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Spatiotemporal variation in reproductive parameters of yellow-bellied marmots

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Abstract Spatiotemporal variation in reproductive rates is a common phenomenon in many wildlife populations, but the population dynamic consequences of spatial and temporal variability in different components of reproduction remain poorly understood. We used 43 years (1962–2004) of data from 17 locations and a capture–mark–recapture (CMR) modeling framework to investigate the spatiotemporal variation in reproductive parameters of yellow-bellied marmots (*Marmota flaviventris*), and its influence on the realized population growth rate. Specifically, we estimated and modeled breeding probabilities of two-year-old females (earliest age of first reproduction), >2-year-old females that have not reproduced before (subadults), and >2-year-old females that have reproduced before (adults), as well as the litter sizes of two-year old and >2-year-old females. Most reproductive parameters exhibited spatial and/or temporal variation. However, reproductive parameters differed with respect to their relative influence on the realized population growth rate (λ). Litter size had a stronger influence than did breeding probabilities on both spatial and temporal variations in λ. Our analysis indicated that λ was proportionately more sensitive to survival than recruitment. However, the annual fluctuation in litter size, abetted by the breeding probabilities, accounted for most of the temporal variation in λ.

Keywords Breeding probability · Capture–mark–recapture (CMR) · Multistate model · Population dynamics · Pradel's reverse-time model · Realized population growth rate · Spatiotemporal population dynamics

Introduction

Variation in environmental conditions over time and space is ubiquitous in nature (Hanski and Gaggiotti 2004; Hanski and Ovaskainen 2003). Such variations can cause changes in vital demographic rates over time and space, and these differences can substantially 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 (Caswell 2001; Coulson et al. 1999, 2000; Heppell et al. 2000). Because population growth rates are highly sensitive to changes in reproductive parameters in many species (e.g., Oli and Armitage 2004; Oli and Dobson 2003; Sæther and Bakke 2000), spatiotemporal variation in these rates can influence the dynamics and persistence of populations. Therefore, a thorough understanding of population dynamics requires a detailed

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understanding of variation in reproductive rates, and of environmental factors that can cause such variation.

Reproduction can be decomposed into two components: 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., Bryant 2005; Jenouvrier et al. 2003; Watson and Moss 1970). A change in breeding probability can cause variation in population growth rate and thus population dynamics, even when average litter or clutch size remains relatively stable. Although spatiotemporal variations in litter (or clutch) size or fecundity rates have been examined for some species (e.g., Bronson 1979; Chamberlain and Crick 2003; Coulson et al. 2000; Gaillard et al. 2000; Jarvinen 1993; Sæther et al. 1999; Tremblay et al. 2003), variations in breeding probability over space and time, and the impact on the population dynamics (i.e., the effect on population growth rate) of such variations have received much less attention. Thus, identifying the impact of spatiotemporal variation in reproductive parameters on population dynamics requires the simultaneous examination of both components of reproduction.

Our objective was to investigate spatiotemporal variations in breeding probability and litter size, and to examine the impact of such variations on the population dynamics of yellow-bellied marmots (*Marmota flaviventris*). We applied multistate capture–mark–recapture (CMR) models to 43 years (1962–2004) of data from 17 discrete habitat patches, and examined spatial and temporal variations in state-specific breeding probabilities. This, combined with analysis of the variation in litter size, enabled us to identify which component of reproduction varied over space and/or time. We also tested a series of hypotheses concerning the effects of several environmental 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, examined the impact of the spatiotemporal variation in components of reproduction on population dynamics, and investigated the relative contribution of survival and recruitment to the realized population growth rate.

Ozgul et al. (2006) provided detailed analysis of the age-specific survival rates of the yellow-bellied marmot population in Colorado. Our study, together with Ozgul et al. (2006), enabled us to compare the spatiotemporal variation in survival and reproductive rates, and evaluate their relative influences on the realized population growth rate. Theory predicts that demographic parameters to which population growth rate is highly sensitive should be less variable than those to which growth rate is less sensitive (Cairns 1992; Gaillard et al. 1998, 2000; Pfister 1998). Oli and Armitage (2004) found that asymptotic growth rate of a yellow-bellied marmot population was generally more sensitive to changes in survival parameters than to reproductive parameters. Thus, we expected survival parameters to be less variable over space or time than reproductive parameters. Furthermore, we expected survival parameters to have a greater relative influence on realized population growth rate than reproductive parameters.

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 (Armitage 2003a; Frase and Hoffmann 1980). The study was conducted in the Upper East River Valley near the Rocky Mountain Biological Laboratory, Gothic, CO, USA (38°57′N, 106°59′W). Marmots in our study area occupy discrete habitat patches. Elevations of marmot sites vary from 2,700 to 3,100 m above sea level. Habitat characteristics vary within and between sites, from rolling grassy meadows to steeper talus slopes (Blumstein et al. 2006; 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 matrilines, 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). Adult marmots breed shortly after emerging from hibernation (Armitage 2003a). Female marmots can reproduce at two years of age, but the probability that a two-year-old female reproduces is generally lower than that of older females, and the median age of first reproduction is three 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). Trapping occurred during late spring and summer months, which is the active season for yellow-bellied marmots. Animal identification number, sex, mass and reproductive condition (Armitage and Wynne-Edwards 2002) were recorded for each animal. We trapped marmots concurrently in 17 sites known to be occupied by marmots (see Ozgul et al. 2006 for the spatial distribution of these sites). We grouped these sites into five categories on the basis of size and quality of habitat patches (four colony and one satellite group). Four major colony sites were: Picnic, River (two adjacent sites were grouped together), Marmot meadow, and Gothic. Satellite sites were typically occupied by few individuals. We assumed that survival and reproductive rates of marmots occupying smaller sites were similar, and grouped all satellite sites together; this was necessary because of the small sample size, which did not permit separate analysis of each satellite site. We used data collected from 748 females that were ≥ 1 year old. Ages for females that were captured as juveniles were known exactly (n = 599), whereas ages for other females (n = 149) were estimated based on body mass (≤ 2 kg = yearling, >2 kg = older, Armitage et al. 1976). Litter size was estimated as the number of weaned juveniles that emerged from natal burrows, and also includes survival of juveniles until weaning.

