, yearlings: 1-2 yrs, and adults: >2 yrs), and four age classes (juveniles: 0-1 yr, yearlings: 1-2 yrs, sub-adults: 2-3 yrs, and adults: >3 yrs). Although our data did not permit analysis of models with >4 age-classes, we believe that the range of age structure considered here is adequate because, in many species of mammals, survival rates of older animals are generally less variable than those of younger animals (Gaillard et al. 1998, Schwartz et al. 1998). We also investigated the spatial variation in age-specific survival rates by testing for the site effect. Next, using the most parsimonious model, we investigated the temporal variation in age- and site-specific survival rates. We considered the additive and interactive effects of site and time on age-specific survival rates (Williams et al. 2001). We note that the order in which site and time effects were included in the model did not influence the results of model selection; testing for the time effect first, and then testing for the site effect resulted in the same final models. To investigate the effect of site quality on spatiotemporal variation in age-specific survival rates, we further grouped eight sites into two major quality types (colony and satellite sites), and tested for time and site effects.

Using the most parsimonious model, we examined the potential influence of environmental covariates on observed spatial and temporal variation in age-specific

survival rates. We tested for the effects of each covariate by modeling the logits of age-specific survival rates as a linear function of a site-specific or temporal covariate. Each temporal covariate was scaled to range between 0 and 1. If the 95% confidence interval for the slope parameter (β) did not include 0, the relationship was considered statistically significant (Williams et al. 2001). Because we only had data on a subset of the environmental factors that could have influenced survival rates, we did not attempt to develop a predictive model with multiple environmental covariates. Instead, our goal was to identify the environmental factors that potentially influenced age-specific survival rates, so we considered the influence of each environmental covariate separately.

We used a Pradel's reverse-time CMR model (Pradel 1996) to estimate and model the realized population growth rate, and to investigate time and site specific population growth rates (λ). RELEASE Tests 2+3 (implemented in Program MARK) were used for assessing goodness-of-fit of the Pradel's model. Spatial and temporal variation in λ was examined as described for the CJS models. Because Pradel's models do not allow for age effect (Franklin 2001), estimates of λ could be biased due to unaccounted differences in age-specific survival rates. Therefore, we also estimated and modeled the realized growth rate of the adult (>2 yrs) segment of the population, and investigated the relative influence of the spatial and temporal variation in age-specific survival rates on adult population growth rate (λ_{ad}).

To assess the relative importance of age-specific survival rates to λ_{ad} , we modeled λ_{ad} directly as a function of these rates (Nichols and Hines 2002, Nichols et al. 2003). Specifically, we asked: which age-specific survival rate most closely covaried (over space and time) with λ_{ad} ? We used site-specific estimates of age-specific survival rates as

a covariate for site effect on λ_{ad} , and time-specific estimates as a covariate for time effect on λ_{ad} . We used the slope parameter (β) to relate the variation in the vital rate to variation in λ_{ad} (Nichols et al. 2003).

Results

Spatiotemporal Variation in Overall Survival Rates

Our general CJS model, $\phi(t * s) \rho(t * s)$, fit the data with a slight under-dispersion ($\chi^2_{150} = 120.2, P = 0.965$). There was strong support for significant variation in the overall (i.e., age structure ignored) annual survival rates both among sites and through time (Table A-1). However, site and time effects were additive, and there was no evidence for interactive effects. The most parsimonious model included site effect, but no time effect, on recapture rates. Three colony sites (River, Picnic, and Marmot Meadow) were the largest and the most intensively studied sites. Constraining the recapture rates for these three sites to have the same value resulted in a more parsimonious model (model #16 in Table A-1). The recapture rate was 0.98 for these three colony sites and 0.79 for the fourth colony site (Gothic). Recapture rates for the north, west, east, and south satellites were 0.91, 0.85, 0.69, and 0.94, respectively.

Age Structure and Spatiotemporal Variation in Age-Specific Survival Rates

Among the candidate models with different age structures, the three age-class model was the most parsimonious (model #2 in Table 3-1). Among the three age-class models, the most parsimonious model indicated that the survival rate of juveniles and yearlings varied significantly among sites, whereas there was less support for site effect in adult survival rates (model #6 in Table 3-1). However, these two models (models #2 & #6) did not differ significantly ($\Delta AICc < 3$), and we chose to continue our analysis with

the model including site effect in all three age classes (model #2 in Table 3-1). Juvenile survival rates were relatively low in three colony sites, Picnic (0.54; 95% CI: 0.46, 0.62), Marmot Meadow (0.53; 95% CI: 0.43, 0.63), and Gothic (0.52; 95% CI: 0.42, 0.62), whereas they were the highest in east (0.78; 95% CI: 0.52, 0.92) and south satellite sites (0.75; 95% CI: 0.60, 0.86) (Fig. 3-2C). Yearling survival rates were the lowest in Marmot Meadow (0.30; 95% CI: 0.19, 0.45) and south satellites (0.33; 95% CI: 0.20, 0.48), and the highest in east satellites (0.78; 95% CI: 0.40, 0.95) (Fig. 3-2B). Adult survival rates were higher in colony sites (0.76; 95% CI: 0.72, 0.80) than in satellite sites (0.64; 95% CI: 0.57, 0.71) (Fig. 3-2A). Adult survival rates were generally higher than juvenile and yearling survival rates in colony sites; however, there was no apparent trend in satellite sites. The greatest spatial variation was observed in the survival of yearlings ($\sigma = 0.11$). Spatial variation in juvenile survival ($\sigma = 0.08$) was slightly lower than in yearling survival, but higher than in adult survival rates ($\sigma = 0.04$).

Analysis of recapture rates with age structure revealed that the model with the modified site effect (s') remained the most parsimonious recapture rate model. Thus, we used the three age-class model with site effect for all age classes as the base survival model and the modified site effect model as the base recapture model (model #2 in Table 3-1) for all subsequent analyses.

Next, we tested for temporal variation in the age-specific survival rates for each site. The best model structure included the additive effect of time on juvenile survival rates, and no time effect on yearling or adult survival rates (model #3 in Table 3-2). Grouping sites into two quality types (colony and satellite sites) resulted in a more parsimonious model for the adult and juvenile survival rates. The model with separate

adult survival rates for colony and satellite sites (model #18 in Table 3-2) was more parsimonious than the model with separate adult survival rates for each of the eight sites (model #10 in Table 3-2), indicating that the observed spatial variation in adult survival rates was due primarily to differences between satellite and colony sites. Juvenile survival rates varied spatially but not temporally in satellite sites, whereas they exhibited substantial temporal variation ($\sigma = 0.20$) in the colony sites (model #18 in Table 3-2; Fig. 3-3C). A model with a similar support ($\Delta AIC_c < 3$; model #19 in Table 3-2) indicated additive effects of time and site on juvenile survival rates within the colonies. We used this final model (model #19 in Table 3-3), which was biologically more plausible, as the base model for evaluating the effect of environmental covariates.

Effect of Environmental Factors

Preceding analyses revealed temporal variation in juvenile survival rates, and spatial variation in the survival rates of all three age-classes. Thus, we examined the influence of temporal and site-specific covariates on juvenile survival rates and of site-specific covariates on the yearling and adult survival rates (see Table B-1 for model details). Site-specific variation in juvenile survival rates was positively influenced by the aspect ($\beta = 0.41$; 95% CI: 0.03, 0.79) and negatively influenced by elevation ($\beta = -0.24$; 95% CI: -0.47, -0.01) of each site. Site-specific variation in yearling survival rates was positively influenced by the elevation ($\beta = 0.26$; 95% CI: 0.01, 0.51). Site-specific variation in adult survival rates was positively influenced by the average group size ($\beta = 0.13$; 95% CI: 0.00, 0.27). Temporal variation in juvenile survival rates in colonies was negatively influenced by the length of permanent snow cover ($\beta = -3.09$; 95% CI: -5.37, -0.85).

Influence on Population Growth Rate

Goodness-of-fit test indicated that the general Pradel's model for the entire population fit the data poorly ($\chi^2_{151} = 422.7, P < 0.001$). We, thus, used a variance inflation factor ($\hat{c} = 2.79$) in parameter estimation and model-selection (White and Burnham 1999, Burnham and Anderson 2002). We used the model structure for survival and recapture rates $\{\phi(t+s) \rho(s')\}$ identified during the preliminary analysis, and estimated the spatial and temporal variation in the realized annual population growth rate, λ . The most parsimonious model indicated only site effect on λ (model #2 in Table 3-3). Site-specific estimates of λ ranged from 0.96 (95% CI: 0.90, 0.99) to 1.09 (95% CI: 1.05, 1.13); estimated realized population growth rates were less than 1.0 in two satellite sites (north and west satellites; Fig. 3-2E). Time-specific estimates of λ ranged from 0.65 (95% CI: 0.45, 0.81) to 1.49 (95% CI: 0.93, 2.05) (Fig. 3-3E).

The general Pradel's model for the adult segment of the population fit the data with a slight under-dispersion ($\chi^2_{56} = 27.6, P = 0.999$). We used the model structure for adult survival and recapture rates $\{\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')\}$ identified previously, and estimated the spatial and temporal variation in the annual realized adult population growth rate, λ_{ad} . The most parsimonious model indicated additive effects of site and time on λ_{ad} (model #8 in Table 3-3). Further grouping of sites into colony and satellites resulted in a more parsimonious model. Parameter λ_{ad} varied only spatially in satellite sites, whereas it varied only temporally in colony sites (model #10 in Table 3-3). A model with a similar support indicated additive effects of time and site on λ_{ad} within the colonies (model #11 in Table 3-3). Site-specific estimates of λ_{ad} ranged from 0.92 (95% CI: 0.86, 0.99) to 1.07 (95% CI: 1.03, 1.11); λ_{ad} was less than 1.0 only in north and west

satellite sites (Fig. 3-2D). Annual estimates of λ_{ad} in colony sites ranged from 0.28 (95% CI: 0.19, 0.47) to 1.83 (95% CI: 1.20, 2.30); λ_{ad} exhibited substantial temporal fluctuations (Fig. 3-3D).

Because of the poor fit of the general Pradel's model (i.e., model for overall population growth rate, λ) to data, we conducted additional analyses focusing on the adult segment of the population. The λ_{ad} covaried most closely with juvenile survival rates over space (Fig. 3-2) as well as over time with a one year lag (Fig. 3-3). Spatial variation in λ_{ad} was significantly influenced by among-site variation in juvenile survival rates ($\beta = 0.36$; 95% CI: 0.14, 0.58; model #12 in Table 3-3), but not by that in yearling ($\beta = -0.03$, 95% CI: -0.19, 0.12; model #13 in Table 3-3) or adult ($\beta = 0.17$; 95% CI: -0.43, 0.77; model #14 in Table 3-3) survival rates. Temporal variation in λ_{ad} was significantly influenced by temporal variation in juvenile survival rates of the preceding year ($\beta = 0.76$, 95% CI: 0.39, 1.12; model #15 in Table 3-3) and yearling survival rates ($\beta = 0.40$, 95% CI: 0.02, 0.79; model #16 in Table 3-3), but not by that in adult survival rates ($\beta = -0.44$, 95% CI: -1.08, 0.19; model #17 in Table 3-3).

Discussion

Spatiotemporal variation in vital demographic rates is a common phenomenon in animal populations, and such variation can have important population dynamic consequences. However, rigorous investigations into population dynamic consequences of spatiotemporal variation in age-specific vital rates require data at large spatial and temporal scales. Consequently, there have been relatively few studies that explicitly considered both sources of variation. Our long-term study of individually-identified animals in several discrete habitat patches provided adequate data for a rigorous

examination of spatiotemporal patterns in age-specific survival rates of yellow-bellied marmots and their population dynamic consequences.

In general, overall survival rates of yellow-bellied marmots varied both spatially and temporally. Detailed analysis of age-specific survival rates indicated that the pattern of variation differed among age classes. The most appropriate age structure was the three age-class model: juveniles (0-1 yr), yearlings (1-2 yrs) and adults (>2), suggesting that the survival rates significantly differed among these three age classes. Previous studies on other ground squirrels reported higher survival rates for adults, and lower rates for young animals (Bronson 1979, Farand et al. 2002). Survival rates of adult yellow-bellied marmots in Colorado were generally higher than those of the younger age classes; however, this trend was consistent only in high quality colony sites. There was no significant difference between the adult and juvenile survival rates in the lower quality satellite sites. Hence, our results indicate that differences in habitat quality can differentially affect age-specific survival rates in sciurid rodent populations. Yearling survival rates were, in general, lower than adult and juvenile survival rates. We note, however, that the estimated survival rates were apparent, rather than true, survival rates. Yearling marmots are much more likely to disperse than juveniles or adults (Van Vuren 1990, Van Vuren and Armitage 1994). As a result, estimates of yearling survival rates were confounded by permanent emigration out of the study area, and therefore, are likely to be underestimated.

Spatial variation in survival rates was observed in all three age classes; however, the degree of spatial variation differed among age classes. The spatial variation in the survival rate of younger animals was greater than that of adults, and it was influenced by

the aspect and the elevation of each site. Juvenile survival rates on southwest facing slopes were higher than those on northeast facing slopes. Aspect of each site determines the amount of exposure to sunlight and duration of snow cover, which in turn, determines the length of the active season and hibernation period at a given site. These factors have been suggested as important determinants of juvenile survival (Van Vuren and Armitage 1991). Bronson (1979) reported no effect of elevation on the survival of juvenile golden-mantled ground squirrels (*Spermophilus lateralis*), whereas survival of juvenile marmots was negatively associated with elevation in our study population. Survival of the juveniles did not differ significantly between satellite and colony sites (see also Lenihan and VanVuren 1996); they were actually higher in two satellite sites (Fig. 3-2C). Juvenile survival rates are likely to be affected by differences in microclimate owing mostly to the differences in aspect and elevation among sites (Armitage 1994).

Adult survival rates differed only between the colony and satellite sites, with generally higher survival rates in colony sites. Colony sites, characterized by large habitat area and more abundant resources (e.g., adequate hibernation opportunity, protection from predation, higher food availability) are usually inhabited by large groups, whereas satellite sites, characterized by smaller habitat area and limited resources, sustain fewer adults (Armitage 1991, 1998). The risk of predation during the active season, and/or mortality during hibernation, are likely to be higher in satellite sites, resulting in lower adult survival. Our results were consistent with those of Armitage and Schwartz (2000) that average group size positively influenced the survival rate of adult animals. Zammuto and Millar (1985) and Bronson (1979) indicated that adult survival rates were higher at higher elevations for some ground squirrel populations. Gillis et al. (2005), on the other

hand, reported that annual survival rates of the adult arctic ground squirrels (*Spermophilus parryii pleisus*) did not vary with elevation, but noted a trade-off between active season and over-winter survival. We did not observe a positive association between elevation and survival of adult marmots. It is important to note that the range of elevational gradient in our study sites was smaller than that in aforementioned studies.

The additive effect of time in the overall survival rates primarily reflected temporal variation in juvenile survival rates; there was no support for the existence of temporal variation in yearling or adult survival rates. A model of synchronous temporal variation in survival rates among colony sites (i.e., the additive effects of time and space) was supported by the data more strongly than was an asynchronous temporal variation model (i.e., the interactive effects of time and space), suggesting that regional climatic factors were likely to be the main cause of such variation (Schwartz and Armitage 2005). Multiple environmental and social factors may act synergistically to influence survival rates of marmots in our metapopulation, and the individual or combined effect of a few factors cannot account for the observed variation. Nonetheless, our results suggest that juvenile survival rates were mainly influenced by environmental factors that determined the duration of snow cover, whereas survival of older animals were mostly influenced by social factors such as group size. The precise mechanisms underlying these effects require further study. Differential predation on adults as a function of site is strongly implicated by previous studies (Van Vuren 2001, Blumstein et al. in press), and prior work also suggests that predation may vary temporally (Armitage 2004).

The variation in age-specific survival rates over space and time were naturally reflected in spatial and temporal variation in population growth rates. Growth rate of the

entire population (λ) and of the adult segment of the population (λ_{ad}) followed a pattern that primarily reflected site-specific differences in juvenile survival rates. Modeling λ_{ad} as a function of age-specific survival rates revealed that spatial variation in λ_{ad} was significantly influenced by survival of juveniles but not of yearlings or adults. Likewise, λ_{ad} closely covaried over time with survival of juveniles with one year time lag. Because survival of yearlings and adults did not vary significantly over time, it seems reasonable to conclude that most of the observed temporal variation in population growth rate was due primarily to temporal variation in survival of juveniles. These results suggest that spatial and temporal variation in population dynamics of yellow-bellied marmots was strongly influenced by spatiotemporal variation in juvenile survival rates.

It has been suggested that vital demographic rates with the greatest potential influence on population growth rate tend to exhibit the least temporal (or spatial) variability (Cairns 1992, Gaillard et al. 1998, Pfister 1998, Gaillard et al. 2000). In yellow-bellied marmots, the projected population growth rate is highly sensitive to variation in juvenile survival rates (Oli and Armitage 2004). However, we found that, among all age-specific survival rates, survival of juveniles was the most variable over space and time. This variation heavily influenced the dynamics of our study population; site-specific and temporal variation in population growth rate closely covaried with, and primarily reflected spatiotemporal variation in survival of juveniles. Thus, the high variability in juvenile survival rates over space and time clearly influenced the dynamics of our study population, and is also likely to be an important determinant of the spatiotemporal variation in the population dynamics of other mammals with similar life history characteristics. Higher spatiotemporal variability in the survival of younger age

classes has been reported for other long-lived vertebrate species (e.g., Douglas and Leslie 1986, Clutton-Brock et al. 1987, Gaillard et al. 1998, Portier et al. 1998); however, its effects on population dynamics were rarely addressed.

We conclude that survival rates of yellow-bellied marmots exhibit both spatial and temporal variation, but that survival of juveniles is more variable over space and time than that of older animals. Spatial and temporal variation in juvenile survival rates strongly influenced the variation in the growth rates of our study population. Given the high variability in survival rates of younger age classes, and the high sensitivity of population dynamics to these rates in several species of mammals (Oli and Dobson 2003), future modeling attempts should thoroughly incorporate the spatiotemporal variation in the survival of younger age classes, and carefully examine population dynamic consequences of such variations. We note, however, that adult survival may have a greater influence than juvenile survival on the population dynamics of some long-lived vertebrates (e.g., Doak et al. 1994, Caswell et al. 1999, Gaillard et al. 2000), suggesting that the generality of our conclusions may be limited to species with life-histories similar to the yellow-bellied marmot.

Table 3-1. Analysis of the age structure and spatial variation in age-specific apparent survival rates for the yellow-bellied marmot, using Cormack-Jolly-Seber models. Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c values (ΔAIC_c), AIC_c weights and number of parameters (#p) are given for each model. Age classes used for this analysis are juvenile (*juv*: 0-1 yr), yearling (*yr* : 1-2 yr), sub-adult (*sub-ad*: 2-3 yr), and adults (*ad*: >1 yr for 2 age-class, >2 yr for 3 age-class, and >3 yr for 4 age-class model). Symbols are: ϕ = apparent annual survival rate, ρ = annual recapture rate, s = site effect, and s' = modified site effect. A period (.) indicates constant value of the parameter. The most parsimonious models are highlighted in bold.