Components of reproduction

We investigated the spatial and temporal variations in two major components of reproduction: (1) breeding probability and (2) litter size. For the analysis of breeding probabilities, we considered four life history states based on age and reproductive status (Fig. 1): (1) yearling (1–2 year), (2) subadult ($\geq$2-year-old females who have not reproduced before), (3) reproductive adult (>2-year-old females who have reproduced during the preceding summer), and (4) nonreproductive adult (>2-year-old females who have reproduced before, but not during the preceding breeding season). We did not include juveniles (0–1 year olds) in our analyses because the earliest age of first reproduction in our study population was two years. We used the multistate CMR model (Brownie et al. 1993; Fujiwara and Caswell 2002; Hestbeck et al. 1991; Williams et al. 2001) implemented in Program MARK (White and Burnham 1999) to estimate and model state-specific annual apparent survival (S), recapture (ρ), and transition (ψ) rates. The transition rate ψ_{xy} indicates the probability of transition from state x in one year to state y the following year, conditional on surviving the period in state x. We estimated the breeding probabilities for each state as the transition rate from each state to the reproductive adult state (ψ_{x3}). Data were insufficient to estimate parameters separately for the two adult states. Therefore, we constrained the survival and recapture rates of reproductive and nonreproductive adults to be the same (i.e., $S_3 = S_4$, $\rho_3 = \rho_4$); we also constrained rates of transition within and between the two adult states to be the same (i.e., $\psi_{33} = \psi_{43}$, $\psi_{34} = \psi_{44}$). We tested these assumptions in a separate analysis and found no support for differences in survival, recapture and breeding probabilities between the two states. Hereafter, we will use ψ_{13} to indicate "breeding probability of two-year-old females" (i.e., the breeding probability of an individual that was a yearling in the previous year and survived the period to become a two-year-old), ψ_{23} to indicate "breeding probability of subadults" (i.e., the breeding probability of an individual that was a subadult the previous year and survived the period), and ψ_{33} to indicate "breeding probability of adults" (i.e., breeding probability of an individual that was an adult the previous year and survived the period). Both yearling recapture rate (ρ_1) and yearling to yearling transition rate (ψ_{11}) were fixed to zero, because surviving yearlings moved to either subadult or adult state. The parameters ψ_{14}, ψ_{21}, ψ_{24}, ψ_{31}, ψ_{32}, ψ_{41}, and ψ_{42} were also fixed at zero, as these transitions were not biologically possible.

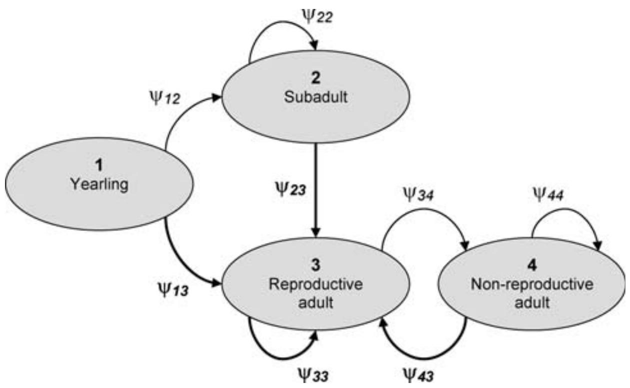

Fig. 1 The four life history states used in the multistate mark–recapture model for the yellow-bellied marmot (*Marmota flaviventris*) population in Gothic, CO. Transition rates are denoted as ψ_{xy}, indicating the probability of transition from state x to state y, conditional on surviving the period in state x. Breeding probabilities are the transitions from each state to reproductive adult state (ψ_{x3}), and are indicated in *bold*. Transitions $\psi_{34} = \psi_{44}$ and $\psi_{33} = \psi_{43}$ are constrained to be the same (see text for details). Transitions ψ_{12}, ψ_{22}, and ψ_{34} are complements of ψ_{13}, ψ_{23}, and ψ_{33}, respectively (e.g., $\psi_{22} = 1 - \psi_{23}$)

We used the program UCARE V2.02 (Choquet et al. 2003) to assess the goodness-of-fit of the general multistate model. The over-dispersion parameter ($\hat{c}$) was calculated as the χ^2 divided by the degrees of freedom (Burnham and Anderson 2002). We used Akaike's information criterion, corrected for small sample size (AIC$_c$) for model comparison, and to identify 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$_c$).

Ozgul et al. (2006) reported for the same study population that there was no evidence for temporal variation in the survival or recapture rates of the yearling or adult marmots. Thus, we tested only for site effects in survival and recapture rates. First, we tested for site effects in each rate by comparing the general model, which included site effect on all parameters $\{S_1(s)\ S_2(s)\ S_3(s)\ \rho_2(s)\ \rho_3(s)\ \psi_{13}(s)\ \psi_{23}(s)\ \psi_{33}(s)\}$, to a series of reduced models in which one of the parameters was constrained to be constant among sites (.) or different between colony and satellite sites (*col/sat*). Next, we constructed a model that included only the effects detected in the previous analysis, and retested for each effect based on this new model. Next, using the most parsimonious model identified, we tested for temporal variation in each transition rate. Due to data limitations, we only tested for additive, not interactive, effect of year.

We used a general linear model (GLM) with an identity link function to test for spatial and temporal variations in litter size. We used the Shapiro–Wilk test to test for normality of residuals (Shapiro and Wilk 1965). Analysis of age effects on litter size revealed that a two age-class model was the most parsimonious, 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) $\geq$3-year-old females. We used AIC$_c$ for model comparison, and to identify the most parsimonious model (Burnham and Anderson 2002). GLM analysis was performed in the program R (R Development Core Team 2005).