No.	Model	AIC_c	ΔAIC_c	AIC_c Weights	#p
1	$\phi_{juv}(s) \phi_{ad}(s) \rho(s')$ *	2666.17	45.89	0.000	22
2	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$**	2622.63	2.35	0.170	30
3	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{sub-ad}(s) \phi_{ad}(s) \rho(s')$ ***	2633.13	12.85	0.001	38
4	$\phi_{juv}(.) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$ **	2625.48	5.20	0.041	23
5	$\phi_{juv}(s) \phi_{yrl}(.) \phi_{ad}(s) \rho(s')$ **	2626.28	6.00	0.027	23
6	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{ad}(.) \rho(s')$**	2620.28	0.00	0.549	23
7	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{ad}(.) \rho(s)$ **	2622.71	2.43	0.163	25
8	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s)$ **	2625.09	4.80	0.050	32
9	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{sub-ad}(.) \phi_{ad}(.) \rho(s')$ ***	2622.32	2.03	0.152	24
10	$\phi_{juv}(s) \phi_{ad}(.) \rho(s')$ *	2674.83	54.55	0.000	15
11	$\phi_{juv}(s) \phi_{yrl}(.) \phi_{ad}(.) \rho(s')$ **	2623.54	3.26	0.082	16

* 2 age-class model

** 3 age-class model

*** 4 age-class model

Table 3-2. Analysis of temporal variation in age-specific apparent survival rates for the yellow-bellied marmot, using age structured Cormack-Jolly-Seber models. Three age-class model was used for these analyses: juvenile (*juv* : 0-1 yr), yearlings (*yrl* : 1-2 yr), and adults (*ad* : >2 yr). Symbols are: *t* = time effect, *t* * *s* = interactive effects of *t* and *s*, and *t* + *s* = additive effects of *t* and *s*. Colony (*col*) and satellite (*sat*) groups are indicated in the subscripts. Other symbols are defined in Table 3-1. The most parsimonious models are highlighted in bold.

No.	Model	AIC _c	Δ AIC _c	AIC _c Weights	#p
1	$\phi_{juv}(s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2622.63	34.25	0.000	30
2	$\phi_{juv}(t) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2613.02	24.64	0.000	49
3	$\phi_{juv}(t+s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2607.26	18.88	0.000	56
4	$\phi_{juv}(t*s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2655.41	67.03	0.000	179
5	$\phi_{juv}(t+s) \phi_{yrl}(t) \phi_{ad}(s) \rho(s')$	2624.92	36.54	0.000	73
6	$\phi_{juv}(t+s) \phi_{yrl}(t+s) \phi_{ad}(s) \rho(s')$	2628.00	39.62	0.000	80
7	$\phi_{juv}(t+s) \phi_{yrl}(s) \phi_{ad}(t) \rho(s')$	2627.00	38.62	0.000	73
8	$\phi_{juv}(t+s) \phi_{yrl}(s) \phi_{ad}(t+s) \rho(s')$	2627.82	39.44	0.000	80
9	$\phi_{juv_col}(t) \phi_{juv_sat}(t) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2602.61	14.23	0.000	68
10	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2598.72	10.35	0.003	52
11	$\phi_{juv_col}(s) \phi_{juv_sat}(t) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2625.62	37.24	0.000	46
12	$\phi_{juv_col}(t) \phi_{juv_sat}(\cdot) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2599.29	10.91	0.002	49
13	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad}(s) \rho(s')$	2599.06	10.68	0.002	55
14	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl_col}(s) \phi_{yrl_sat}(\cdot) \phi_{ad}(s) \rho(s')$	2602.33	13.95	0.000	49
15	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl_col}(\cdot) \phi_{yrl_sat}(s) \phi_{ad}(s) \rho(s')$	2600.15	11.77	0.001	49
16	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(s) \phi_{ad_sat}(\cdot) \rho(s')$	2592.50	4.12	0.062	49
17	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(s) \rho(s')$	2594.58	6.20	0.022	49
18	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	2588.38	0.00	0.486	46
19	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	2588.67	0.29	0.421	49

Table 3-3. Analysis of temporal and spatial variation in the growth rate of the entire population (λ) and adult (animals >2 yrs old) segment of the population (λ_{ad}), using Pradel's reverse-time models. Site-specific covariates for λ_{ad} are juvenile (juv_s), yearling (yrl_s), and adult (ad_s) survival rates, and temporal covariate for λ_{ad} are juvenile survival rate of the previous year (juv_{t-1}), and yearling (yrl_t) and adult (ad_t) survival rates of the current year. Other symbols are defined in Tables 3-1 and 3-2. The most parsimonious models are highlighted in bold.

No.	Model	AIC _c	Δ AIC _c	AIC _c Weights	#p
Entire population:					
1	$\phi(t+s) \rho(s') \lambda(\cdot)$	2994.63	13.92	0.001	41
2	$\phi(t+s) \rho(s') \lambda(s)$	2982.24	1.53	0.318	48
3	$\phi(t+s) \rho(s') \lambda(t)$	2994.64	13.93	0.001	67
4	$\phi(t+s) \rho(s') \lambda(t+s)$	2980.71	0.00	0.681	74
Adult segment of the population:					
5	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad}(\cdot)$	2183.36	67.29	0.000	9
6	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad}(s)$	2162.98	46.91	0.000	16
7	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad}(t)$	2158.97	42.90	0.000	35
8	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad}(t+s)$	2127.72	11.65	0.003	42
9	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(t) \lambda_{ad_sat}(t)$	2140.51	24.44	0.000	36
10	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(t) \lambda_{ad_sat}(s)$	2120.58	4.51	0.090	37
11	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(t+s) \lambda_{ad_sat}(s)$	2122.19	6.12	0.040	42
12	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(t+juv_s) \lambda_{ad_sat}(juv_s)$	2116.07	0.00	0.857	35
13	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(t+yrl_s) \lambda_{ad_sat}(yrl_s)$	2126.46	10.39	0.005	35
14	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(t+ad_s) \lambda_{ad_sat}(ad_s)$	2126.33	10.25	0.005	35
15	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(juv_{t-1}+s) \lambda_{ad_sat}(s)$	2151.99	35.91	0.000	17
16	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(yrl_t+s) \lambda_{ad_sat}(s)$	2161.01	44.94	0.000	17
17	$\phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s') \lambda_{ad_col}(ad_t+s) \lambda_{ad_sat}(s)$	2163.21	47.14	0.000	17

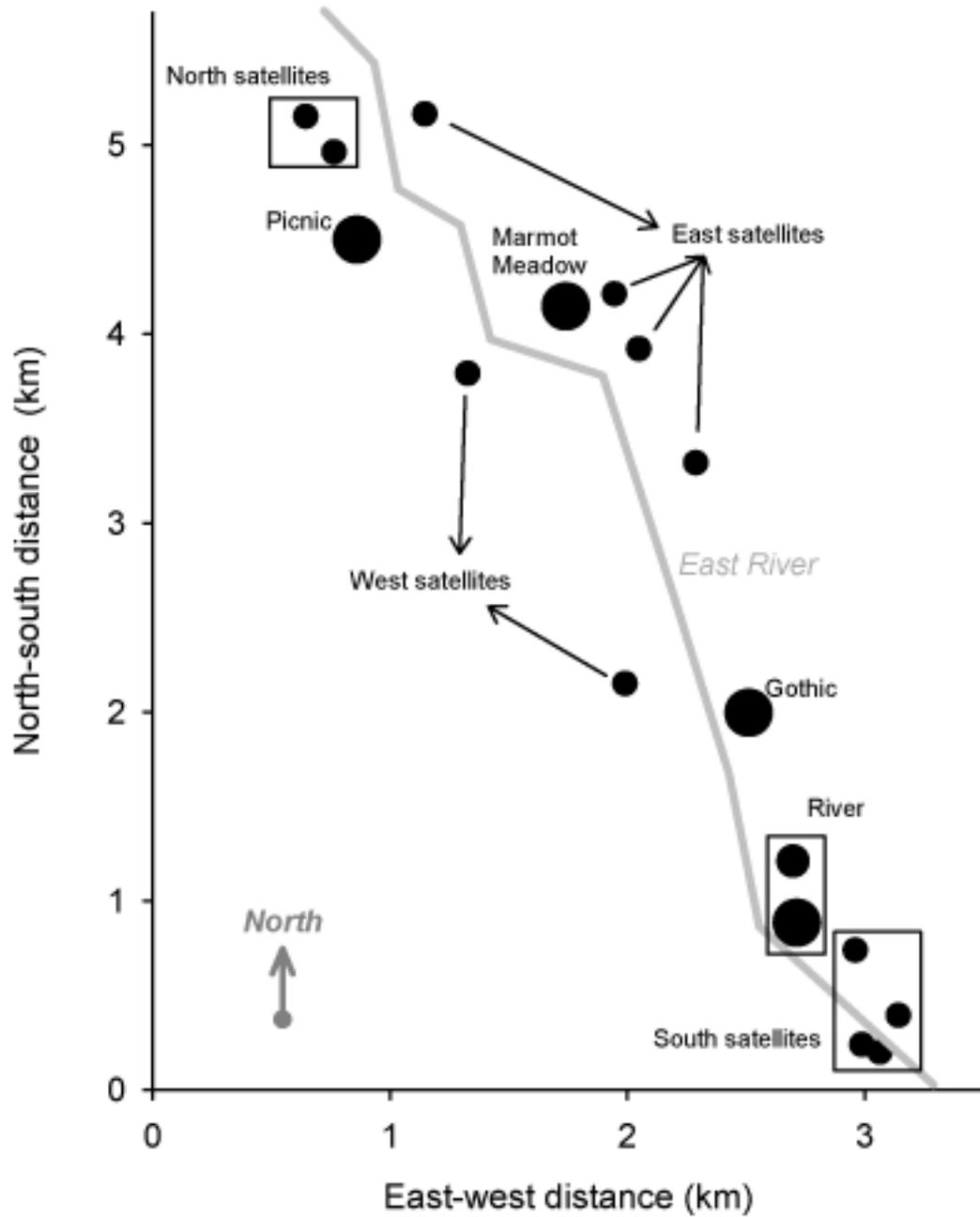


Figure 3-1. The spatial structure of the yellow-bellied marmot metapopulation in Colorado, U.S.A. Seventeen sites are grouped into four colonies (River, Gothic, Marmot Meadow and Picnic) and four satellite groups (south, west, east, and north satellites).

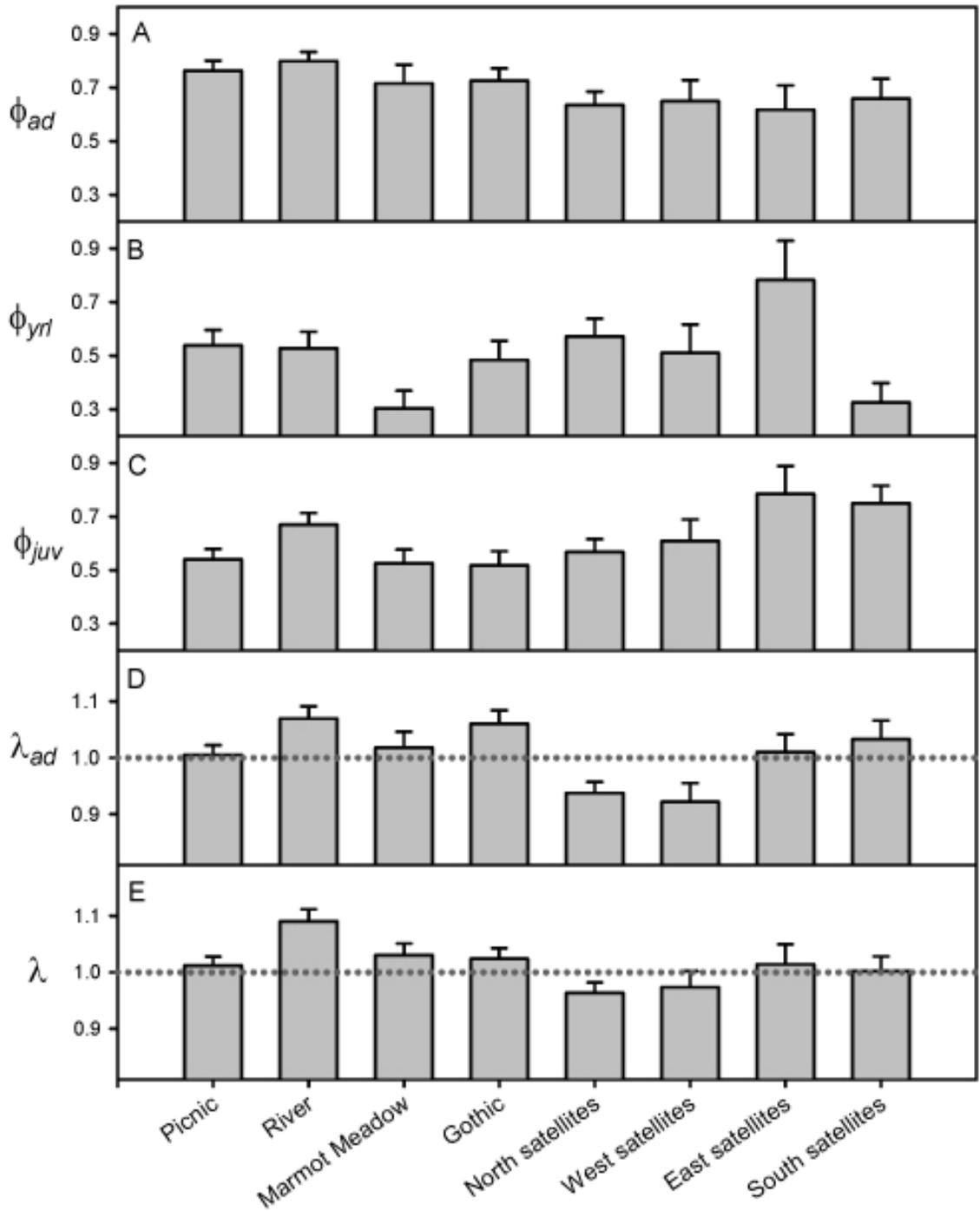


Figure 3-2. Spatial variation in annual (A) adult (ϕ_{ad}), (B) yearling (ϕ_{yrl}), and (C) juvenile (ϕ_{juv}) survival rates. Mean values and standard errors were estimated using model #2 in Table 3-1. Spatial variation in the growth rate of the (D) adult segment of the population (λ_{ad}) and (E) entire population (λ). Mean values and standard errors were estimated using model #6 and model #2 in Table 3-3, respectively.

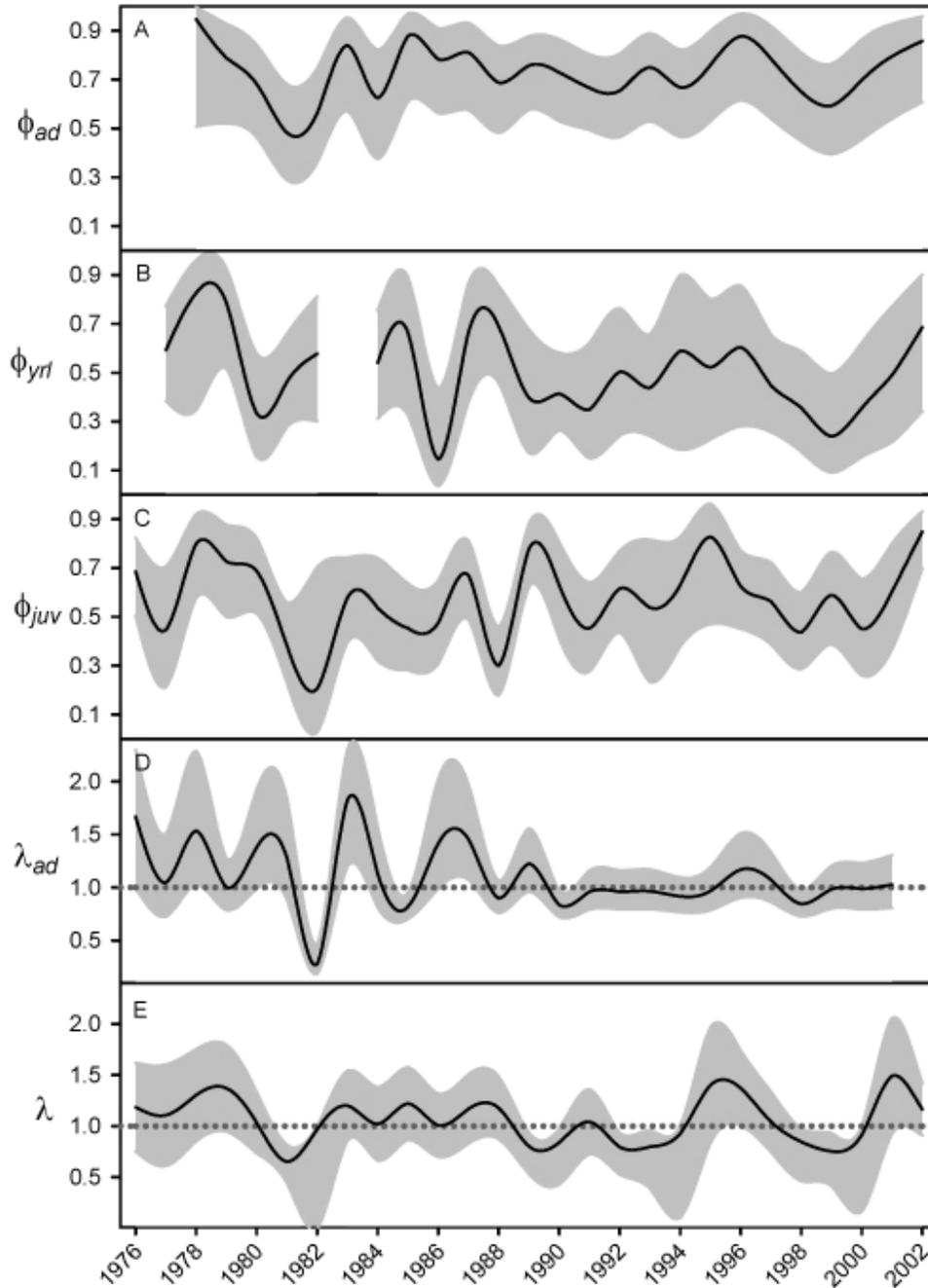


Figure 3-3. Temporal variation in annual (A) adult (ϕ_{ad}), (B) yearling (ϕ_{yrl}) and (C) juvenile (ϕ_{juv}) survival rates from 1976 to 2003. Mean values (solid line) and 95% confidence intervals (gray shade) were estimated using model #7, model #5, and model #18 in Table 3-2, respectively. The gap in B indicates that the parameter was not estimable. Temporal variation in the growth rate of the (D) adult segment of the population (λ_{ad}) with one year lag, and (E) entire population (λ). Mean values (solid line) and 95% confidence intervals (gray shade) were estimated using the model #10 and model #3 in Table 3-3, respectively.