Effect of environmental factors

Using the most parsimonious models identified in the preceding analyses, we examined the potential influence of environmental factors on breeding probabilities and litter size. We considered the influence of extrinsic and intrinsic environmental factors that can potentially influence components of reproduction. Extrinsic factors included elevation and slope aspect (NE vs. SW facing) of each site and climatic variables for each year of the study, whereas intrinsic factors included population-level characteristics (see Appendix A). We used principal components analysis (PCA) to reduce the number of climatic variables used in the analyses (see Appendix B for details on PCA).

We investigated the effect of each covariate on breeding probabilities by modeling the logit of each transition rate as a linear function of extrinsic and intrinsic covariates in Program MARK. The influence of the aforementioned covariates on litter size was examined by modeling litter size as a linear function of each of extrinsic and intrinsic covariates. Because we only had data on a subset of environmental factors that could have influenced reproductive parameters, we investigated the influence of each covariate separately. The influence of a covariate on a parameter was evaluated by comparing the difference in AIC$_c$ (ΔAIC$_c$) between models with and without the covariate; ΔAIC$_c$ >2 was taken as an evidence of support for the relationship between the parameter and the covariate. The 95% confidence interval for the slope parameter (β) indicated the direction and magnitude of the relationship (e.g., Blums et al. 2003; Ozgul et al. 2006). Proportion of variation explained by each covariate was assessed by comparing the deviances of constant, covariate and general models (e.g., Barbraud et al. 2000; Gaillard et al. 1997). The general model was time-dependent in the case of time-specific covariates, and site-dependent in the case of site-specific covariates. Total amount of variation explained by the general model was calculated as the difference in deviances between general and constant models. Similarly, the amount of variation explained by a covariate was calculated as the difference in deviances between the covariate and constant models. The proportion of variation explained by a covariate was calculated as the variation explained by the covariate divided by the total amount of variation; this quantity is analogous to a squared correlation coefficient (r^2, Schemper 1990).

Influence on population growth rate

We used Pradel's reverse-time CMR model (Nichols and Hines 2002; Pradel 1996) to examine the spatiotemporal variation in realized population growth rate. For these analyses, we used mark–recapture data from 42 years, and estimated annual realized population growth rate (λ) and seniority parameter (γ) for the female segment of the population. RELEASE Tests 2 + 3 (implemented in Program MARK) were used to assess the goodness-of-fit of the global model. Spatial and temporal variations in λ were examined as described for multistate models.

To assess the relative importance of different components of reproduction to λ, we used the standardized estimates of each component as a covariate in Program MARK and modeled λ directly as a function of these rates (Nichols and Hines 2002; Nichols et al. 2003). Specifically, we asked: which components of reproduction covary most closely with λ? We used site-specific estimates of breeding probabilities and litter size as covariates for the site effect on λ, and time-specific estimates as covariates for the year effect on λ. We used the slope parameter (β) to relate the variation in the vital rate to variation in λ (Nichols et al. 2003). The proportion of variation explained by each vital rate (r^2) was assessed by comparing model deviance with deviances of constant and general (site- or time-dependent) λ models (e.g., Barbraud et al. 2000; Gaillard et al. 1997). Next, we estimated the relative contributions of survival and recruitment to λ (Nichols et al. 2000). Recruitment is the per capita rate of addition of new individuals to the population per unit time (i.e., the number of individuals entering the population between years i and $i + 1$ per individual already in the population at year i, Pradel 1996). The seniority rate (γ) and its complement ($1 - \gamma$) can be interpreted as the relative contributions of survival and recruitment, respectively, to the realized population growth rate (Nichols et al. 2000). Thus, $\gamma > 0.5$ would indicate a greater relative influence of survival on the realized population growth rate than of recruitment. Pradel's model does not differentiate between reproduction and immigration as different sources of recruitment. However, recruitment in our study population was almost entirely from reproduction (Schwartz et al. 1998).

Results

Survival, recapture, and breeding probabilities

The goodness-of-fit test for the general multistate model provided no evidence of lack of fit ($\chi^2_{265} = 156.9, P > 0.99$), but indicated under-dispersion in the data ($\hat{c} = 0.59$). The most parsimonious model indicated a site effect on the recapture rates of subadult and adult marmots, a site effect on the yearling survival rate, a colony/satellite effect on subadult and adult survival rates, no site effect on the breeding probability of two year olds, and a site effect on the breeding probabilities of subadults and adults (model 4 in Table 1). However, a comparison of models 4 and 2 indicated that there was no strong evidence of a site effect on yearling survival ($\Delta\mathrm{AIC}_c < 2$). We chose the model with no site effect on yearling survival (model 2) for further analyses, because this model had fewer parameters than the model with a site effect on yearling survival (model 4). Recapture rates (mean ± SE) for subadults were 0.94 ± 0.03 in Picnic, 0.89 ± 0.04 in River, 0.71 ± 0.15 in Marmot meadow, 0.43 ± 0.09 in Gothic, and 0.69 ± 0.07 in satellite sites. Recapture rates for adults were 0.99 ± 0.01 in Picnic, 0.96 ± 0.02 in River, 0.97 ± 0.03 in Marmot meadow, 0.87 ± 0.04 in Gothic, and 0.86 ± 0.04 in satellite sites. The survival rate of yearlings did not vary substantially among sites (0.45 ± 0.02), whereas those of subadult and adults varied between colony and satellite sites. Subadult survival rates were 0.65 ± 0.03 in colonies and 0.48 ± 0.04 in satellites, whereas adult survival rates were 0.74 ± 0.02 in colonies and 0.63 ± 0.04 in satellites. We note that these estimates are apparent, rather than true, survival rates, and are confounded by permanent emigration.

The breeding probability of two year olds (ψ_{13}) did not vary substantially among sites (0.25 ± 0.03), whereas those

Table 1 Analysis of spatial variation in state-specific apparent survival, recapture, and transition rates for the yellow-bellied marmot population in Gothic, CO using multistate mark–recapture models

No.	Survival model	Recapture model	Transition model	$\Delta\mathrm{AIC}_c$	AIC_c weight	#*p*	Deviance
1	S_1 (*site*) S_2 (*site*) S_3 (*site*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (*site*) ψ_{23} (*site*) ψ_{33} (*site*)	11.2	0.001	40	3361.4
2	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	0.3	0.212	26	3378.5
3	S_1 (*col/sat*) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	1.4	0.122	27	3377.6
4	S_1 (*site*) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	0.0	0.250	30	3370.2
5	S_1 (.) S_2 (*site*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	0.5	0.190	29	3372.7
6	S_1 (.) S_2 (.)S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	9.1	0.003	25	3389.3
7	S_1 (.) S_2 (*col/sat*) S_3 (.)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	5.3	0.018	25	3385.5
8	S_1 (.) S_2 (*col/sat*) S_3 (*site*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	4.7	0.023	29	3376.9
9	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*col/sat*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	24.6	0.000	23	3408.8
10	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (.)ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	25.4	0.000	22	3411.6
11	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*col/sat*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	5.7	0.015	23	3389.8
12	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (.)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*site*)	12.1	0.001	22	3398.3
13	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (*col/sat*) ψ_{23} (*site*) ψ_{33} (*site*)	1.0	0.149	27	3377.2
14	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (*site*) ψ_{23} (*site*) ψ_{33} (*site*)	6.2	0.011	30	3376.4
15	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (.) ψ_{33} (*site*)	9.2	0.002	22	3395.4
16	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*col/sat*) ψ_{33} (*site*)	11.2	0.001	23	3395.3
17	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (.)	10.2	0.002	22	3396.4
18	S_1 (.) S_2 (*col/sat*) S_3 (*col/sat*)	ρ_2 (*site*) ρ_3 (*site*)	ψ_{13} (.) ψ_{23} (*site*) ψ_{33} (*col/sat*)	11.6	0.001	23	3395.7

Differences in Akaike's information criterion corrected for small sample size ($\Delta\mathrm{AIC}_c$), AIC_c weights, number of parameters (#*p*), and deviances are given for each model. Each age class is indicated as a subscript: yearling ($_1$), subadult ($_2$), and adult ($_3$). Symbols are: S, apparent annual survival rate; ρ, annual recapture rate; ψ_{xy}, transition rate from state x to state y; *site*, site effect; *col/sat*, site effect constrained to be colony or satellite. A period (.) indicates constant value of the parameter (model with intercept only)

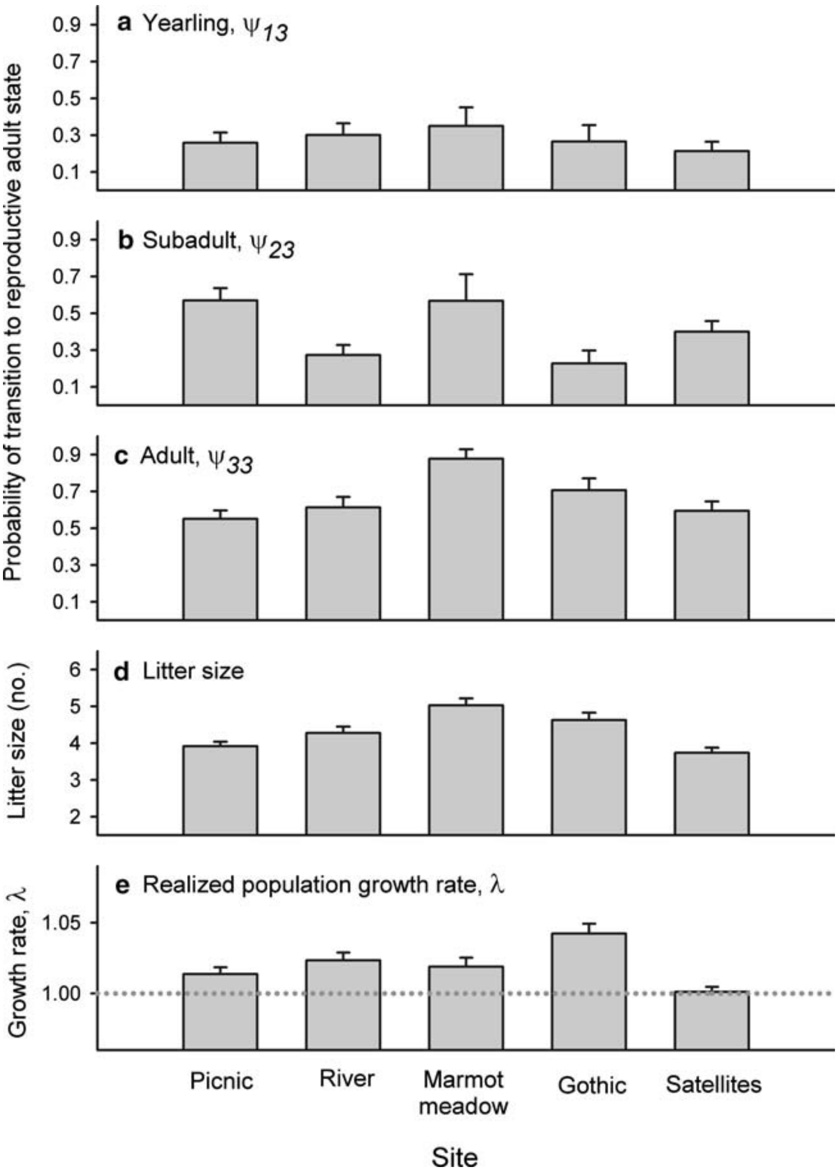

Fig. 2a–e Estimated probabilities of transition (mean + SE) from **a** yearling (ψ_{13}), **b** subadult (ψ_{23}), **c** adult (ψ_{33}) states to the reproductive adult state, as well as **d** litter size and **e** realized population growth rate (λ) for each site (Picnic, River, Marmot meadow, Gothic, and Satellites). Means and SE were estimated using model 14 (ψ_{13}), model 2 (ψ_{23} and ψ_{33}) in Table 1; model 10 (litter size) in Table 3 and model 3 (λ) in Table 4