CHAPTER 4
SPATIOTEMPORAL VARIATION IN THE REPRODUCTIVE PARAMETERS OF
THE YELLOW-BELLIED MARMOT

Spatiotemporal variation in reproductive rates is a common phenomenon in many wildlife populations, but population dynamic consequences of spatial and temporal variability in different components of reproduction (e.g., breeding probability, number of offspring produced) remain poorly understood. We used 43 years (1962 -2004) of data from 17 locations and capture-mark-recapture (CMR) modeling framework to investigate the spatiotemporal variation in reproductive parameters of the yellow-bellied marmot (*Marmota flaviventris*), and its influence on the realized population growth rate. Specifically, we estimated and modeled the litter size, and the probability of breeding the following year of the yearling (i.e., pre-reproductive), non-reproductive adult and reproductive adult females. The breeding probabilities of the non-reproductive and reproductive adults and the litter size varied over space, whereas only the breeding probability of the reproductive adults varied over time. We also tested a series of hypotheses concerning the effects of key environmental and social factors on the observed variation in each component of reproduction. We used a reverse-time CMR model to investigate the influence of components of reproduction on the realized population growth rate. The litter size and the breeding probability of the non-reproductive adults had a significant influence on the realized population growth rate. Our results indicate that the recruitment into the adult segment of the population is likely

to be the critical component of the population dynamics of the yellow-bellied marmots and other mammals with similar life history characteristics.

Introduction

Many species live in discrete habitat patches that occur either naturally or due to human-caused fragmentation of once contiguous habitats (Hanski and Ovaskainen 2003, Hanski and Gaggiotti 2004). Habitat patches may experience different sets of environmental conditions, such as resource availability, predation pressure, and microclimatic conditions. Additionally, environmental conditions in each habitat patch may change over time. Such spatiotemporal variation in environmental factors can cause differences in vital demographic rates over time and space, and these differences can significantly influence the dynamics, regulation, and persistence of populations (Kareiva 1990, Pulliam and Danielson 1991, Tilman and Kareiva 1997).

Reproduction is an important life history trait that can be particularly sensitive to spatiotemporal variation in the environment (Roff 1992, Stearns 1992, Heppell et al. 2000, Caswell 2001). Changes in the environmental or social conditions can significantly influence reproductive rates (e.g., Coulson et al. 1999, Coulson et al. 2000). Because population growth rates are highly sensitive to changes in reproductive parameters in many species (e.g., Sæther and Bakke 2000, Oli and Dobson 2003, Oli and Armitage 2004), spatiotemporal variation in these rates can play a significant role on the dynamics and persistence of populations. Therefore, a thorough understanding of population dynamics over space and time requires a detailed understanding of spatiotemporal variation in reproductive rates, and of environmental and/or social factors that can cause such variation.

Reproduction can be considered as being composed of two parts: breeding probability and number of offspring produced (Lebreton et al. 1990, Nichols et al. 1994). The probability that an individual of reproductive age reproduces in a given breeding season is typically less than 1.0, and this probability can vary over space or time (e.g., Watson and Moss 1970, Jenouvrier et al. 2003, Bryant 2005). Spatiotemporal variation in breeding probability can cause spatiotemporal variation in population dynamics even when average litter or clutch size remains relatively stable. Although spatiotemporal variation in litter (or clutch) size or fecundity rates have been examined for some species (e.g., Bronson 1979, Jarvinen 1993, Sæther et al. 1999, Coulson et al. 2000, Gaillard et al. 2000, Chamberlain and Crick 2003, Tremblay et al. 2003), variation in breeding probability over space and time, and population dynamic consequences of such variations have received much less attention. Discerning the population dynamic consequences of spatiotemporal variation in reproductive parameters necessitates simultaneous examination of variation in both components of reproduction (i.e., breeding probability and number of offspring produced). However, few studies have simultaneously considered spatial and temporal variation in both components of reproduction or investigated population dynamic consequences of such variation.

Our objective was to investigate the spatiotemporal variation in breeding probability and litter size, and to examine the population dynamic consequences of such variation in the yellow-bellied marmot (*Marmota flaviventris*). We applied multistate capture-mark-recapture (CMR) models to 43 years (1962 - 2004) of data from 17 discrete habitat patches, and examined both spatial and temporal variation in the breeding probability. We also investigated the spatial and temporal variation in litter size; this,

combined with spatiotemporal variation in breeding probability, enabled us to discern which component of reproduction varied over space or time. We also tested a series of hypotheses concerning the effects of key environmental and social factors on the observed variation in each component. Finally, using a Pradel's reverse-time CMR model, we estimated and modeled the realized population growth rate, and examined population dynamic consequences of the spatiotemporal variation in components of reproduction.

Materials and Methods

Study Area and Species

The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent, occupying montane regions of the western North America (Frase and Hoffmann 1980, Armitage 2003a). The study was conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38° 57' N, 106° 59' W). The marmots in our study area occupy discrete habitat patches (Fig. 2-1). The elevation of marmot sites varies from 2700 to 3100 m above sea level. Habitat characteristics vary within and between sites from rolling grassy meadows to steeper talus slopes (Svendsen 1974, Blumstein et al. in press). These distinct habitat patches vary in size and quality, ranging from satellite sites as small as 0.01 ha, to colony sites as large as 7.2 ha. Colony sites are occupied by one or more matriline, each typically consisting of one male, two or more closely related adult females, yearlings, and juveniles, whereas satellite sites are typically occupied by a single adult female, her litter, and sometimes an adult male (Armitage 1991, 1998). Marmots breed shortly after emergence from hibernation (Armitage 2003a). The yellow-bellied marmot first breeds at 2 years of age, less than a quarter of 2-year-old females reproduce, and the median age of first reproduction is 3

years (Schwartz et al. 1998). The biology of yellow-bellied marmots in Colorado is described in detail by Armitage (1991, 2003a).

Field Methods and Data

From 1962 to 2004, yellow-bellied marmots were live-trapped and individually marked using numbered ear tags (details in Armitage 1991). Animal identification number, sex, mass and reproductive condition were recorded for each animal. Trapping concurrently occurred in 17 sites known to be occupied by marmots. We grouped these sites into five categories on the basis of site quality and location. Four major colony sites were grouped separately: Picnic, River (two adjacent sites were grouped together), Marmot Meadow, and Gothic. Satellite sites were typically occupied by few individuals. We assumed that reproductive rates of marmots occupying these low-quality sites were similar. Therefore, all the satellite sites were grouped together. We used data collected from 748 females that were ≥ 1 year old. Ages for the females that were captured as juveniles were known exactly, whereas ages for other females were estimated based on body mass (≤ 2 kg = yearling, > 2 kg = adult, Armitage et al. 1976). Litter size was the number of weaned young that emerged from the natal burrows.

Components of Reproduction

We investigated the spatial and temporal variation in two major components of reproduction: (1) the breeding probability and (2) the litter size. Female marmots can reproduce at 2 years of age, but the probability that 2-year old females reproduce is generally lower than that of older females (Schwartz et al. 1998). Therefore, we considered three life history states based on age and reproductive status (Fig. 4-1): (1) yearling (1-2 yrs; pre-reproductive), (2) non-reproductive adult (females ≥ 2 yrs and do not breed in a given year) and (3) reproductive adult (females ≥ 2 yrs and breed in a given

year) states. We used the multistate CMR model (Hestbeck et al. 1991, Brownie et al. 1993, Williams et al. 2001, Fujiwara and Caswell 2002) implemented in Program MARK (White and Burnham 1999) to estimate and model state-specific survival, recapture, and transition rates. The transition rate ψ_{xy} indicates the probability of transition from state x to state y , conditional on surviving the period in state x . Specifically, we estimated the transition rate from each state to the reproductive state: ψ_{13} (probability of a yearling breeding the following year as a two year-old conditional on survival), ψ_{23} (probability of a non-reproductive adult breeding the following year conditional on survival), and ψ_{33} (probability of a reproductive adult breeding again the following year conditional on survival) (Fig. 4-1). Hereafter, we will use "the breeding probability" to indicate "the probability of breeding the following year conditional on survival", for simplicity. Both yearling recapture (ρ_1) and yearling to yearling transition rates (ψ_{11}) were fixed to zero, as all the yearlings either die or move to one of the adult states. Transition rates from non-reproductive to yearling (ψ_{21}) and reproductive to yearling state (ψ_{31}), which were biologically impossible, were also fixed to zero. Transitions ψ_{12} , ψ_{22} , and ψ_{32} are complements of ψ_{13} , ψ_{23} , and ψ_{33} , respectively (e.g., $\psi_{32} = 1 - \psi_{33}$).

We used Program UCARE V2.02 (Choquet et al. 2003) to test the goodness-of-fit of the general multistate model. We used quasi-likelihood adjusted Akaike's Information Criterion, corrected for small sample size (QAIC_c) for model comparison, and for the identification of the most parsimonious model from a candidate model set (Burnham and Anderson 2002). Model comparison was based on the differences in QAIC_c values, ΔQAIC_c . We used QAIC_c weight as a measure of relative support for each model. There was no significant temporal variation in the survival or recapture rates of the yearling or

adult marmots (Ozgul et al. in press-a). Therefore, we tested only for the site effect in these rates. First, we tested for site effect on recapture rates of the non-reproductive and reproductive adults. We then proceeded to test for site effect on the survival rate of yearlings, non-reproductive adults and reproductive adults. Finally, we tested for both site and time effects on state-specific transition rates (i.e., breeding probabilities).

We used a general linear model (GLM) to test for spatial and temporal variation in the litter size. Analysis of age effects on litter size revealed that two age-class (2 year old, and older females) model was the most parsimonious model, a result consistent with earlier findings that two year old females generally produce smaller litters than older females (Schwartz et al. 1998). Thus, we grouped females into two age classes for investigating spatial and temporal variation in litter size: (1) two year old females and (2) older females. We used AIC_c for model comparison, and for the identification of the most parsimonious model (Burnham and Anderson 2002). GLM analysis was performed in Program R (R Development Core Team 2005).

Effect of Environmental and Social Factors

Using the most parsimonious models identified in the preceding analyses, we examined the potential influence of the environmental and social factors on breeding probabilities and litter size. We considered the influence of three sets of covariates that can potentially influence components of reproduction: (1) site-specific, (2) climatic, and (3) social factors (Appendix C, Table C-1). We tested for the effect of each covariate on the breeding probabilities by modeling the logit of each transition rate as a linear function of the site-specific, climatic, or social covariates. The influence of the aforementioned covariates on the litter size was examined similarly by modeling the litter size as a linear function of each of the site-specific, climatic, or social covariates. Because we only had

data on a subset of the environmental and social factors that could have influenced reproductive parameters, we considered the influence of each covariate separately. If the 95% confidence interval for the slope parameter (β) did not include 0, the relationship was considered statistically significant (Williams et al. 2001).

Influence on Population Growth Rate

We used Pradel's reverse-time CMR model (Pradel 1996, Nichols and Hines 2002) to examine the spatiotemporal variation in the realized population growth rate, and to investigate the influence of each component of reproduction on the realized population growth rates (λ). RELEASE Tests 2+3 (implemented in Program MARK) were used for assessing goodness-of-fit of the Pradel's model. Previous analysis (Ozgul et al. in press-a) indicated a poor fit of the general Pradel's model (i.e., model for overall population growth rate, λ) to data. Therefore, we conducted our analyses focusing on the growth rate of the adult (≥ 2 yrs) segment of the population (λ_{ad}). Spatial and temporal variation in λ_{ad} was examined as described for the multistate models. To assess the relative importance of different components of reproduction to adult population growth rate, we modeled λ_{ad} directly as a function of these rates (Nichols and Hines 2002, Nichols et al. 2003). Specifically, we asked: which components of reproduction significantly influenced spatial and temporal variation in λ_{ad} ? We used site-specific estimates of transition rates and litter size as covariates to test for site effect on λ_{ad} , and time-specific estimates as covariates to test for time effect on λ_{ad} . Each component of reproduction would influence the adult segment of the population with a time lag. Time-specific estimates of the transition rates were included with a two year lag (e.g., ψ_{23} during 1996-97 period would influence λ_{ad} during 1998-99), whereas those of the litter size were included with a one

year lag (e.g., litter size during 1996 would influence λ_{ad} during 1997-98). We used the slope parameter (β) to relate the variation in the vital rate to variation in λ_{ad} (Nichols et al. 2003).

Results

Survival, Recapture, and Breeding Probability

The goodness-of-fit test of the general multistate model indicated a slight overdispersion ($\chi^2_{III} = 121.4$, $P = 0.24$). Thus, we used the calculated value of the overdispersion parameter ($\hat{c} = 1.09$) for parameter estimation and quasi-likelihood adjustment for model comparison. The most parsimonious model (model #22 in Table 4-1) included a constant recapture rate of 1.00 ($SE < 0.01$) for the reproductive adults, and site effect on the recapture rates of non-reproductive adults. Recapture rates (mean \pm SE) for non-reproductive adults in Picnic, River, Marmot Meadow, and Gothic colonies were 0.96 ± 0.02 , 0.88 ± 0.04 , 0.56 ± 0.11 , and 0.51 ± 0.07 , respectively. Recapture rate for non-reproductive adults in satellite sites was 0.62 ± 0.05 . The survival rates for yearlings (0.46 ± 0.03) and reproductive adults (0.76 ± 0.02) were constant, whereas survival rates of non-reproductive adults varied among sites. Survival rate of non-reproductive adults in Picnic, River, Marmot Meadow, and Gothic colonies was 0.73 ± 0.04 , 0.66 ± 0.04 , 0.40 ± 0.09 , and 0.60 ± 0.05 , respectively, and in satellite sites it was 0.50 ± 0.03 . Next, we investigated the spatial and temporal variation in each transition rate. The most parsimonious model indicated no spatial or temporal variation in ψ_{13} (0.25 ± 0.03). However, it is important to note that ψ_{13} was inestimable for the majority of the sampling periods. The parameter ψ_{23} did not vary over time, but showed spatial variation ranging from 0.31 ± 0.05 (River) to 0.59 ± 0.14 (Marmot Meadow) (Fig. 4-2). The parameter ψ_{33}

exhibited both spatial and temporal variation. It varied from 0.47 ± 0.06 (Satellites) to 0.82 ± 0.07 (Marmot Meadow) among sites (Fig. 4-2), and from 0.11 ± 0.11 (1991) to 0.90 ± 0.10 (2003) over time (Fig. 4-3). There were no significant differences between colonies and satellites in any of the three transition rates (Table 4-1).

Litter Size

The most parsimonious model for litter size included the additive effects of site and age, but no time effect (model #4 in Table 4-2). Estimates of litter size ranged from 3.74 ± 0.14 (satellites) to 5.03 ± 0.19 (Marmot Meadow) among sites. The litter size for two year old females (3.79 ± 0.16) was slightly lower than that of older females (4.22 ± 0.08). The second best model (model #6 in Table 4-2) indicated only site effect, but this model was less supported by the data ($\Delta AIC_c = 3.48$).

Effects of Environmental and Social Factors

We examined the influence of environmental and social factors on each transition rate using the most parsimonious model identified above (model #22 in Table 4-1). Among the site-specific factors considered (Appendix C), the aspect significantly influenced ψ_{23} ($\beta = -0.64$, 95% CI: -1.06, -0.22) and ψ_{33} ($\beta = 0.61$, 95% CI: 1.21, 0.01); breeding probability was lower for non-reproductive adults and higher for reproductive adults in southwest facing sites than in northeast facing sites. The parameter ψ_{23} was positively influenced by elevation ($\beta = 0.44$, 95% CI: 0.12, 0.77). Among social factors (Appendix C), residency status significantly influenced ψ_{23} ($\beta = 0.61$, 95% CI: 0.16, 1.06); probability of breeding was higher for resident non-reproductive females than immigrant non-reproductive females. The parameter ψ_{23} was positively influenced by the average group size ($\beta = 0.26$, 95% CI: 0.10, 0.42) and the relative number of adults ($\beta =$

0.46, 95% CI: 0.11, 0.80). The parameter ψ_{13} was negatively influenced by the relative number of yearlings ($\beta = -0.75$, 95% CI: -1.14, -0.36) and the relative number of adults ($\beta = -0.50$, 95% CI: -0.69, -0.31) present in the site. Parameter ψ_{33} was negatively influenced by the principal components representing the severity of the preceding winter ($\beta = -0.31$, 95% CI: -0.02, -0.60) and the onset of the present summer ($\beta = -0.34$, 95% CI: -0.03, -0.64), and it was positively influenced by the principal component representing precipitation during the previous summer ($\beta = 0.41$, 95% CI: 0.69, 0.12) (Appendix C).

We examined the influence of environmental and social factors on litter size using the most parsimonious model identified above (model #4 in Table 4-2). Litter size was significantly influenced by the aspect ($\beta = 0.58$, 95% CI: 0.26, 0.89); it was slightly higher in southwest facing sites (4.45 ± 0.12) than in northeast facing sites (3.89 ± 0.11). No other environmental or social factors significantly influenced litter size.

Influence on Population Growth Rate

The general Pradel's model for the adult segment of the population fit the data with a slight underdispersion ($\chi^2_{118} = 52.2$, $P = 0.999$). We used the most parsimonious model identified for the adult survival and recapture rates $\{\phi_{ad}(s) \rho(s)\}$, and modeled the spatial and temporal variation in the annual realized adult population growth rate, λ_{ad} . The most parsimonious model indicated only the time effect, but no site effect, on λ_{ad} (model #2 in Table 4-3). A model with less support indicated additive effects of time and site on λ_{ad} (model #1 in Table 4-3). Annual estimates of λ_{ad} ranged from 0.54 ± 0.05 (1983) to 1.68 ± 0.23 (2003) indicating substantial temporal fluctuations (Fig. 4-3). The λ_{ad} was positively influenced by the temporal variation in ψ_{23} ($\beta = 0.28$, 95% CI: 0.04,

0.51) and litter size ($\beta = 0.65$, 95% CI: 0.37, 0.94), but not by that in ψ_{33} ($\beta = -0.01$, 95% CI: 0.18, -0.20). We did not include ψ_{13} in this analysis, because ψ_{13} was not estimable for the majority of the periods. The λ_{ad} ranged from 1.01 ± 0.01 (Marmot Meadow) to 1.04 ± 0.01 (Gothic), but did not vary significantly among sites (Fig. 4-1). Thus, variation in some reproductive parameters over space did not contribute substantially to spatial variation in λ_{ad} .

Discussion

Spatiotemporal variation in reproduction is a common phenomenon in many animal populations, and such variation can have important demographic consequences. However, rigorous investigation of spatiotemporal variation in reproduction and its demographic consequences requires data at large spatial and temporal scales. Our long term study of yellow-bellied marmots provided sufficient data for a thorough investigation of the spatiotemporal variation in different components of reproduction. Specifically, we addressed the following questions: Which components of reproduction varied over time and among sites? Which environmental or social factors potentially influenced the observed variation? And, finally, what are the population dynamic consequences of the observed variations in these demographic rates?

Components of reproduction in yellow-bellied marmots exhibited both spatial and temporal variation. However, the degree of variation differed among different components of reproduction. The breeding probability of the yearlings did not exhibit spatial or temporal variation. In general, only a quarter of the two year old females bred successfully. The breeding probability of the non-reproductive adults showed significant spatial, but not temporal, variation. However, it was always higher than the breeding

probability of the yearlings, indicating significant effect of age on the breeding probability. The breeding probability of the reproductive adults showed both spatial and temporal variation. Nonetheless, it was generally higher than the breeding probability of the non-reproductive adults, indicating that females that have reproduced in a given year are also more likely to reproduce the following year. The litter size varied among sites and between two age classes. Two year old females, which are all first time breeders, generally have smaller litters compared to older females, indicating that mother's age and experience might influence litter size (Schwartz et al. 1998).