of subadults (ψ_{23}) and adults (ψ_{33}) did (Fig. 2a–c). Breeding probabilities of adults were generally higher than those of subadults. Breeding probabilities of subadults were 0.57 ± 0.07 in Picnic, 0.27 ± 0.05 in River, 0.57 ± 0.14 in Marmot meadow, 0.23 ± 0.07 in Gothic, and 0.40 ± 0.06 in satellite sites. Breeding probabilities of adults were 0.55 ± 0.05 in Picnic, 0.61 ± 0.06 in River, 0.88 ± 0.05 in Marmot meadow, 0.71 ± 0.06 in Gothic, and 0.59 ± 0.05 in satellite sites.

Next, we investigated temporal variation in breeding probabilities (Table 2). We did not detect substantial temporal variation in the breeding probability of two year olds; this parameter was inestimable for the majority of the sampling periods (model 7 in Table 2; Fig. 3a). On the other hand, breeding probabilities of subadult and adults showed temporal variation (Fig. 3b,c). Breeding probability of subadults varied from 0.12 ± 0.11 (1973–1974) to 0.84 ± 0.14 (1995–1996), and those of adults varied from 0.17 ± 0.15 (1968–1969) to 0.88 ± 0.08 (1987–1988).

Litter size

The test of normality of residuals using the model with the additive effects of year, site and age (model 4 in Table 3) revealed no departure from a normal distribution (Saphiro–Wilk normality test: $W = 0.99$, $p = 0.58$). The most parsimonious model for litter size included the additive effects of site and age, but no year effect (model 7 in Table 3). Estimates of litter size ranged from 3.74 ± 0.14 (satellites) to 5.03 ± 0.19 (Marmot meadow) among sites (Fig. 2d).

Table 2 Analysis of temporal variation in state-specific transition rates for the yellow-bellied marmot population in Gothic, CO using multistate mark–recapture models

No.	Transition model	ΔAIC_c	AIC_c weight	#*p*	Deviance
1	ψ_{13} (.) ψ_{23} (site) ψ_{33} (site)	22.11	0.000	26	3378.5
2	ψ_{13} (year) ψ_{23} (site) ψ_{33} (site)	52.76	0.000	67	3327.1
3	ψ_{13} (.) ψ_{23} (year) ψ_{33} (site)	19.65	0.000	52	3324.0
4	ψ_{13} (.) ψ_{23} (site) ψ_{33} (year)	22.48	0.000	56	3318.9
5	ψ_{13} (.) ψ_{23} (site + year) ψ_{33} (site)	12.57	0.002	56	3309.0
6	ψ_{13} (.) ψ_{23} (site) ψ_{33} (site + year)	6.59	0.036	60	3295.0
7	ψ_{13} (.) ψ_{23} (site + year) ψ_{33} (site + year)	0.00	0.962	91	3226.4

In all of the models, survival and recapture rates are modeled based on model 2 in Table 1: $\{\phi_1\,(.)\ \phi_2\,(c/s)\ \phi_3\,(c/s)\ \rho_2\,(s)\ \rho_3\,(s)\}$. Symbols are: *year*, year effect; *site + year*, additive effects of site and year. Other symbols are defined in Table 1

The average litter size for two-year-old females (3.79 ± 0.16) was slightly lower than that of older females (4.22 ± 0.08). Annual estimates of average litter size varied from 2.60 ± 0.68 (1982) to 5.58 ± 0.44 (2002) (Fig. 3d).

Effects of environmental factors

We examined the influence of environmental factors on breeding probabilities using model 7 in Table 2 (for model comparison tables, see Appendices C and D). Among the extrinsic factors considered, aspect of the site (NE- vs. SW-facing) influenced ψ_{33} ($\beta = 0.58$, 95% CI: 0.16, 1, $r^2 = 0.41$) and ψ_{23} ($\beta = -0.84$, 95% CI: −1.37, −0.32, $r^2 = 0.60$). Breeding probability of adults was higher in southwest-facing sites than in northeast-facing sites; interestingly, this pattern was reversed for subadults. Elevation of sites had a small but negative influence on ψ_{33} ($\beta = -0.29$, 95% CI: 0.17, −0.63, $r^2 = 0.05$), whereas it had a positive influence on ψ_{23} ($\beta = 0.63$, 95% CI: 0.19, 1.08, $r^2 = 0.48$). Resident subadult females had slightly higher breeding probability compared to immigrants ($\beta = 0.43$, 95% CI: −0.11, 0.97, $r^2 = 0.25$).

Parameter ψ_{33} was negatively influenced by the principal component representing the severity of the winter ($\beta = -0.26$, 95% CI: −0.51, 0, $r^2 = 0.07$), and positively influenced by the principal component representing precipitation during previous summer ($\beta = 0.26$, 95% CI: 0.02, 0.5, $r^2 = 0.08$). Parameter ψ_{23} was negatively influenced by the principal component representing the onset of the summer ($\beta = -0.22$, 95% CI: −0.51, 0.8, $r^2 = 0.04$). However, the proportion of temporal variation in ψ_{23} and ψ_{33} explained by the climatic factors (i.e., r^2 values) were very small.