Spatiotemporal variation in age-specific survival rates of the yellow-bellied marmots in Colorado and the population dynamic consequences were reported elsewhere (Ozgul et al. in press-a). Yet, our study revealed that the survival of non-reproductive adults was generally lower than that of reproductive adults. There was no evidence that reproduction was costly as measured by changes in either the survival rate or the probability of breeding the following year (Nichols et al. 1994). Contrary to the predictions of life history theory (Stearns 1992), reproductive females generally survived better, and also were more likely to breed the following year compared to non-reproductive females (see also Oli and Armitage 2003).

Several environmental and social factors can act simultaneously to influence components of reproduction in mammals (e.g., Clutton-Brock et al. 1987, Stenseth et al. 1996, Leirs et al. 1997, Coulson et al. 2000). We found that different components of reproduction in yellow-bellied marmots were influenced by different sets of environmental or social factors. The breeding probability of the reproductive adults and litter size were influenced mostly by the climatic factors, whereas the breeding

probabilities of the yearlings and non-reproductive adults were influenced mostly by social factors. The breeding probability of yearlings is lower when the number of yearlings and adults in the colony are larger. These results are consistent with earlier studies suggesting that reproductive suppression might play a dominant role in causing delayed age of first reproduction (Armitage 1999, Blumstein and Armitage 1999, Armitage and Schwartz 2000, Armitage 2003c, Oli and Armitage 2003). The breeding probability of the non-reproductive adults was influenced by the residency status; a non-reproductive resident adult had significantly higher probability of breeding than a non-reproductive immigrant. Group size had a positive effect on this breeding probability, indicating social enhancement of reproduction (Armitage 1998, Armitage and Schwartz 2000).

Environmental factors that significantly influenced the breeding probability of the reproductive adults included precipitation during the previous summer, winter severity, and early summer environmental conditions. All of these factors can potentially influence the physical condition of a female, and thus her likelihood of breeding (Armitage 1994, 1996, Lenihan and Van Vuren 1996). The spatial variation in this breeding probability was influenced by the aspect of marmot sites; on northeast facing sites, where the length of the active season is shorter and the hibernation period is longer, breeding probability of the reproductive adults was lower. Our results suggest that the breeding probability of the females that had bred at least once is mostly governed by the environmental conditions, rather than the social conditions. A change in the breeding probability of the reproductive adults is likely to be a consequence of the trade-off between somatic and reproductive efforts in reaction to a change in environmental

conditions (Stearns 1992, Oli 1999). This interpretation is strongly supported by studies of other species of marmots in which reproductive skipping occurs because females are unable to gain sufficient mass to both survive hibernation and reproduce in the year following reproduction (Armitage and Blumstein 2002).

Litter size was influenced by the aspect of marmot sites; sites located on southwest facing slopes had relatively higher litter size than sites on northeast facing slopes. Lengths of the active season and hibernation period have been suggested as important determinants of litter size (Van Vuren and Armitage 1991, Schwartz and Armitage 2002).

Spatiotemporal variation in the population growth rate is a result of variation in vital demographic rates. Given that components of reproduction varied over time and/or space, we asked how these variations influenced the population growth rate. The realized growth rate of the adult segment of the population (λ_{ad}) showed significant fluctuations during the study period (see also Ozgul et al. in press-a). Among all reproductive parameters, litter size and the breeding probability of the non-reproductive adults significantly influenced the temporal variation in λ_{ad} . The observed spatial or temporal variation in the breeding probability of the reproductive adults did not significantly influence the observed variation in λ_{ad} . Thus, litter size and the breeding probability of the non-reproductive adults are likely to be the major components of reproduction with important influence on population growth rate.

Survival of younger animals and reproductive rates have been suggested to be important drivers of population dynamics in many species of mammals (e.g., Gaillard et al. 2000). Our results, combined with those of Ozgul et al. (in press-a), indicate that litter size and juvenile survival, abetted by the breeding probability of the non-reproductive

adults, are likely to be the main demographic factors driving the dynamics of the yellow-bellied marmot population. These vital rates (survival of young animals, litter size, and breeding probability) are the components of recruitment into the adult segment of the population. They are generally more sensitive to variation in extrinsic factors, thus exhibit a greater degree of variation over space and time. Consequently, they play a predominant role in the observed fluctuations in population growth rate. Therefore, we suggest that recruitment into adult segment of the population is likely to be the critical component of the population dynamics of the yellow-bellied marmot (Armitage 1973, 2003b), and other species with similar life history characteristics.

We conclude that components of reproduction in yellow-bellied marmots exhibit both spatial and temporal variation, but that the pattern of variation differs among the components. However, only litter size and the breeding probability of the non-reproductive adults significantly influenced the realized population growth rate. The spatiotemporal variation in the components of recruitment into the adult population is likely to be the main demographic factor driving the dynamics of the yellow-bellied marmot population.

Table 4-1. Analysis of state-specific apparent survival, recapture, and transition rates for the yellow-bellied marmot using a multistate mark-recapture model. Differences in quasi-likelihood adjusted Akaike's Information Criterion corrected for small sample size (ΔQAIC_c), QAIC_c weights and number of parameters (#p) are given for each model. Each age class is indicated as a subscript: yearling ($_1$), non-reproductive adult ($_2$), and reproductive adult ($_3$). Symbols are: ϕ = apparent annual survival rate, ρ = annual recapture rate, ψ_{xy} = transition rate from state x to state y , s = site effect, t = time effect, $s + t$ = additive effects of s and t , and cs = site effect constrained to be colony or satellite. A period (.) indicates constant value of the parameter. Parameters ρ_{11} , ψ_{11} , ψ_{21} , and ψ_{31} are fixed at 0. Parameters ψ_{12} , ψ_{22} , and ψ_{32} are complements of ψ_{13} , ψ_{23} , and ψ_{33} , respectively (e.g., $\psi_{22} = 1 - \psi_{23}$).

No.	Survival model	Recapture model	Transition model	ΔQAIC_c	QAIC_c Weights	#p
1	$\phi_1(s) \phi_2(s) \phi_3(s)$	$\rho_2(s) \rho_3(s)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	36.04	0.000	37
2	$\phi_1(s) \phi_2(s) \phi_3(s)$	$\rho_2(cs) \rho_3(s)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	43.76	0.000	36
3	$\phi_1(s) \phi_2(s) \phi_3(s)$	$\rho_2(.) \rho_3(s)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	42.95	0.000	35
4	$\phi_1(s) \phi_2(s) \phi_3(s)$	$\rho_2(s) \rho_3(cs)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	34.03	0.000	36
5	$\phi_1(s) \phi_2(s) \phi_3(s)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	32.65	0.000	35
6	$\phi_1(cs) \phi_2(s) \phi_3(s)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	31.83	0.000	32
7	$\phi_1(.) \phi_2(s) \phi_3(s)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	30.49	0.000	31
8	$\phi_1(.) \phi_2(cs) \phi_3(s)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	34.35	0.000	28
9	$\phi_1(.) \phi_2(.) \phi_3(s)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	45.02	0.000	27
10	$\phi_1(.) \phi_2(s) \phi_3(cs)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	25.76	0.000	28
11	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(s) \psi_{23}(s) \psi_{33}(s)$	26.41	0.000	27
12	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(cs) \psi_{23}(s) \psi_{33}(s)$	20.58	0.000	24
13	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(s) \psi_{33}(s)$	20.62	0.000	23
14	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(cs) \psi_{33}(s)$	31.39	0.000	20
15	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(.) \psi_{33}(s)$	30.51	0.000	19
16	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(s) \psi_{33}(cs)$	23.99	0.000	20
17	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(s) \psi_{33}(.)$	26.51	0.000	19
18	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(t) \psi_{23}(s) \psi_{33}(s)$	25.62	0.000	50
19	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(t) \psi_{33}(s)$	56.01	0.000	57
20	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(s+t) \psi_{33}(s)$	48.08	0.000	61
21	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(s) \psi_{33}(t)$	12.69	0.002	51
22	$\phi_1(.) \phi_2(s) \phi_3(.)$	$\rho_2(s) \rho_3(.)$	$\psi_{13}(.) \psi_{23}(s) \psi_{33}(s+t)$	0.00	0.998	55

Table 4-2. Analysis of the spatial, temporal, and age-specific variation in litter size for the yellow-bellied marmot, using a general linear model. Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c (ΔAIC_c), AIC_c weights and degrees of freedom are given for each model. Symbols are: *year* = time effect, *site* = site effect and *age* = age effect. A plus sign (+) denotes additive effects. A period (.) indicates constant value of the parameter.

No.	Model	AIC_c	ΔAIC_c	AIC_c Weights	Degrees of freedom
1	Litter size (<i>year</i> + <i>site</i> + <i>age</i>)	1773.73	19.06	0.000	49
2	Litter size (<i>year</i> + <i>site</i>)	1781.86	27.19	0.000	48
3	Litter size (<i>year</i> + <i>age</i>)	1806.56	51.89	0.000	45
4	Litter size (<i>site</i> + <i>age</i>)	1754.67	0.00	0.851	7
5	Litter size (<i>year</i>)	1812.33	57.65	0.000	44
6	Litter size (<i>site</i>)	1758.15	3.48	0.149	6
7	Litter size (<i>age</i>)	1786.02	31.35	0.000	3
8	Litter size (.)	1788.61	33.93	0.000	2

Table 4-3. Analysis of the temporal and spatial variation in growth rate of the adult (animals ≥ 2 yrs old) segment of the population (λ_{ad}), using Pradel's reverse-time models. Site-specific covariates for λ_{ad} are site-specific estimates of litter size ($litter^s$), and site-specific transition rates from non-reproductive adult (ψ^s_{23}) and reproductive adult (ψ^s_{33}) states to reproductive adult state. Temporal covariates for λ_{ad} are annual estimates of litter size ($litter^t$), and time-specific transition rates from yearling (ψ^t_{13}), non-reproductive adult (ψ^t_{23}), and reproductive adult (ψ^t_{33}) states to reproductive adult state. Other symbols are defined in Table 4-1.

No.	Model	AIC _c	Δ AIC _c	AIC _c Weights	#p
1	$\phi(s) \rho(s) \lambda_{ad}(s+t)$	4456.17	4.19	0.043	56
2	$\phi(s) \rho(s) \lambda_{ad}(t)$	4451.98	0.00	0.351	52
3	$\phi(s) \rho(s) \lambda_{ad}(s)$	4517.21	65.23	0.000	15
4	$\phi(s) \rho(s) \lambda_{ad}(\cdot)$	4512.99	61.01	0.000	11
5	$\phi(s) \rho(s) \lambda_{ad}(\psi^t_{23})$	4509.69	57.71	0.000	12
6	$\phi(s) \rho(s) \lambda_{ad}(\psi^t_{33})$	4515.03	63.05	0.000	12
7	$\phi(s) \rho(s) \lambda_{ad}(litter^t)$	4495.72	43.74	0.000	12
8	$\phi(s) \rho(s) \lambda_{ad}(\psi^s_{13}+t)$	4453.91	1.93	0.134	53
9	$\phi(s) \rho(s) \lambda_{ad}(\psi^s_{23}+t)$	4453.30	1.31	0.182	53
10	$\phi(s) \rho(s) \lambda_{ad}(\psi^s_{33}+t)$	4453.86	1.88	0.137	53
11	$\phi(s) \rho(s) \lambda_{ad}(litter^s+t)$	4453.65	1.66	0.153	53

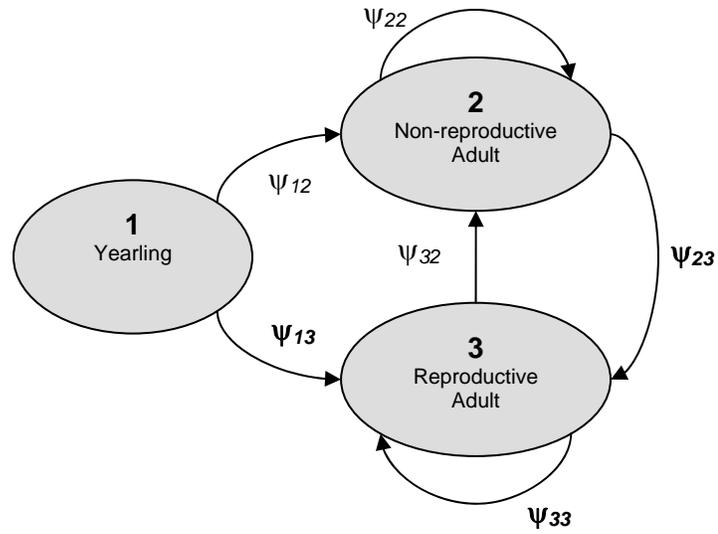


Figure 4-1. The life cycle graph for the yellow bellied marmot, with three life history states (yearling, non-reproductive adult and reproductive adult). Transition rates are denoted as ψ_{xy} = probability of moving from state x to state y , conditional on surviving the period in state x . Transitions ψ_{12} , ψ_{22} , and ψ_{32} are complements of ψ_{13} , ψ_{23} , and ψ_{33} (e.g., $\psi_{22} = 1 - \psi_{23}$).

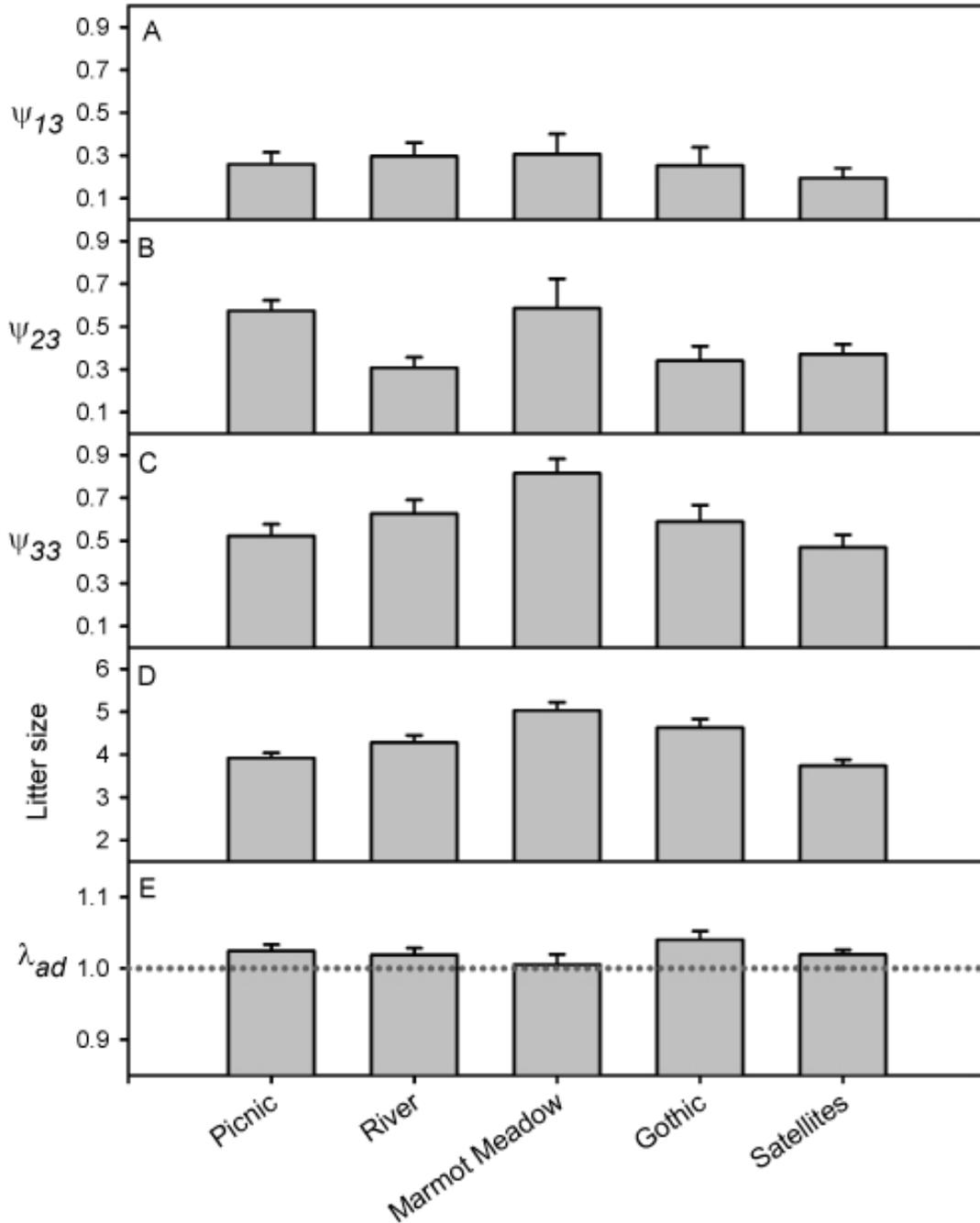


Figure 4-2. Site-specific estimates (mean \pm SE) of transition rates from (A) yearling (ψ_{13}), (B) non-reproductive adult (ψ_{23}), and (C) reproductive adult (ψ_{33}) states to the reproductive adult state. Mean values and standard errors were estimated using model #11, model #22, and model #13 in Table 4-1, respectively. Site-specific estimates of (D) litter size and (E) the realized growth rate of the adult population (λ_{ad}). Mean values and standard errors were estimated using model #4 in Table 4-2 and model #3 in Table 4-3, respectively.

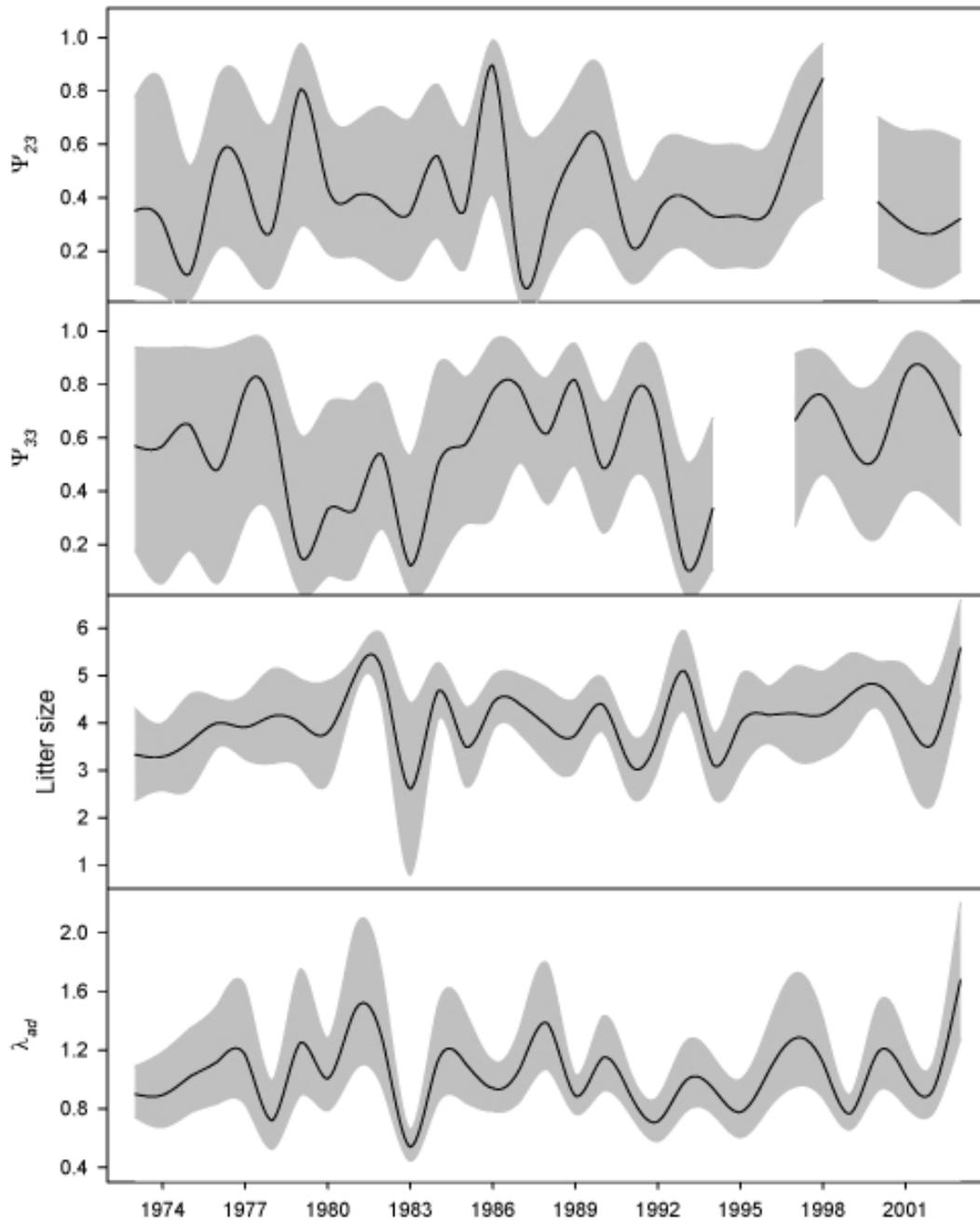


Figure 4-3. Temporal variation in transition rates from (A) non-reproductive adult (ψ_{23}) and (B) reproductive adult (ψ_{33}) states to reproductive adult state with two years lag. Mean values (solid line) and 95% confidence intervals (gray shade) were estimated using model #19 and model #21 in Table 4-1, respectively. Temporal variation in (C) the litter size with one year lag, and (D) the realized growth rate of the adult segment of the population (λ_{ad}). The gaps in 4A and 4B indicate that these parameters were not estimable for those years. Mean values and 95% confidence intervals were estimated using model #3 in Table 4-2, and model #2 in Table 4-3, respectively.

CHAPTER 5
THE INFLUENCE OF LOCAL DEMOGRAPHIC PROCESSES ON THE REGIONAL
DYNAMICS OF A YELLOW-BELLIED MARMOT METAPOPOPULATION

The dynamics of spatially structured populations are determined by the local demographic processes, and by the interactions among local populations (i.e., dispersal). However, few studies of long-lived vertebrates have empirically investigated the relative importance of local demography and dispersal on regional population dynamics. We investigated the dynamics of a spatially structured population of the yellow-bellied marmot in Colorado, USA using data collected from 17 local populations over 43 years. Local projected population growth rates ranged from 0.85 to 1.04, and varied among sites. Retrospective analysis of life-table response experiments revealed that variation in yearling survival, followed by variations in the survival of juveniles and reproductive adults made the largest contributions to the spatial variation in population growth rates. Using a vec-permutation matrix approach, we developed a matrix metapopulation model and investigated the relative influence of local demographic rates and the dispersal rate on metapopulation dynamics. Prospective elasticity analysis revealed that the metapopulation growth rate was most sensitive to survival of the reproductive adults, followed by that of the two younger age classes. The potential influence of dispersal on the metapopulation growth rate was lower than that of the aforementioned demographic rates. The dynamics of the yellow-bellied marmot metapopulation depended heavily on a small number of good quality colony sites, and the metapopulation growth rate was highly sensitive to the changes in the demographic rates of these sites. These results

underscore the need for the explicit consideration of the local demographic processes for understanding the dynamics and persistence of demographically and spatially structured populations.

Introduction

Spatial heterogeneity is a common feature of wildlife populations, and can influence dynamics and persistence of population at local and regional scales (Andrewartha and Birch 1954, Levins 1969, Hanski 1999). It has been suggested that a complete understanding of the population dynamics necessitates an understanding of the influence of spatial processes (Pulliam 1988, Kareiva 1990, Tilman and Kareiva 1997). Consequently, both theoretical ecologists and conservation biologists rely on metapopulation theory and models to understand the influence of spatial heterogeneity on population dynamics (e.g., Lankester et al. 1991, Lahaye et al. 1994, Akçakaya and Atwood 1997, Hokit et al. 2001). Although there are still gaps between theory and practice, metapopulation models have been moderately successful in explaining and predicting population dynamics in fragmented landscapes (Hanski 1999, Akçakaya and Sjørgen-Gulve 2000, Sjørgen-Gulve and Hanski 2000).

Several models with varying degrees of complexity have been developed to investigate the dynamics of spatially structured populations (for a review see Akçakaya and Sjørgen-Gulve 2000). However, detailed demographic data at multiple sites are difficult to collect; consequently, most empirical studies of metapopulation dynamics have used simple models that do not require detailed demographic data (e.g., stochastic patch occupancy models, logistic regression models). Such models of metapopulation dynamics typically emphasize the role of regional processes such as dispersal and synchrony among local populations, but they do not explicitly consider the role of within-

population demographic processes on the dynamics and persistence of populations at regional scales. Ironically, regional processes such as dispersal can be heavily influenced by local demography (e.g., Burgman et al. 1993, Lahaye et al. 1994, Lopez and Pfister 2001). Spatial variation in population dynamics is a consequence of local differences in demographic parameters (Caswell 2000, Oli and Armitage 2004, Bruna and Oli 2005). Moreover, dispersal is strongly dependent on local demographic processes such as population density (Bowler and Benton 2005, Matthysen 2005). However, consideration of local population dynamics often requires more data than those required by simpler models (Akçakaya 2000a). As a result very few studies, particularly of long-lived vertebrates, have investigated the relative role of local demographic processes in determining metapopulation dynamics.

Retrospective demographic techniques provide an adequate framework for identifying vital rates that contribute the most to the observed spatial variation in λ 's (Caswell 2000, Oli and Armitage 2004, Bruna and Oli 2005). However, a thorough understanding of metapopulation dynamics also requires information on the regional processes such as dispersal of individuals. Dispersal connects otherwise disjunct populations inhabiting different sites, and spatial correlation in demographic rates can link the fates of separate populations (Hanski 1998, Morris and Doak 2002). Investigating the relative influence of demographic and regional processes on the dynamics and persistence of populations requires models that simultaneously consider local demographic processes as well as regional processes.

A group of models, matrix metapopulation models (i.e. spatially and demographically structured models), incorporate local demographic processes and

regional processes in modeling the population dynamics across multiple sites (Akçakaya 2000a). These models form the basis of several spatially-explicit population viability analyses, which have proven to be useful in conservation biology (for reviews see Akçakaya 2000b, Beissinger and McCullough 2002, Akçakaya et al. 2004). However, most of these studies are based on model simulations, as predicting future changes in population size often prevents the use of analytical methods (Morris and Doak 2002). Recent developments in matrix metapopulation models (i.e., multi-site matrix models) allows estimating metapopulation growth rates and evaluating the absolute or proportional sensitivity of metapopulation growth rate to model parameters (Hunter and Caswell in press). Using a special permutation matrix called the vec-permutation matrix, Hunter and Caswell (in press) show how to construct a metapopulation model from a simple block-diagonal formulation of the demographic and dispersal processes. Their approach provides an analytical framework for the perturbation analysis of metapopulation models that simultaneously considers local demographic processes as well as dispersal among local populations.

In this study, we used a stage-structured matrix population model to investigate the spatial variation in population dynamics of a yellow-bellied marmot (*Marmota flaviventris*) metapopulation in East River Valley, Colorado. First, we used a random design life-table response experiment analysis to identify the key demographic rates that made the largest contributions to the observed spatial variation in population growth rate (λ). Next, using the recently developed vec-permutation matrix approach (Hunter and Caswell in press), we developed a matrix metapopulation model that connected the local population dynamics via dispersal. Finally, using a prospective perturbation analysis of

the matrix metapopulation model, we investigated the relative influence of demographic rates and the dispersal rate on the metapopulation growth rate (λ_{MP}), and evaluated the relative influence of each site to λ_{MP} .

Materials and Methods

Study Area and Species

The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent, occupying montane regions of the western North America (Frase and Hoffmann 1980, Armitage 2003a). This study was conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, Colorado (38° 57' N, 106° 59' W). The marmots in our study area occupied discrete habitat patches that varied in size and quality (Armitage 1991, 1998). We identified 17 distinct sites (hereafter, “sites”) within the study area, and grouped these sites into 8 categories on the basis of site quality and location (for details see Ozgul et al. in press-a). Four major colonies, which were higher quality sites, were considered separately: (1) Picnic, (2) River (two sites), (3) Marmot Meadow and (4) Gothic. Satellite sites, which were lower quality sites, were grouped with respect to their location: (5) north satellites (2 sites), (6) west satellites (2 sites), (7) east satellites (4 sites) and (8) south satellites (4 sites).

Previous studies have shown that survival and reproductive rates of individual marmots differed among life-history stages (Armitage and Downhower 1974, Schwartz et al. 1998, Oli and Armitage 2004, Ozgul et al. in press-a, Ozgul et al. in review). Also, a vast majority of dispersers are yearlings, and about 45% of yearling females disperse out of natal sites (Armitage 1984, Van Vuren 1990). The biology of yellow-bellied marmots in Colorado is described in detail by Armitage (1991, 2003a).

Field Methods

From 1962 to 2004, yellow-bellied marmots were live-trapped and individually marked using numbered ear tags (details in Armitage 1991). Animal identification number, sex, mass and reproductive condition were recorded for each animal. Trapping concurrently occurred in 17 sites known to be occupied by marmots. Ages for the females that were captured as juveniles were known exactly, whereas ages for other females were estimated based on body mass (≤ 2 kg = yearling, > 2 kg = adult, Armitage et al. 1976). Litter size was estimated as the number of weaned young that emerged from the natal burrows (Schwartz et al. 1998, Oli and Armitage 2004).

Local Population Dynamics

We used a post-breeding census, stage-structured matrix model to investigate the local population dynamics at each site. We modeled only the female segment of the population, because it was difficult to estimate fecundity for males. We considered two age and two stage classes. The two age classes were juveniles (0-1 yr) and the yearlings (1-2 yrs). Adult marmots (≥ 2 yrs) were divided into two reproductive stages: pre-reproductive adults (≥ 2 yrs and have not reproduced yet) and reproductive adults (≥ 2 yrs and have reproduced right before the census). This stage structure is depicted as a life-cycle graph (Fig. 5-1), which can be expressed in population projection matrix form as:

$$\begin{bmatrix} 0 & S_y \psi_y l s_y / 2 & S_p \psi_p l s_a / 2 & S_r \psi_r l s_a / 2 \\ S_j & 0 & 0 & 0 \\ 0 & S_y (1 - \psi_y) & S_p (1 - \psi_p) & 0 \\ 0 & S_y \psi_y & S_p \psi_p & S_r \end{bmatrix},$$

where S_x = the probability of an individual in state x surviving until the following year's census, ψ_x = the probability of an individual in stage x breeding the following year (just

before the next census) conditional on survival, and l_{s_x} = average litter size of a female in stage x . Because this model is based on post-breeding census and breeding takes place just before the next census, all stages except the juvenile stage have a non-zero probability of breeding before the next census (Fig. 5-1). The parameters S_j and S_y were estimated for each site using an age-structured Cormack-Jolly-Seber model (Ozgul et al. in press-a), whereas the parameters S_p , S_r , ψ_y , ψ_p and ψ_r were estimated for each site using a multistate capture-mark-recapture (CMR) model (Ozgul et al. in review). Parameter estimates were based on maximum likelihood CMR analysis of long-term trapping data, and were undertaken in coordination with the development of this model. The litter sizes were estimated for each site using a general linear model (Ozgul et al. in press-a); litter size differed only between the yearling females (l_{s_y}) and older females (l_{s_a}) (Schwartz et al. 1998). Because the sex ratios of the litter were even (Armitage 1991, 2002), we divided the litter size by two to estimate the number of female offspring per female.

The model structure given above is slightly different than the model used for parameter estimation in Ozgul et al. (in review). The pre-reproductive stage in our model includes only those adult females that have not yet reproduced (nulliparous females), whereas the non-reproductive stage in Ozgul et al. (in review) includes the pre-reproductive adults and also those adults that have reproduced before, but not this year. This was because the available data limited the estimable parameters to only two adult stages. As a result, we used the parameter estimates of the non-reproductive stage from Ozgul et al. (in review) to parameterize the pre-reproductive stage in our model.

For each site, the projected population growth rate (λ) was estimated as the dominant eigenvalue of the population projection matrix. We estimated covariance among demographic variables using data from the entire study period, and estimated approximate variance of λ using the series approximation method (i.e. "delta method", Caswell 2001).

We investigated the sensitivity of λ to proportional changes in the elements of the population projection matrix for each site (de Kroon et al. 2000, Caswell, 2001 #31). As some of the projection matrix elements are functions of the same vital rates (S_i, ψ_i, l_{s_i}), we also calculated lower-level elasticities for each site (Caswell 2001). The details of the elasticity analysis are given in Appendix D.

We also used stochastic simulations to estimate the elasticity of stochastic population growth rate (λ_s) to vital rates (Morris and Doak 2002). By perturbing each mean, variance, or covariance of the vital rates one at a time, we simulated the model long enough to arrive at a good estimate of λ_s , and then estimated the elasticity as

$$E_x^s = \frac{\Delta \lambda_s}{\Delta x} \frac{x}{\lambda_s},$$

$$\frac{\Delta \lambda_s}{\Delta x} = \frac{\lambda_{s, new} - \lambda_{s, original}}{x_{new} - x_{original}},$$

where x is the entity (mean, variance, or covariance of the vital rates) being perturbed,

and $\frac{\Delta \lambda_s}{\Delta x}$ is the sensitivity of λ_s to x (Morris and Doak 2002). We estimated the process

variance by discounting the sampling variance using White's (2000) method. We

assumed that the correlations among vital rates were identical for all sites, and estimated

the correlations using the mean annual values for the entire population during the last 27

years. We assumed that survival and breeding probabilities were beta distributed, and litter size was lognormally distributed (Morris and Doak 2002). In each simulation we generated correlated vital rates using the estimated correlation matrix (Morris and Doak 2002). We used a 5% change in each rate, and simulated population dynamics for 500 years with 500 replicates.

Next, we used a random design life-table response experiment (LTRE) analysis to investigate the actual contribution of the covariation among demographic parameters to observed spatial variation in λ (Caswell 2001):

$$V(\lambda) \approx \sum_{ij} \sum_{kl} Cov(a_{ij}, a_{kl}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}},$$

where $Cov(a_{ij}, a_{kl})$ is the covariance of projection matrix elements a_{ij} and a_{kl} , and sensitivities were evaluated at the mean matrix. We also calculated the contributions to $V(\lambda)$ in terms of lower-level parameters x_i . In this case the variance $V(\lambda)$ was calculated as:

$$V(\lambda) \approx \sum_{kl} Cov(x_i, x_j) \frac{\partial \lambda}{\partial x_i} \frac{\partial \lambda}{\partial x_j},$$

where the sensitivities were evaluated at the mean value of the parameter (Caswell 2001).

Metapopulation Dynamics

We used Hunter & Caswell's (in press) vec-permutation matrix approach to model the metapopulation dynamics by combining demographic and dispersal data from 17 sites. Their method provides a technique to formulate the metapopulation projection matrix using a similar approach to the formulation of a single population projection matrix. In a single population projection matrix, the number of columns (or rows) is equal to the number of stage classes within a single population, whereas in a metapopulation

projection matrix, the number of columns is equal to the number of local populations \times the number of stage classes. To facilitate the formulation of the metapopulation projection matrix, Hunter & Caswell (in press) decomposes the projection matrix into two major components: the demography matrix and the dispersal matrix. We assumed that demography and dispersal occurred sequentially within the projection interval; demographic changes occurred within each site and then dispersal redistributed individuals among sites. The corresponding metapopulation projection equation can be written as:

$$\underbrace{\begin{bmatrix} \mathbf{n}_1 \\ \vdots \\ \mathbf{n}_{17} \end{bmatrix}}_{\mathbf{N}_{t+1}} = \underbrace{\mathbf{P}^T \mathbf{M} \mathbf{P} \mathbf{B}}_{\mathbf{A}} \underbrace{\begin{bmatrix} \mathbf{n}_1 \\ \vdots \\ \mathbf{n}_{17} \end{bmatrix}}_{\mathbf{N}_t},$$

where \mathbf{N}_t is the metapopulation vector at time t , written in terms of stage distributions within each site, and \mathbf{n}_i is the population vector of the i^{th} site. The matrix product $\mathbf{A} = \mathbf{P}^T \mathbf{M} \mathbf{P} \mathbf{B}$ is the metapopulation projection matrix (Hunter and Caswell in press). \mathbf{B} is the block-diagonal matrix for demography:

$$\mathbf{B} = \begin{pmatrix} \mathbf{K}_1 & 0 & \dots & 0 \\ 0 & \mathbf{K}_2 & \dots & 0 \\ & & \ddots & \\ 0 & 0 & \dots & \mathbf{K}_{17} \end{pmatrix},$$

where the i^{th} diagonal block \mathbf{K}_i is a 4x4 demographic projection matrix for site i . \mathbf{M} is the block-diagonal matrix for dispersal:

$$\mathbf{M} = \begin{pmatrix} \mathbf{L}_1 & 0 & 0 & 0 \\ 0 & \mathbf{L}_2 & 0 & 0 \\ 0 & 0 & \mathbf{L}_3 & 0 \\ 0 & 0 & 0 & \mathbf{L}_4 \end{pmatrix},$$

where the i^{th} diagonal block \mathbf{L}_i is a column stochastic (the sum of each column is 1), 17x17 dispersal matrix for stage i . \mathbf{P} is the 68 x 68 vec-permutation matrix, and \mathbf{P}^T is the transpose of \mathbf{P} , where \mathbf{P} is defined as (Hunter and Caswell in press):

$$\mathbf{P} = \sum_{i=1}^4 \sum_{j=1}^{17} \mathbf{E}_{ij} \otimes \mathbf{E}_{ij}^T$$

where \mathbf{E}_{ij} is a 4 x 17 matrix with 1 in the (i,j) position and zeros elsewhere and \otimes denotes the Kronecker matrix product (Hunter and Caswell in press).

Dispersal. The majority of dispersers were yearlings (Armitage 1984, Van Vuren 1990), so we assumed that only yearlings dispersed among sites. A 10-year radio-telemetry study indicated that ~45% of the female yearlings dispersed, and that many animals dispersed outside of the study area (Van Vuren 1990). In our analysis, we assumed that the Colorado metapopulation was a closed system, and that 45% of female yearlings dispersed from each site, and forced these individuals to disperse inside the metapopulation based on distances among sites. We also assumed that the survival rate of disperser yearlings were equal to that of resident yearlings [Van Vuren, 1994 #98]. These assumptions were necessary, because the dispersal matrices needed to be column stochastic. To understand the influence of dispersal rate on the metapopulation dynamics, we repeated our analyses using four additional levels of dispersal rate: two lower (25% and 35%) and two higher (55% and 65%) than estimated dispersal rate of 45%.