We examined the influence of extrinsic and intrinsic factors on litter size using model 7 in Table 3 (for model comparison tables see Appendix E). Elevation ($\beta = -0.34$, 95% CI: −0.55, −0.12, $r^2 = 0.03$) and aspect ($\beta = 0.55$, 95% CI: 0.27, 0.82, $r^2 = 0.04$) influenced litter size, but the magnitude of this effect was relatively small. Litter size was slightly lower at higher elevations, and slightly higher in southwest facing sites (4.45 ± 0.12) than in northeast facing sites (3.89 ± 0.11). No other extrinsic or intrinsic factors substantially influenced litter size.

Influence on population growth rate

The goodness-of-fit test for Pradel's model indicated no evidence of lack of fit, but revealed a slight under-dispersion in the data ($\chi^2_{237} = 180.9$, $P = 0.997$). We used the most parsimonious model identified for annual survival and recapture rates $\{S\ (s)\ \rho\ (s)\}$, and tested for spatial and temporal variations in the annual realized population growth rate, λ. The most parsimonious model indicated additive effects of site and year on λ (model 1 in Table 4). Site-specific estimates of λ varied from 1.00 ± 0.01 (Satellites) to 1.04 ± 0.01 (Gothic) (Fig. 2e), whereas annual estimates ranged from 0.69 ± 0.04 (1981–1982) to 1.51 ± 0.13 (2003–2004) indicating substantial temporal variation (Fig. 3e). All reproductive parameters influenced both spatial and temporal variations in λ, but the pattern of influence varied among parameters. Litter size had the strongest influence on site-specific variation in λ ($\beta = 0.011$, 95% CI: 0.006, 0.016, $r^2 = 0.56$). The influence of ψ_{13} ($\beta = 0.008$, 95% CI: 0.004, 0.013, $r^2 = 0.35$) was greater than that of ψ_{23} ($\beta = -0.007$, 95% CI: −0.012, −0.001, $r^2 = 0.19$) and ψ_{33} ($\beta = 0.007$, 95% CI: 0.001, 0.013, $r^2 = 0.19$). Interestingly, ψ_{23} negatively influenced λ; where the breeding probability of subadults was higher, λ was generally lower (Fig. 2). Litter size had the strongest influence also on temporal variation in λ ($\beta = 0.077$, 95% CI: 0.055, 0.099, $r^2 = 0.24$). Parameters ψ_{13} ($\beta = 0.091$, 95% CI: 0.055, 0.127, $r^2 = 0.14$), ψ_{23} ($\beta = 0.104$, 95% CI: 0.067, 0.14, $r^2 = 0.17$), and ψ_{33} ($\beta = 0.063$, 95% CI: 0.037, 0.089, $r^2 = 0.12$) also influenced λ, but the magnitude of the influence was small.

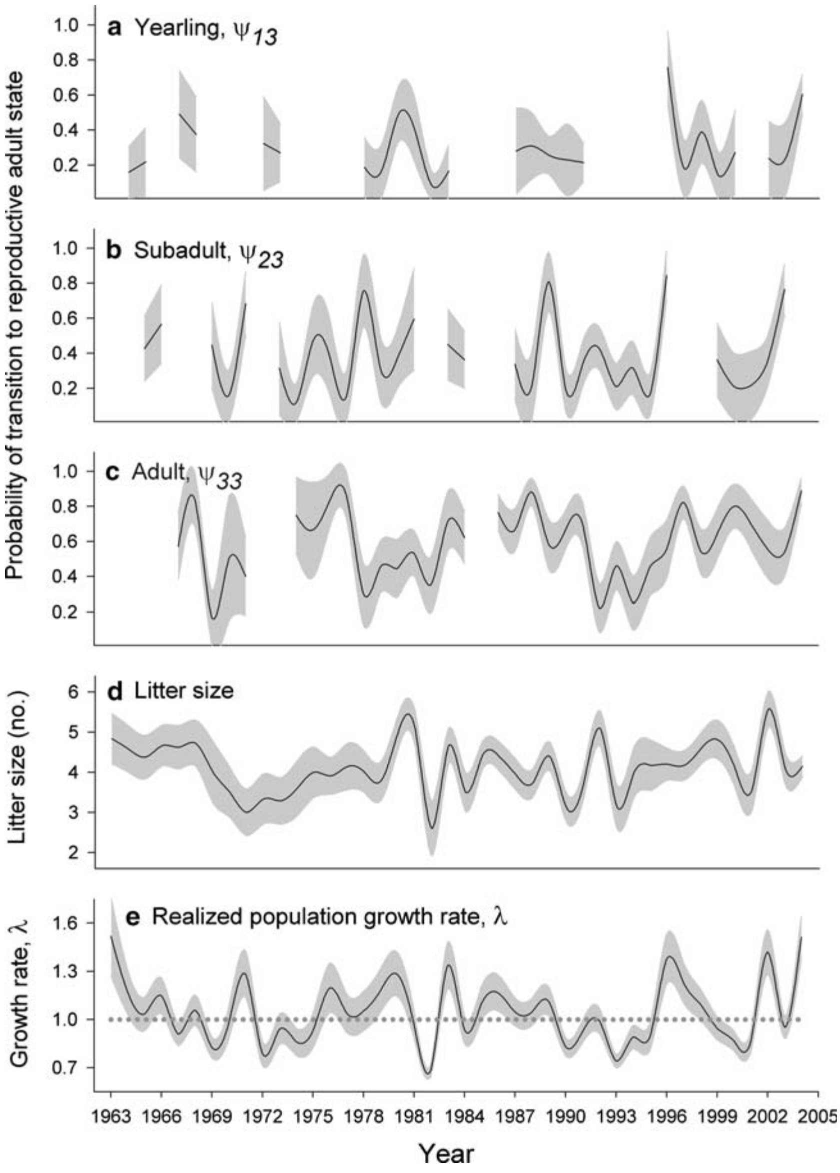

Fig. 3a–e Variation from 1963 to 2005 in probability of transition (mean ± SE) from **a** yearling (ψ_{13}), **b** subadult (ψ_{23}), and **c** adult (ψ_{33}) states to the reproductive adult state, as well as **d** litter size, and **e** realized population growth rate. Mean values (*solid lines*) and standard errors (*shaded area*) were estimated using model 2 (ψ_{13}), model 3 (ψ_{23}) and model 4 (ψ_{33}) in Table 2; model 9 (litter size) in Table 3 and model 2 (λ) in Table 4