We estimated the distance-dependence of dispersal based on the dispersal distances of 38 radio-tagged yearling marmots (Van Vuren 1990). Proportion of individuals dispersing to each distance class (in km) was used as the dependent variable (D), and the mid-point of each distance class as the independent variable (d) in the exponential model (Akçakaya and Atwood 1997, Hanski 1999):

$$D = a \cdot e^{-\frac{d}{b}}$$

where a and b are model parameters. The parameter b is the average dispersal distance, and it was estimated at 1.44 km for female marmots (Van Vuren 1990). The model was fitted with $a = 0.084$ and b fixed at 1.44 km. We used the estimated D to distribute the dispersing individuals among sites. The resulting dispersal matrix is column stochastic (the sum of each column is 1) with the probability of staying at the natal site (0.55) along the diagonal.

The metapopulation growth rate λ_{MP} was estimated as the dominant eigenvalue of the metapopulation projection matrix \mathbf{A} . The sensitivity of the λ_{MP} to changes in demography (\mathbf{S}_B) and dispersal (\mathbf{S}_M) were calculated using results of Caswell and Trevisan (1994) and Lesnoff et al. (2003):

$$\mathbf{S}_B = \mathbf{P}^T \mathbf{M}^T \mathbf{P} \mathbf{S}_A$$

$$\mathbf{S}_M = \mathbf{P} \mathbf{S}_A \mathbf{B}^T \mathbf{P}^T$$

where \mathbf{S}_A is the sensitivity matrix of the metapopulation matrix, \mathbf{A} (Hunter and Caswell in press). In each case, the elasticity matrices were calculated as:

$$\mathbf{E}_B = \frac{1}{\lambda_{MP}} \mathbf{B} \circ \mathbf{S}_B$$

$$\mathbf{E}_M = \frac{1}{\lambda_{MP}} \mathbf{M} \circ \mathbf{S}_M$$

The sensitivities and elasticities relevant to demographic and dispersal parameters appear in the 4 x 4 diagonal blocks of \mathbf{S}_B and \mathbf{E}_B and the 17x17 diagonal blocks of \mathbf{S}_M and \mathbf{E}_M , respectively. The sums of the diagonal blocks of \mathbf{E}_B quantify proportional contributions of the demography in each site to λ_{MP} (Hunter and Caswell in press). The

sensitivity and elasticity of λ_{MP} to lower-level vital rates and dispersal rates were calculated using the chain rule as described previously (Caswell 2001).

Results

Local Population Dynamics

Local λ 's (*mean* \pm *SE*) showed substantial variation among sites. It was the highest in the River colony (1.043 ± 0.039) and the lowest in the south satellites (0.848 ± 0.052). In general, λ was higher in colony sites (Picnic: 1.016 ± 0.049 , Marmot Meadow: 0.964 ± 0.065 , Gothic: 0.974 ± 0.068) than in satellite sites (North: 0.876 ± 0.045 , West: 0.849 ± 0.052 , East: 0.907 ± 0.059). The λ estimated using a single projection matrix for the entire population was 0.977 ± 0.084 , which was similar to that reported by Schwartz et al. (1998) and Oli and Armitage (2004).

Elasticity of λ to changes in the lower-level vital rates did not vary substantially among sites (Fig. 5-2). In all sites, elasticity of local λ was the highest to S_r , and the second highest to S_j and S_y (elasticity values were the same for the two rates in all sites). The summed elasticity of λ to the survival of the pre-reproductive classes (S_j , S_y , S_p) was very close to that of reproductive class (S_r). As for the deterministic elasticities, stochastic growth rate λ_S had the highest elasticity to the mean values of adult survival rates in all sites (Fig. 5-3). However, elasticity of λ_S to changes in other vital rates varied among sites. The detailed results of elasticity analyses are given in Appendix D.

The largest spatial variance was observed in the fertility of the reproductive adult stage, and it also made the largest contribution to $V(\lambda)$ (Fig. 5-4). The fertility rate of pre-reproductive females and its covariance with fertility rate of reproductive females were

large, but these made very small contribution to $V(\lambda)$. Variances in the probability of transition from yearling to pre-reproductive stage and from juvenile to yearling stage had positive contributions, and the covariance between the growth from yearling to pre-reproductive stage and the fertility of the reproductive stage had negative contributions, to $V(\lambda)$.

We also calculated the contributions to $V(\lambda)$ in terms of lower level vital rates: S_j , S_y , S_p , S_r , ψ_y , ψ_p , ψ_r , l_{S_y} , and l_{S_a} . The largest variances and covariances were observed in l_{S_y} and l_{S_a} ; however, these did not make significant contribution to $V(\lambda)$ (Fig. 5-5). The largest contribution to $V(\lambda)$ came from variances in S_y , S_a , and S_j , in that order. The covariance between yearling survival and the litter size for the adults had a negative effect on $V(\lambda)$.

Metapopulation Dynamics

We analyzed the metapopulation dynamics for five different levels of dispersal rate (25%, 35%, 45%, 55%, and 65%). At the estimated 45% dispersal rate, λ_{MP} was 0.971, indicating a small annual decline. This estimate was very close to the λ estimated using a single population matrix for the entire region (0.977). The λ_{MP} decreased with increasing dispersal rate (Fig. 5-6).

We first examined the influence of the demography in each site on λ_{MP} (Fig. 5-6). At the estimated 45% dispersal rate, λ_{MP} was most sensitive to demographic rates of two River colonies, which were the sites with the highest λ 's (Fig. 5-6C). The sum of the proportional influence of the demography of colony sites (0.933) was substantially greater than that of satellite sites (0.067). At lower dispersal levels, the two sites with the highest λ had a substantially greater influence on λ_{MP} , than the rest of the sites had (Fig.

5-6A,B). At higher dispersal levels, the two sites with the highest local λ 's still had the greatest influence on λ_{MP} (Fig. 5-6D,E). However, as dispersal increased the influence of the demography in other sites on λ_{MP} increased significantly; at 65% dispersal, the sum of the proportional influence of colony sites decreased to 0.803, and that of satellite sites increased to 0.197.

Next, we calculated the elasticity of λ_{MP} to the vital demographic rates and the dispersal rate, treating these rates as lower-level parameters. We summed the elasticities of the vital demographic rates across all the sites. We again used five different levels of dispersal rate and examined the elasticity of the λ_{MP} to each vital rate (Fig. 5-7). The overall elasticity pattern was the same in all five dispersal levels; λ_{MP} was most sensitive to survival rates (particularly S_r), followed by the l_{s_a} and ψ_r . As expected, λ_{MP} was negatively influenced by the dispersal rate; as the proportion of yearlings dispersing from a site increased, λ_{MP} decreased. However, the potential influence of dispersal on λ_{MP} was much lower than that of the demographic rates.

The elasticity of λ_{MP} to dispersal was the highest at the 55% dispersal rate; higher or lower dispersal rates resulted in a decline in this elasticity value. As the dispersal rate increased from 25% to 65%, the elasticity of λ_{MP} to the survival of the reproductive adults increased, and the elasticity of λ_{MP} to all the other demographic rates decreased. Only the elasticity of λ_{MP} to the breeding probability of the pre-reproductive adults showed a small increase at the 65% dispersal level. It is important to note that these changes in the elasticity values were small, and did not affect the overall elasticity pattern (Fig. 5-7).

These results indicated that λ_{MP} was heavily influenced by the demography of the colony sites with the highest growth rates, particularly by the survival of the reproductive adults in these sites. To analyze the influence of each colony site on λ_{MP} , we calculated λ_{MP} by excluding one, two, three, and four of the colony sites. The λ_{MP} decreased from 0.971 to 0.941 in the absence of the best site (River), and to 0.917, 0.910, and 0.886 in the absence of the best two, three and four colony sites (Picnic, Gothic, and Marmot Meadow), respectively.

Discussion

Consideration of local demographic processes can be important for a better understanding of regional population dynamics (Burgman et al. 1993, Lahaye et al. 1994), but it often requires more data than those required by simpler models (Akçakaya 2000b). As a result, very few studies, particularly of long-lived vertebrates, have investigated the influence of local population dynamics in determining population dynamics at regional scales. Although the role of spatial heterogeneity on population dynamics is well established, the relative roles of demography and dispersal on the dynamics of population at local and regional scales is not well understood. Our long-term study of individually-identified animals in several discrete habitat patches has provided data necessary for a rigorous examination of the local population and metapopulation dynamics of yellow-bellied marmots.

As a result of spatial variation in environmental factors, the survival and reproductive rates of the female yellow-bellied marmots varied among sites (Ozgul et al. in press-a, Ozgul et al. in review). Naturally, these variations influenced local population dynamics, as indicated by substantial variation in local λ 's among sites. However,

population growth rates in most of the sites had indicated that these populations were decreasing, and could not persist without dispersal from the few high quality sites, clearly indicating the interplay between regional and local demographic processes.

Although the demographic rates and the local λ 's showed spatial variation, the elasticity patterns did not vary significantly among sites; local λ 's had, overall, higher elasticity to the mean values of the survival rates than to those of reproductive rates, as is true for many long-lived species (Pfister 1998). Local λ 's were the most sensitive to the survival of the reproductive adults, followed by the survival of the two younger age classes.

Caswell (2001) argued that the deterministic sensitivities, in general, were good approximations of the sensitivity values of the stochastic models. Similar to the deterministic analysis, the stochastic growth rate (λ_S) was most sensitive to proportional changes in the survival of the reproductive adult. However, unlike the deterministic analysis, the elasticity pattern for the rest of the vital rates varied significantly among sites. Juvenile and yearling survival rates and the breeding probability of the reproductive adults had differential influence on λ_S among sites. These results indicate the importance of considering the temporal covariation of the vital rates for identifying those rates that potentially influence the population growth rate.

Ozgul (in press-a) and Ozgul (in review) investigated the vital rates that covaried most closely with the realized growth rate of the adult segment of the population (λ_{ad}). The LTRE analysis revealed that the variation in yearling survival, followed by variation in survival of reproductive adults and juveniles made the largest contributions to the spatial variation in λ . Although survival of female yearlings was not as influential as the

survival of the reproductive adults, the significant variation in this rate contributed the most to the variation in local λ 's. Survival of reproductive adults was generally very high in all the sites and did not show substantial variation among sites. Nonetheless, even the very small variation in this rate caused a significant variation in local λ 's. As predicted by theoretical studies, the most influential vital rate was buffered by the environment and showed the least amount of variation among sites (Pfister 1998); however, even the small variation in this rate significantly contributed to the spatial variation in local dynamics.

Demographic analysis of the local populations helped elucidate the demographic basis of spatial variation in population growth rates. However, local populations of yellow-bellied marmots in Colorado are interconnected through dispersal, and understanding the regional dynamics requires an additional consideration of the role of dispersal. Thus, we used a recently developed matrix metapopulation model (Hunter and Caswell in press) to investigate the metapopulation dynamics. Although the available data allowed us to parameterize only a simple dispersal model, we used the resulting metapopulation model to perform asymptotic analyses and to investigate the relative influence of local demography on regional dynamics.

Our results suggest that a few colony sites are the major drivers of the regional population dynamics; the two major colony sites were more influential on λ_{MP} compared to all the other sites. These results are consistent with those from a study based on a simple patch occupancy model (Ozgul et al. (in press-b)). The dependence of regional persistence on a small number of high quality sites has been suggested as a general rule in long-lived species (Harrison 1991, Schoener 1991, Beier 1993), and has been observed in other species that shared similar life-history characteristics (e.g., *Ochotona princeps*,

Moilanen et al. 1998). The higher the λ of a local population, the more likely that it served to increase λ_{MP} ; excluding the highest quality sites significantly decreased λ_{MP} (see also Ozgul et al. in press-b). These results emphasized the importance of local population dynamics of these few high quality sites for regional persistence. Therefore, we also investigated the relative influence of local demographic rates and the dispersal rate on regional population dynamics. Similar to the local population dynamics, the survival of reproductive adults, followed by the survival of juvenile and yearlings, were the most influential vital rates on λ_{MP} . As expected, the dispersal rate negatively influenced λ_{MP} ; however, the magnitude of the influence of dispersal on λ_{MP} was lower than that of the demographic rates. Increasing or decreasing the dispersal levels did not have a significant effect on this elasticity pattern. Overall, demographic rates that were most influential on local population dynamics of the best quality sites were also the most influential vital rates on regional population dynamics.

In general, lower quality sites had a very small influence on λ_{MP} . At higher dispersal levels, the influence of lower quality sites on λ_{MP} increased, but the overall λ_{MP} decreased. These results indicated a mainland-island or source-sink type population dynamics (Pulliam 1988, Harrison 1989), in which the viability of the metapopulation depends on the fate of the best quality sites. However, lower quality sites had a small but meaningful contribution to the regional persistence of the yellow-bellied marmot metapopulation (Ozgul et al. in press-b). It is important to note that our analysis of asymptotic dynamics did not address the potential contribution of lower quality sites to the regional persistence. In our model, $\lambda > 1$ indicated a growing local population, whereas $\lambda < 1$ indicated a declining local population; the former always increased the

λ_{MP} , whereas the latter decreased λ_{MP} . However, no single local population is invulnerable to extinction over time. Lower quality sites can contribute to regional persistence especially when local extinctions are asynchronous and balanced by local recolonization (Hanski 1999). To investigate the importance of the lower quality sites on regional persistence, one may choose an approach that would include the environmental and demographic stochasticities, a form of density dependence in both demographic and dispersal rates, and also a level of asynchrony among local population dynamics. A simulation based approach may be necessary to include these features using a matrix metapopulation modeling framework (Morris and Doak 2002). However, such an approach requires more parameter estimates, which may be difficult to obtain.

In conclusion, the dynamics of the yellow-bellied marmot metapopulation mainly depended on a few colony sites, and the metapopulation growth rate was highly sensitive to changes in the demography of these high quality sites. The relative influence of dispersal on the metapopulation growth rate was lower than that of the demographic rates. Most commonly used models of metapopulation dynamics emphasize the importance of regional processes, but do not explicitly consider the role of within-population demographic processes. However, our results suggest that local demographic processes can be at least as important as, if not more important than the regional processes in governing the dynamics and persistence of the spatially structured populations of yellow-bellied marmots and other species that share similar life-history characteristics.

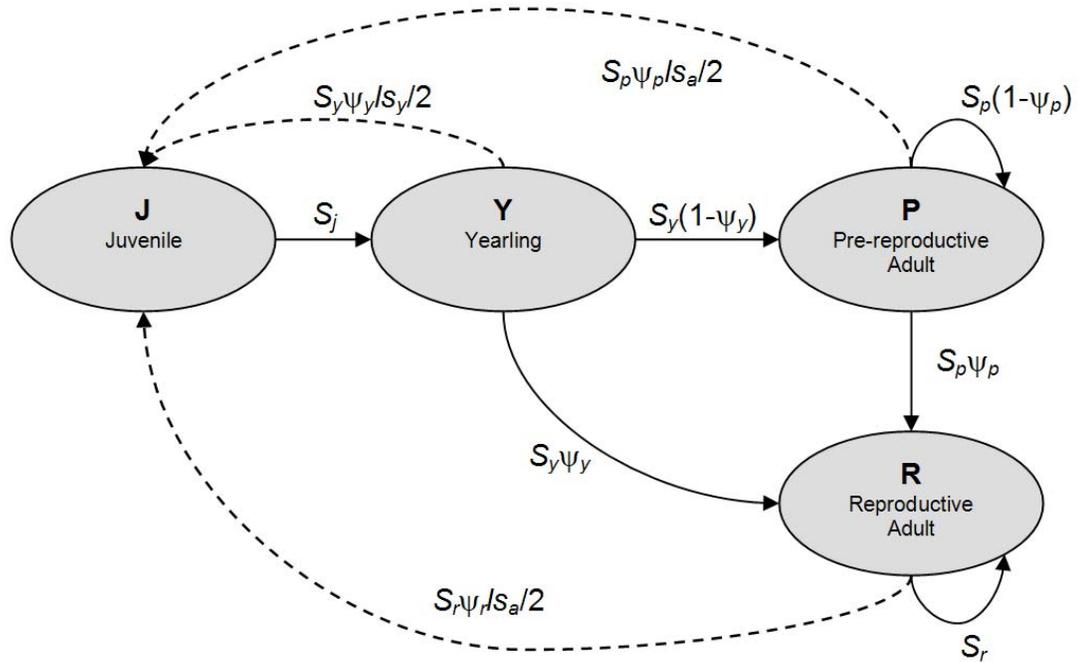


Figure 5-1. The life cycle graph for the yellow bellied marmot, with four life history stages: juvenile (j), yearling (y), pre-reproductive adult (p), and reproductive adult (r). S_x denotes the probability of an individual in stage x surviving until the next census. ψ_x denotes the probability of an individual in stage x breeding right before the next census, conditional on survival. l_{s_y} and l_{s_a} denote the litter size for the yearling and adult stages, respectively.

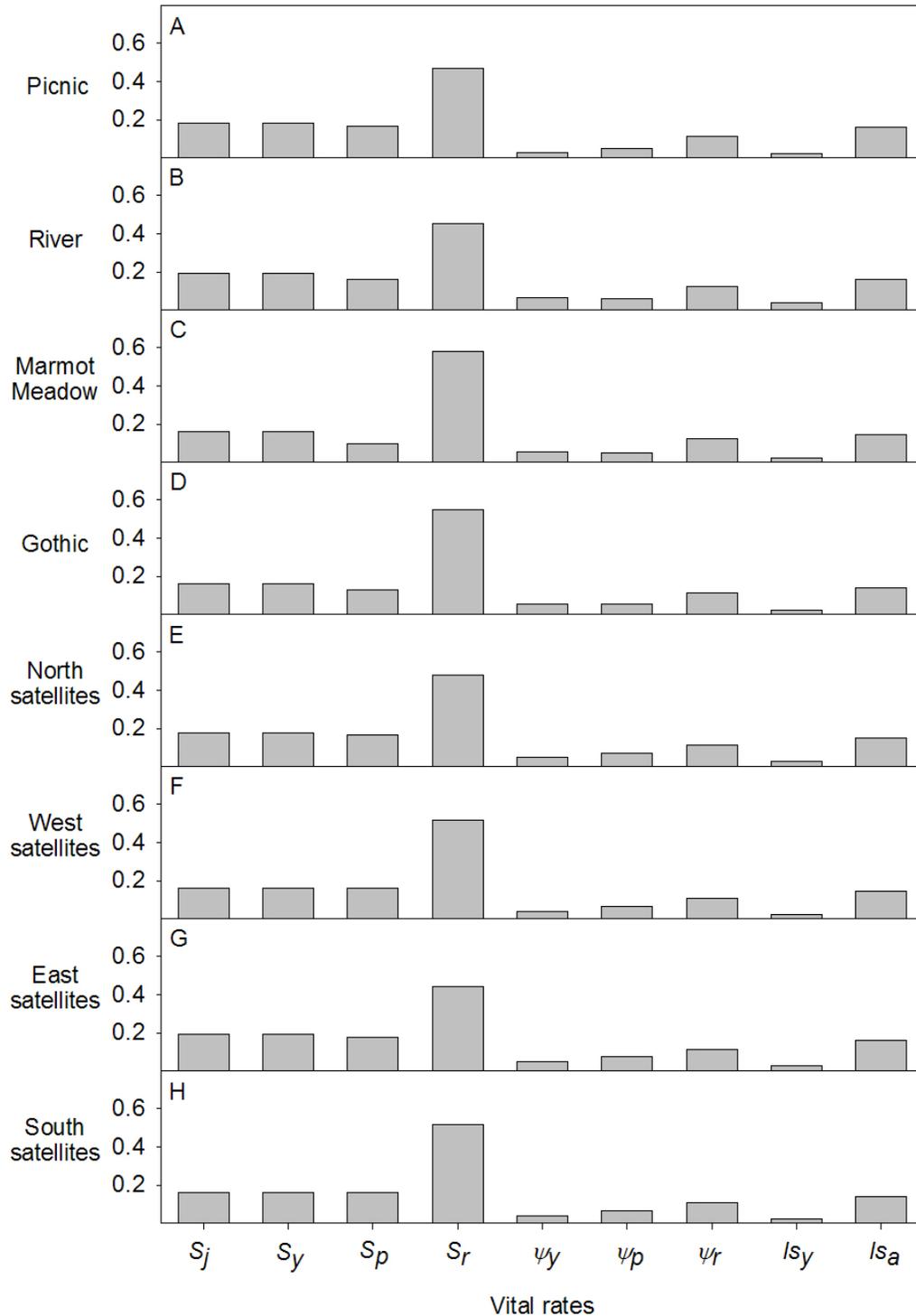


Figure 5-2. Elasticity (proportional sensitivity) of the projected population growth rate (λ) to the vital rates. Elasticities are given for each site group: (A) Picnic colony, (B) River colonies, (C) Marmot Meadow colony and (D) Gothic colony, (E) north satellites, (F) west satellites, (G) east satellites and (H) south satellites. See Fig.5-1 for definitions of the vital rates.

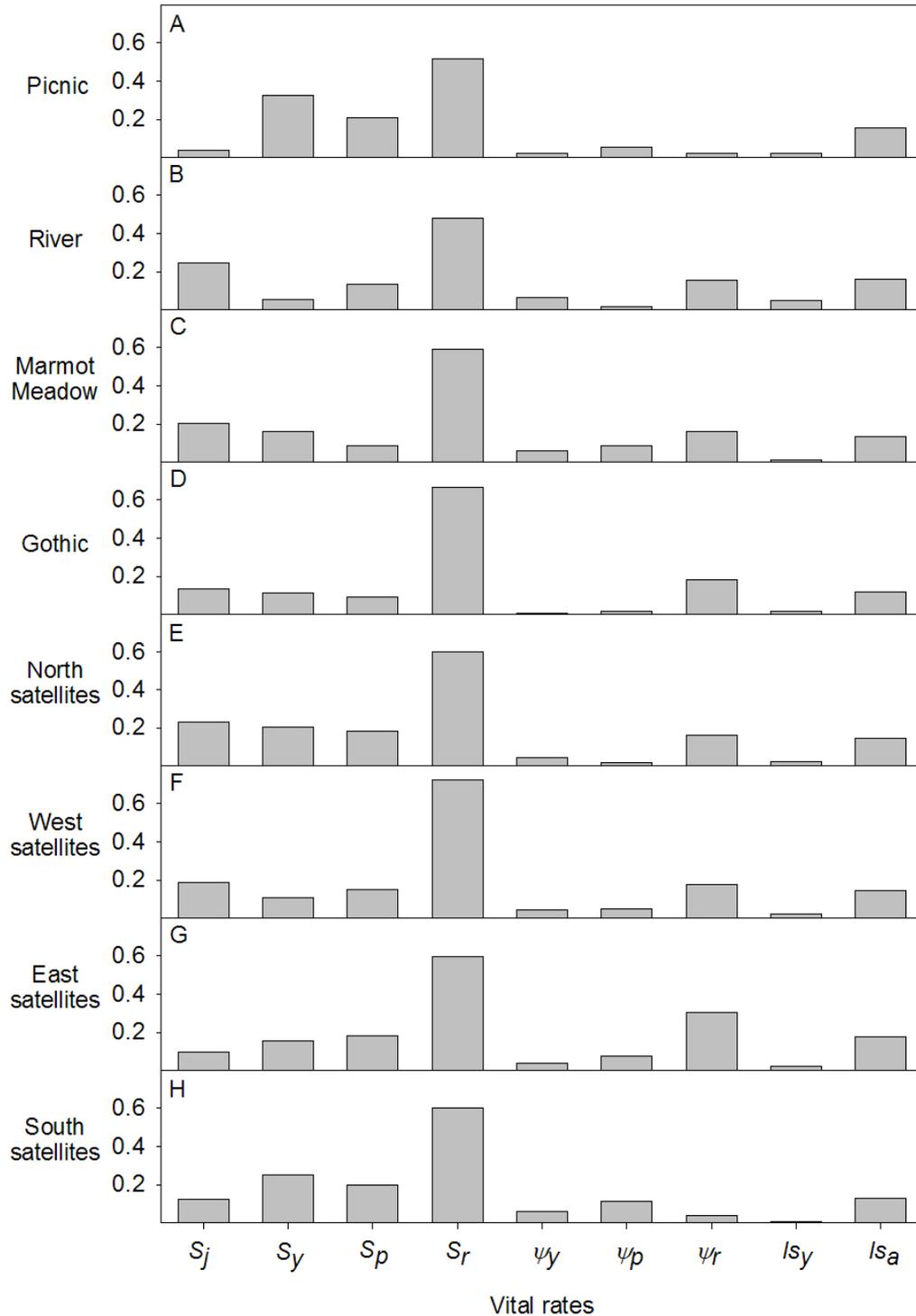


Figure 5-3. Elasticity (proportional sensitivity) of the stochastic population growth rate (λ_s) to the mean values of the vital rates. Elasticities are given for each site group: (A) Picnic colony, (B) River colonies, (C) Marmot Meadow colony and (D) Gothic colony, (E) north satellites, (F) west satellites, (G) east satellites and (H) south satellites. See Fig.5-1 for definitions of the vital rates.

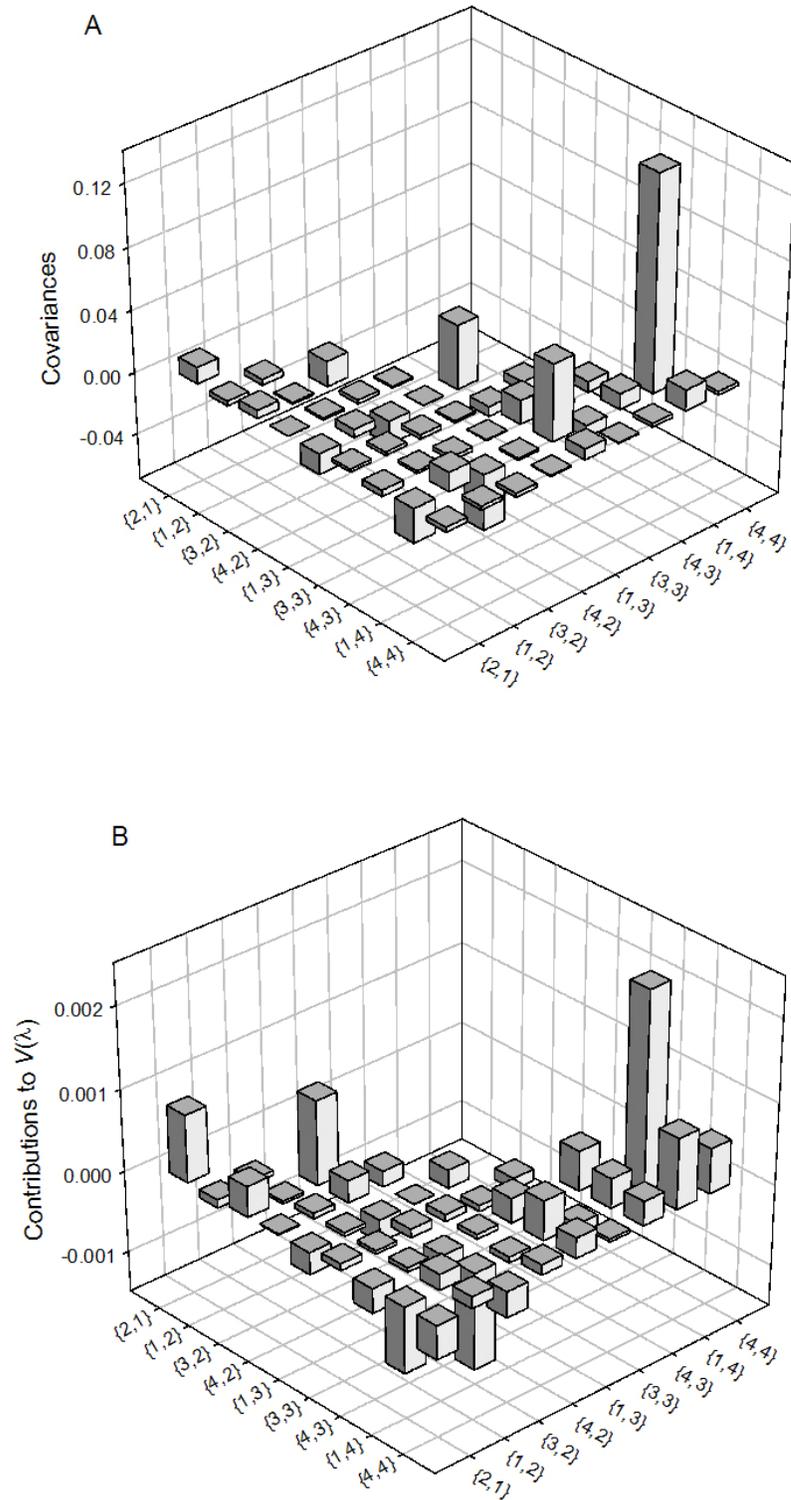


Figure 5-4. (A) The covariances of the projection matrix elements among sites. (B) The contributions of the covariances to the variation in projected growth rates among sites, $V(\lambda)$. $\{i, j\}$ denotes the matrix element in the i^{th} row and j^{th} column of the projection matrix.

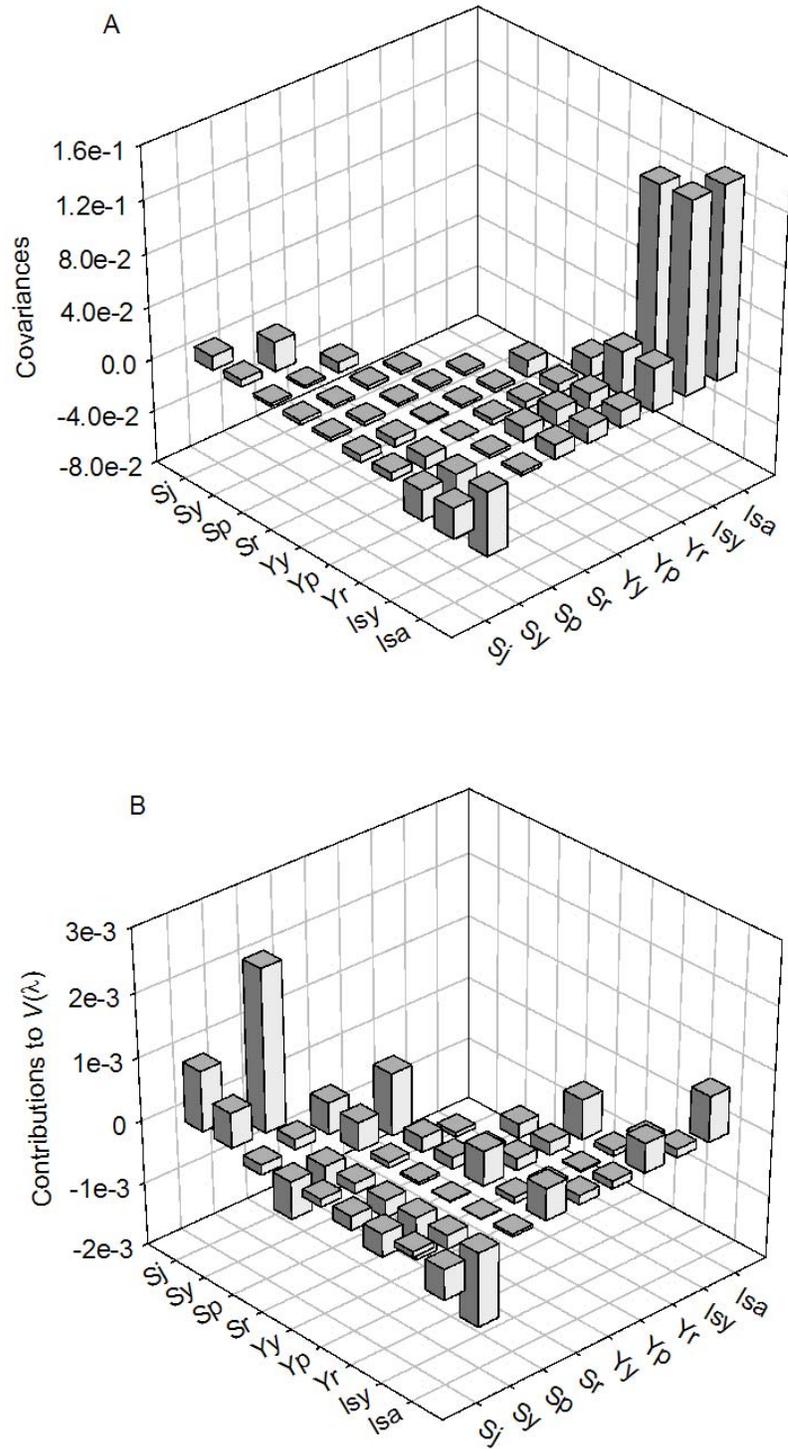


Figure 5-5. (A) The covariances of the vital rates among sites. (B) The contributions of the covariances to the variation in projected growth rates among sites, $V(\lambda)$. See Fig.5-1 for definitions of the vital rates.

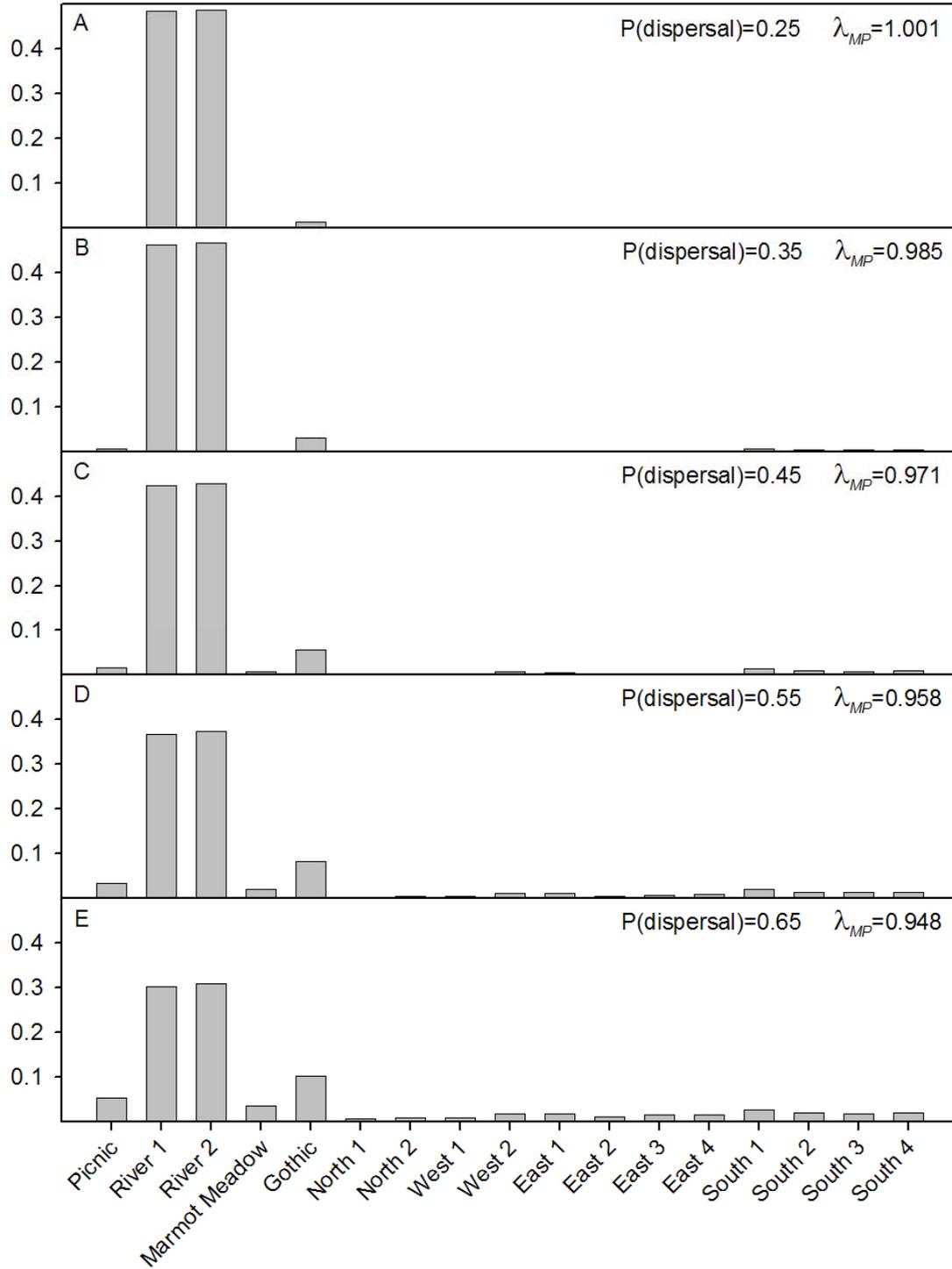


Figure 5-6. Proportional influence of the demography in each of the 17 sites on metapopulation growth rate (λ_{MP}), calculated as the sums of the diagonal blocks of the elasticity matrix, E_B (see text for details). Proportional influences are given for five different levels of dispersal: (A) 25%, (B) 35%, (C) 45%, (D) 55%, and (E) 65% dispersal rate.