The seniority parameter (γ) of the Pradel's reverse time CMR model quantifies the relative contribution of apparent survival, whereas $(1 - \gamma)$ quantifies the relative contribution of recruitment to λ (Nichols and Hines 2002; Nichols et al. 2000). We investigated whether and to what extent the relative contribution of survival and recruitment varied over time or among sites. Annual estimates of γ ranged from 0.39 ± 0.06 (1962–1963) to 0.89 ± 0.05 (1998–1999), indicating temporal variation in the relative contributions of apparent survival and recruitment to λ. Apparent survival contributed to λ more than recruitment did in 34 out of the 43 years of the study ($\gamma > 0.5$). The seniority parameter γ was less variable among sites (Picnic: 0.62 ± 0.02, River: 0.64 ± 0.02, Marmot meadow: 0.56 ± 0.03, Gothic: 0.58 ± 0.02, and Satellites: 0.53 ± 0.02); the contribution of apparent survival was higher than that of recruitment at all sites ($\gamma > 0.5$).

Discussion

Spatiotemporal variation in reproduction is ubiquitous in many wildlife populations, and such variation can have important demographic consequences. However, rigorous investigation of spatiotemporal variation in reproduction and its demographic consequences requires long-term data from several local populations. Our long-term study of yellow-bellied marmots provided adequate data for a thorough examination of the spatiotemporal variation in

Table 3 Analysis of the spatial, temporal, and age-specific variations in litter size for the yellow-bellied marmot population in Gothic, CO, using a general linear model

No.	Model	ΔAIC$_c$	AIC$_c$ weight	*df*	Deviance
1	Litter (*year* + *site* + *age* + *year*:*site* + *year*:*age* + *site*:*age*)	411.0	0.000	207	561.6
2	Litter (*year* + *site* + *age* + *year*:*site* + *year*:*age*)	388.4	0.000	203	564.2
3	Litter (*year* + *site* + *age* + *year*:*site*)	276.6	0.000	177	604.4
4	Litter (*year* + *site* + *age*)	19.1	0.000	49	914.8
5	Litter (*year* + *site*)	27.2	0.000	48	935.3
6	Litter (*year* + *age*)	51.9	0.000	45	1000.4
7	Litter (*site* + *age*)	0.0	0.733	7	1073.1
8	Litter (*site* + *age* + *site*:*age*)	3.3	0.138	11	1062.0
9	Litter (*year*)	57.7	0.000	44	1017.8
10	Litter (*site*)	3.5	0.129	6	1085.7
11	Litter (*age*)	31.3	0.000	3	1165.9
12	Litter (.)	33.9	0.000	2	1177.2

Differences in Akaike's information criterion corrected for small sample size (ΔAIC$_c$), AIC$_c$ weights, and degrees of freedom (*df*) are given for each model. Symbols are: *year*, year effect; *site*, site effect; *age*, age effect. A plus sign (+) denotes additive effects, and a colon (:) denotes interaction effect. A period (.) indicates a constant value of the parameter (model with intercept only)

Table 4 Analysis of the temporal and spatial variations in realized population growth rate of the yellow-bellied marmot population in Gothic, CO, using Pradel's reverse-time models

No.	Model	ΔAIC$_c$	AIC$_c$ weight	#*p*	Deviance
1	$\phi\ (s)\ \rho\ (s)\ \lambda\ (s + t)$	0.00	0.987	56	2498.9
2	$\phi\ (s)\ \rho\ (s)\ \lambda\ (t)$	25.53	0.000	52	2532.7
3	$\phi\ (s)\ \rho\ (s)\ \lambda\ (s)$	106.81	0.000	15	2689.8
4	$\phi\ (s)\ \rho\ (s)\ \lambda\ (.)$	134.04	0.000	11	2725.2
5	$\phi\ (s)\ \rho\ (s)\ \lambda\ (\psi^{s}_{13} + t)$	15.70	0.000	53	2520.8
6	$\phi\ (s)\ \rho\ (s)\ \lambda\ (\psi^{s}_{23} + t)$	21.31	0.000	53	2526.5
7	$\phi\ (s)\ \rho\ (s)\ \lambda\ (\psi^{s}_{33} + t)$	21.34	0.000	53	2526.5
8	$\phi\ (s)\ \rho\ (s)\ \lambda\ (litter^{s} + t)$	8.68	0.013	53	2513.8
9	$\phi\ (s)\ \rho\ (s)\ \lambda\ (s + \psi^{t}_{13})$	82.38	0.000	16	2663.4
10	$\phi\ (s)\ \rho\ (s)\ \lambda\ (s + \psi^{t}_{23})$	76.58	0.000	16	2657.6
11	$\phi\ (s)\ \rho\ (s)\ \lambda\ (s + \psi^{t}_{33})$	86.70	0.000	16	2667.7
12	$\phi\ (s)\ \rho\ (s)\ \lambda\ (s + litter^{t})$	62.62	0.000	16	2643.6

Symbols are: ϕ, overall apparent survival rate; ρ, overall recapture rate; λ, realized population growth rate. Site-specific covariates for λ are site-specific estimates of litter size (*litter*^{s}), and breeding probabilities of two-year-olds (ψ^{s}_{13}), subadults (ψ^{s}_{23}) and adults (ψ^{s}_{33}). Temporal covariates for λ are annual estimates of litter size (*litter*^{t}), and breeding probabilities of two-year-olds (ψ^{t}_{13}), subadults (ψ^{t}_{23}), and adults (ψ^{t}_{33}). Other symbols are defined in Tables 1 and 2

reproductive parameters. Specifically, we addressed the following questions:

- Which components of reproduction varied over time and among sites?
- Which environmental factors potentially influenced the observed variation?
- How did variation in reproductive parameters influence realized population growth rate?