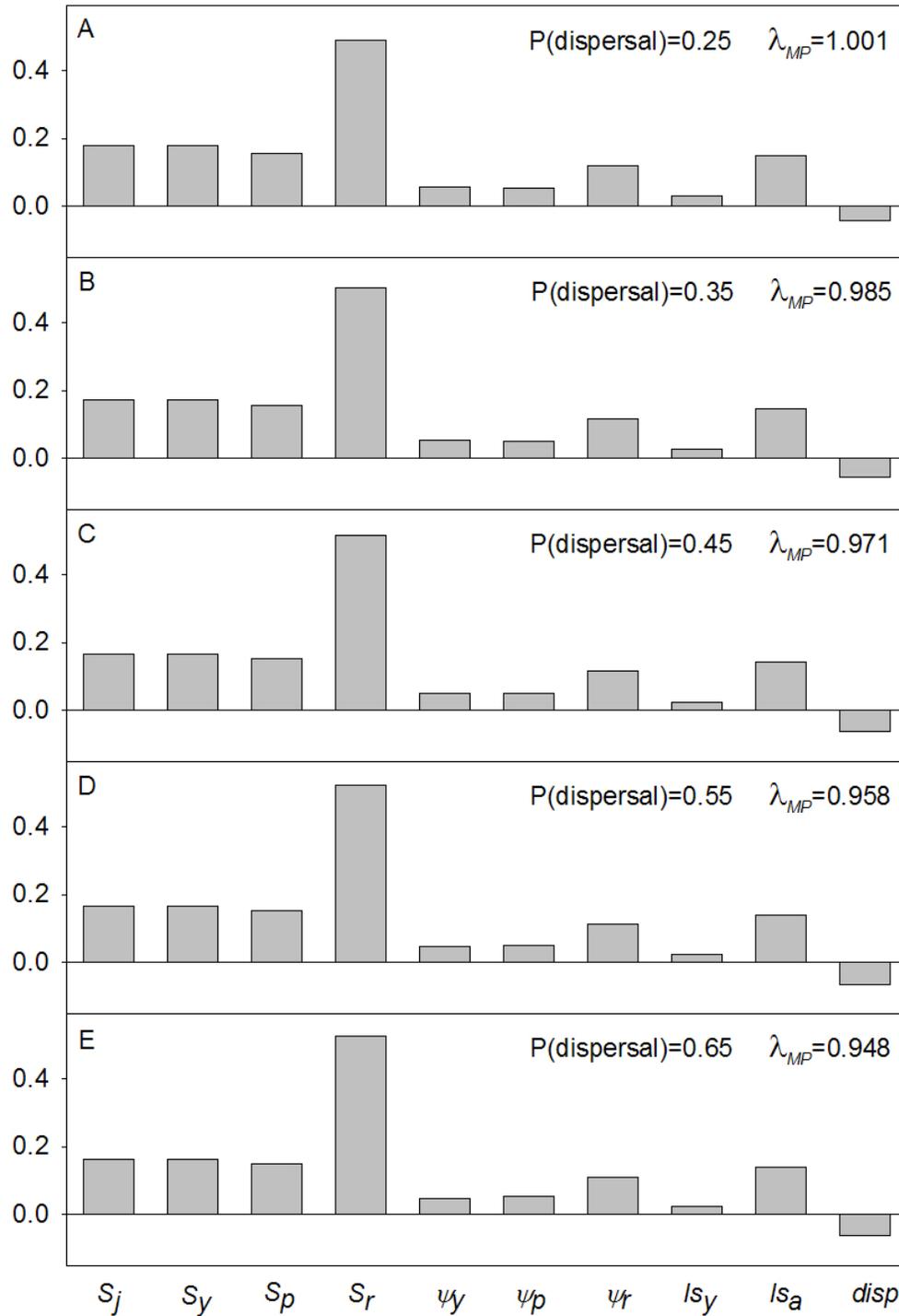


Figure 5-7. Proportional influence of each vital rate and the dispersal rate ($disp$) on λ_{MP} . The elasticity values for the vital demographic rates are summed across all the sites. Proportional influences are given for five different levels of dispersal: (A) 25%, (B) 35%, (C) 45%, (D) 55%, and (E) 65% dispersal rate. See Fig.5-1 for definitions of the vital rates.

CHAPTER 6 CONCLUSION

The gap between theory and practice in ecology makes it difficult to select an appropriate modeling approach for addressing conservation needs of wildlife populations that live in spatially heterogeneous landscapes. The application of metapopulation models is often constrained by the lack of sufficient data. Therefore, the majority of metapopulation studies are based on simple models with fewer data requirements and on species with simple life-histories. In this research, I analyzed the population dynamics of a socially complex, long-lived mammal species that lives in a spatially structured population. I investigated the factors and processes that influenced the dynamics of a yellow-bellied marmot metapopulation in Colorado using two different spatially explicit modeling approaches with different degrees of complexity. My specific objectives were (1) to investigate the relative influence of particular sites and site quality on metapopulation persistence, (2) to investigate the spatial heterogeneity in demographic rates and its influence on population dynamics, (3) to determine the relative influence of demographic rates and the dispersal rate on the metapopulation dynamics, and (4) to compare the utility of two metapopulation models with different degrees of complexity.

In Chapter 2, I used a stochastic patch occupancy model and investigated the relative influence of particular sites, site quality, network characteristics, and regional stochasticity on the persistence of the yellow-bellied marmot metapopulation. Results of these analyses indicated that the dynamics of the yellow-bellied marmot metapopulation mainly depended on a few high quality sites, and the regional persistence was highly

sensitive to changes in the quality of these sites. Nonetheless, I also found that the lower quality sites made a significant contribution to the long-term persistence of the yellow-bellied marmot metapopulation. The importance of lower quality sites for the metapopulation dynamics suggests that the yellow-bellied marmot system is not a typical mainland-island system, but shows characteristics of a metapopulation in which the extinction–recolonization dynamics play a significant role. These analyses, based on simple site occupancy data, provided several useful insights regarding the dynamics and persistence of the yellow-bellied marmot metapopulation. However, the high sensitivity of metapopulation persistence to local population size, particularly in high quality sites, demanded a more elaborate investigation of the local demographic processes.

Patch occupancy models do not consider the demographic processes within local populations. In chapters 3 and 4, I investigated the spatiotemporal variation in local demographic processes. Survival and reproduction are the two major components of the local demographic processes, and spatiotemporal variations in these rates potentially influence both local and regional population dynamics. Age-specific survival rates of yellow-bellied marmots exhibited both spatial and temporal variation, but survival of younger animals was more variable over space and time than that of adults. Spatial and temporal variation in juvenile survival rates strongly influenced the variation in the realized population growth rate. Also, the components of reproduction in yellow-bellied marmots exhibited both spatial and temporal variation, but the pattern of variation differed among the components. Only the litter size and the breeding probability of the non-reproductive adults significantly influenced the temporal variation in the realized population growth rate. These analyses indicated that juvenile survival and litter size,

followed by the breeding probability of the non-reproductive adults, were likely to be the main demographic factors driving the temporal dynamics of the yellow-bellied marmot population. These vital rates were the components of recruitment into the adult segment of the population; they were more sensitive to the variation in extrinsic factors, thus exhibiting a greater degree of variation over space and time. Consequently, they play a predominant role in influencing the fluctuations in the realized population growth rate. Therefore, recruitment into the adult population is likely to be the critical component of the population dynamics of the yellow-bellied marmot and of other species with similar life history characteristics.

In Chapter 5, I parameterized a stage-structured matrix model for each population, and investigated the demographic causes of the observed spatial variation in projected population growth rate. The survival of the reproductive adults, followed by the survival of the two young age classes, was potentially the most influential demographic parameter on the local population dynamics. The variation in female yearling survival, followed by the variation in the survival of reproductive adults and juveniles, made the largest contributions to the observed variation among local population dynamics.

Using a demographically and spatially structured matrix metapopulation model, I investigated the relative influence of local demographic rates and the dispersal rate on metapopulation dynamics. Only a small number of colony sites ultimately governed the dynamics of the yellow-bellied marmot metapopulation. analysis of the patch occupancy model also led to the same conclusion. The projected metapopulation growth rate was highly sensitive to the changes in the local demography of these high quality sites, particularly to changes in the survival of the reproductive adults. The magnitude of the

influence of dispersal on metapopulation dynamics was lower than that of the demographic rates. Interestingly, demographic rates that were most influential on the local population dynamics of the best quality sites were also the vital rates with the greatest influence on metapopulation dynamics.

Many wildlife species live in fragmented populations, and identifying the relative importance of local and regional processes is an important issue in conservation decision-making. Several approaches to modeling the dynamics of spatially structured populations have emphasized the importance of regional processes without explicitly considering the role of local demographic processes. However, my results have demonstrated the importance of incorporating local demographic processes for understanding the dynamics of spatially structured populations of yellow-bellied marmots and other species that share similar life-history characteristics. In conclusion, the findings of this research provide a thorough understanding of the population dynamics of a socially complex, long-lived mammal species that live in a spatially structured population.

APPENDIX A
ANALYSIS OF SPATIAL AND TEMPORAL VARIATION IN OVERALL
APPARENT ANNUAL SURVIVAL RATES

Table A-1. Analysis of spatial and temporal variation in overall apparent annual survival rates for the yellow-bellied marmot using Cormack-Jolly-Seber models. Akaike's Information Criterion corrected for small sample size (AIC_c), differences in AIC_c values (ΔAIC_c), AIC_c weights and number of parameters are given for each model. Symbols are: ϕ = apparent annual survival rate, ρ = annual recapture rate, t = time effect, s = site effect, s' = modified site effect, $t*s$ = interactive effects of site and time, $t+s$ = additive effects of site and time. A period (.) indicates constant value of the parameter. The most parsimonious models are highlighted in bold.

no.	Model	AIC_c	ΔAIC_c	AIC_c Weights	Number of parameters
1	ϕ (.) ρ (.)	2729.81	76.22	0	2
2	ϕ (.) ρ (s)	2684.00	30.41	0	9
3	ϕ (.) ρ (t)	2723.05	69.46	0	28
4	ϕ (s) ρ (.)	2720.99	67.39	0	9
5	ϕ (s) ρ (s)	2675.06	21.46	0	16
6	ϕ (s) ρ (t)	2715.61	62.02	0	35
7	ϕ (t) ρ (.)	2707.40	53.81	0	28
8	ϕ (t) ρ (s)	2661.58	7.98	0.013	35
9	ϕ (t) ρ (t)	2712.62	59.03	0	54
10	ϕ (t+s) ρ (.)	2701.15	47.56	0	35
11	ϕ (t+s) ρ (s)	2655.68	2.08	0.258	42
12	ϕ (t+s) ρ (t)	2706.45	52.86	0	61
13	ϕ (t*s) ρ (.)	2798.83	145.24	0	217
14	ϕ (t*s) ρ (s)	2762.83	109.24	0	224
15	ϕ (t*s) ρ (t)	2818.19	164.60	0	243
16	ϕ (t+s) ρ (s')	2653.59	0.00	0.729	40

APPENDIX B
EFFECT OF ENVIRONMENTAL COVARIATES ON THE SPATIAL AND
TEMPORAL VARIATION IN AGE-SPECIFIC SURVIVAL RATES

Table B-1. A table showing the effect of environmental covariates on the spatial and temporal variation in age-specific survival rates. The base model used for the covariate analysis is $\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$ (see Table 3-2). Site-specific covariates are elevation (*elev*), aspect (*asp*), slope (*slope*), and average group size (*size*), and temporal covariates are length of the growing season (*grw.ssn*), duration of permanent snow cover (*snw.cvr*), annual snow fall (*snw.fall*), annual precipitation (*prep*), monthly mean summer temperature (*temp*), first Julian date of bare ground (*bare*), and first Julian date of permanent snow pack (*snw.pck*). Other symbols are defined in Table 3-2.

No.	Model	ΔAIC_c	AIC _c Weights	Number of Parameters
Base models:				
1	$\phi_{juv_col}(t) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	1.77	0.122	46
2	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	2.06	0.106	49
Spatial variation in juvenile survival:				
3	$\phi_{juv_col}(t+elev) \phi_{juv_sat}(elev) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	0.48	0.233	44
4	$\phi_{juv_col}(t+asp) \phi_{juv_sat}(asp) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	0.00	0.297	44
5	$\phi_{juv_col}(t+slope) \phi_{juv_sat}(slope) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	3.87	0.043	44
6	$\phi_{juv_col}(t+size) \phi_{juv_sat}(size) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	3.90	0.042	44
Spatial variation in yearling survival:				
7	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(elev) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	3.18	0.060	43
8	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(asp) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	4.29	0.035	43
9	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(slope) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	7.37	0.007	43
10	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(size) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	3.92	0.042	43
Spatial variation in adult survival:				
11	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad}(elev) \rho(s')$	11.55	0.001	49
12	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad}(asp) \rho(s')$	10.02	0.002	49
13	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad}(size) \rho(s')$	7.91	0.006	49
14	$\phi_{juv_col}(t+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad}(slope) \rho(s')$	8.46	0.004	49
Temporal variation in juvenile survival in colony sites:				
15	$\phi_{juv_col}(grw.ssn+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	27.42	0.000	25
16	$\phi_{juv_col}(prep+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	27.78	0.000	25
17	$\phi_{juv_col}(temp+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	26.04	0.000	25
18	$\phi_{juv_col}(snw.cvr+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	20.86	0.000	25
19	$\phi_{juv_col}(snw.fall+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	27.61	0.000	25
20	$\phi_{juv_col}(snw.pck+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	26.19	0.000	25
21	$\phi_{juv_col}(bare+s) \phi_{juv_sat}(s) \phi_{yrl}(s) \phi_{ad_col}(\cdot) \phi_{ad_sat}(\cdot) \rho(s')$	27.93	0.000	25

APPENDIX C
ENVIRONMENTAL COVARIATES FOR THE COMPONENTS OF
REPRODUCTION

Site-specific factors. We considered two site-specific factors that influence the local micro-climatic conditions: (1) elevation (m) and the (2) aspect (i.e. slope direction: 1 = southwest, 0 = northeast). The Upper East River Valley stretches in a southeast - northwest direction, gaining elevation towards the northwest. Marmot sites on the west side of the East River Valley have steeper slopes facing northeast (38° - 98°), whereas sites on the east side are located on gradually inclined meadows generally facing southwest (183° - 280°).

Climatic factors. We investigated climatic factors at three different time periods: The climatic factors of (1) the previous summer, (2) the previous winter, and (3) the present summer (Table C-1). We used principal components analysis (Varimax rotation with Kaiser normalization) to reduce the number of environmental variables in each time period to be used in subsequent analyses. We extracted two components that explained 58.3% of the variation in the previous summer's climatic factors. The first component alone explained 29.6% of the variation, and it represented the overall precipitation. Summer precipitation (0.93) and late summer precipitation (0.92) both loaded highly on this component. The second component explained 28.7% of the variation, and it represented the growing season. The Julian date of snowmelt loaded highly negatively (-0.93) and the length of the growing season loaded highly positively (0.90) on this component. We extracted one component that explained 56.8% of the variation in the

previous winter's climatic factors. This component represented the winter severity; average snow pack loaded highly positively (0.89), followed by the length of the snow pack (0.75), while average winter temperature loaded negatively (-0.59) on this component. We extracted one component that explained 76.7% of the variation in the present year's climatic factors. This component represented the onset of the summer; the Julian date of snowmelt loaded highly positively (0.93), followed by the early summer precipitation (0.79), while the early summer temperature loaded highly negatively (-0.90) on this component.

Social factors. We considered five social factors: (1) Residency status of the female (resident vs. immigrant), (2) the average number of adult (≥ 2 yrs) females (i.e. average group size), and the weighted number of (3) breeding, (4) adult (≥ 2 yrs), and (5) yearling (1-2 yrs) females at the focal site at a given year. The weighted numbers were calculated by dividing the number of individuals by the site-specific averages over 43 years.

Table C-1. List of covariates used during the analysis of the effect of environmental factors on the breeding probabilities and on litter size of the yellow-bellied marmot.

Factor	Period	Reference
Site-specific factors:		
Elevation (m)	constant	
Aspect (northeast = 0, southwest = 1)	constant	
Previous summer's climatic factors:		
Summer precipitation {May-Sep} (cm) ^a	1962-2004	(Armitage 1994) (Salsbury and Armitage 2003) (Schwartz and Armitage 2002)
Late summer precipitation {Jul-Sep} (cm) ^a	1962-2004	(Armitage 1994)
Julian date of first killing frost ^a	1962-2004	
Late summer temperature (°C) ^a	1962-2004	(Schwartz and Armitage 2005)
Length of growing season (days) ^{a, b}	1975-2004	(Schwartz and Armitage 2002) (Schwartz and Armitage 2005)
Julian date of last bare ground ^b	1975-2004	(Armitage 2003b)
Julian date of snowmelt ^b	1975-2004	(Van Vuren and Armitage 1991)
Previous winter's climatic factors:		
Average winter snow pack (cm) ^b	1975-2004	(Inouye et al. 2000)
Length of the snow pack (days) ^b	1975-2004	(Inouye et al. 2000)
Average winter temperature (°C) ^b	1975-2004	(Schwartz and Armitage 2005)
Present summer's climatic factors:		
Julian date of snowmelt ^b	1975-2004	(Armitage 2003b)
Early summer temperature {Apr-May} (°C) ^a	1962-2004	(Schwartz and Armitage 2005)
Early summer precipitation {Apr-May} (cm) ^a	1962-2004	(Armitage 1994)
Social factors:		
Residency (resident = 1 / immigrant = 0)	constant	
Average adult population size	constant	
Number of breeding females	1962-2004	
Number of adult females	1962-2004	
Number of yearlings	1962-2004	

APPENDIX D
ELASTICITY ANALYSIS OF LOCAL POPULATION DYNAMICS

Elasticity value for each matrix entry is given by the formulae (Caswell 2001):

$$e_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \frac{a_{ij}}{\lambda},$$

$$\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_i}{\langle \mathbf{w}, \mathbf{v} \rangle},$$

where, $\frac{\partial \lambda}{\partial a_{ij}}$ is the sensitivity of λ to (changes in) the matrix element a_{ij} . \mathbf{w}_i and \mathbf{v}_i are the associated right and left eigenvectors corresponding to stable-stage distribution and stage-specific reproductive values, respectively. $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of vectors \mathbf{w} and \mathbf{v} .

As some of the projection matrix elements are functions of the same vital rates (S_i , ψ_i , $l s_i$), we calculated lower-level elasticities for each site using the chain rule (Caswell 2001):

$$e_x = \frac{\partial \lambda}{\partial x} \frac{x}{\lambda},$$

$$\frac{d\lambda}{dx} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x},$$

where $\frac{\partial \lambda}{\partial x}$ is the sensitivity of λ to the vital rate x .

Elasticity of local λ to changes in matrix elements did not vary substantially among sites. In all the sites, elasticity of λ was the highest to the survival of the reproductive adults, and second highest to the survival of the juveniles. Overall, elasticity

for the fertility of the reproductive adults ranked third in seven sites and for the growth from yearling to reproductive adult stage in one site.

Elasticity of local λ to changes in lower-level vital rates did not vary substantially among sites either (Fig. 5-3). In all the sites, elasticity of local λ was the highest to S_r , and the second highest to S_j and S_y (elasticity values were the same for the two rates in all the sites). Overall, elasticity for S_p ranked fourth in six sites, and for l_{s_a} in two sites. We also calculated the summed elasticity of λ to the survival rates for the three pre-reproductive classes (S_j , S_y , S_p) and compared it to that of reproductive adults (S_r). The summed elasticity of λ to the survival of the pre-reproductive classes was very close to that of reproductive classes; it was slightly higher in four sites (Picnic, River, north satellites, and east satellites) and slightly lower in the rest of the sites (Gothic, Marmot Meadow, west satellites and south satellites).

As for the deterministic elasticities, λ_S had the highest elasticity to the mean values of adult survival rates in all sites (Fig. 5-4). However, elasticity of λ_S to changes in other vital rates varied significantly among sites (Fig. 5-4). Elasticity for S_j ranked second in four sites, for S_y in two sites, and for ψ_r in two sites. Elasticity for S_p ranked third in three sites, for ψ_r in two sites, and for S_j , S_y and l_{s_a} , each in one site. Elasticity for l_{s_a} ranked fourth in three sites, for S_p in two sites, and for S_y and ψ_r , each in one site. There was a relatively low effect on λ_S of the small changes in variances in and covariances among vital rates. The summed elasticity of λ to the survival of the pre-reproductive classes was again close to that of reproductive classes; it was slightly higher in two sites (Picnic and north satellites) and lower in the rest of the sites (River, Gothic, Marmot Meadow, west satellites, east satellites and south satellites).

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BIOGRAPHICAL SKETCH

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