Most reproductive parameters exhibited spatial and/or temporal variations (see also Ozgul et al. 2006), but their influences on population dynamics varied, with some reproductive parameters influencing the realized population growth rate more profoundly than the others.

The breeding probability of two year olds did not vary substantially among sites or years. Overall, only a quarter of two-year-old females reproduced successfully. Breeding probabilities of both subadult (>2-year-old females who have not reproduced before) and adult (>2-year-old females who have reproduced before) showed spatial and temporal variations. Breeding probability of subadults was, on average, higher than that of two-year olds, indicating an age effect on breeding probability. Breeding probability of adults was generally higher than that of subadults (except in the Picnic colony), suggesting that adults were more likely to reproduce than subadults (Armitage 1998). Litter size varied among sites and between two age classes. Two-year-old females, which were all first-time breeders, generally had smaller litters compared to older females, indicating that mother's age and experience might influence litter size (Schwartz et al. 1998).

The pattern of influence of environmental factors on reproductive parameters of yellow-bellied marmots varied among parameters, a finding consistent with similar studies of other species of mammals (e.g., Clutton-Brock et al. 1987; Coulson et al. 2000; Leirs et al. 1997; Stenseth et al. 1996). In general, spatial variation in reproductive parameters was partially explained by the aspect (NE- vs. SW-facing) and elevation. Adult females at southeast-facing and lower elevation sites had slightly higher breeding probabilities, possibly due to longer active seasons in these sites. However, influences of aspect and elevation on subadults are more difficult to explain. Among the extrinsic environmental factors considered, there was evidence for weak effects of winter severity and summer precipitation on temporal variation in adult breeding probability. A change in adult breeding probability is likely to be a consequence of the tradeoff in nutrient allocation between somatic and reproductive efforts in response to changes in extrinsic environmental conditions (Oli 1999). This interpretation is supported by studies of other species of marmots in which adult females skip reproduction for ≥ 1 year, because they are unable to gain sufficient mass to both survive hibernation and reproduce (Armitage and Blumstein 2002).

Not surprisingly, spatial and temporal variations in reproductive rates and survival rates (Ozgul et al. 2006) caused the realized growth rate (λ) of our study population to vary over space and time. We found that litter size was the most influential reproductive parameter on both spatial and temporal variations in λ, followed by breeding probabilities. Interestingly, ψ_{23} negatively influenced λ; one possible explanation for this is that subadult breeding probabilities might be higher at suboptimal sites, where competition for resources and reproductive suppression is lower. Ozgul et al. (2006) found that, among age-specific survival rates, survival of juveniles (0–1 year) had the largest influence on temporal variation in λ. The survival of young animals, litter size, and breeding probabilities are components of recruitment into the adult segment of the population. These parameters are generally more sensitive to extrinsic factors compared to adult survival rates, and exhibit a greater degree of variation over space and time (e.g., Gaillard et al. 2000), and these variations were translated into fluctuations in realized population growth rate. Therefore, recruitment into the adult segment of the population is likely to be the critical determinant of temporal variation in population dynamics of yellow-bellied marmots (Armitage 1973, 2003b).

Sensitivity analysis involving the asymptotic (i.e., long-term) population growth rate has received wide use in ecological studies (e.g., Caswell 2001; Oli and Dobson 2003; Stahl and Oli 2006), but a similar analysis involving the realized population growth rate (observed growth rate of a population from time t to t +1) has received little attention. Nichols et al. (2000) showed that the seniority parameter γ of the reverse time CMR model (Nichols and Hines 2002; Nichols et al. 2000) quantifies the proportional sensitivity (or elasticity sensu Caswell 2001; de Kroon et al. 1986) of the realized population growth rate to the apparent survival, whereas $(1 - \gamma)$ quantifies the elasticity of the growth rate to recruitment (reproduction and immigration). Using this approach, we examined the elasticity of λ to survival and recruitment parameters. We found that λ was proportionately more sensitive to changes in survival than recruitment in 34 out of the 42 years of the study. Although Pradel's model does not differentiate between reproduction and immigration as different sources of recruitment, recruitment in our study population was predominantly from reproduction (Schwartz et al. 1998). These results are similar to the elasticity analysis involving the asymptotic population growth rate, which indicated that the growth rate was proportionately more sensitive to changes in juvenile survival (Oli and Armitage 2004). The similarity in the elasticities of asymptotic and realized population growth rates to demographic parameters is interesting, because these growth rates are estimated and interpreted differently (Caswell 2001; Nichols and Hines 2002).

Although the observations regarding the spatiotemporal variation in reproductive parameters were not surprising, the pattern of variation compared to those observed in age-specific survival rates (Ozgul et al. 2006) was insightful. It has been suggested that vital demographic rates with the greatest potential influence on population growth rate tend to exhibit the least amount of variability (Cairns 1992; Gaillard et al. 1998, 2000; Pfister 1998). Our study and that of Oli and Armitage (2004) showed that both realized and asymptotic growth rates of the yellow-bellied marmot population were generally more sensitive to changes in survival parameters than to reproductive parameters. Thus, we expected reproductive parameters to be more variable than survival parameters over time, and our results were generally consistent with this expectation. In our study population, juvenile survival rates (a demographic parameter to which population growth rate was highly sensitive) varied spatially and temporally, but spatial or temporal variations in survival of adult marmots were insubstantial (Ozgul et al. 2006).

We conclude that components of reproduction in yellow-bellied marmots exhibit both spatial and temporal variations, but that the pattern of variation differs among components. Population growth rate was, in general, more sensitive to changes in survival than to changes in reproduction. However, litter size, abetted by breeding probabilities, contributed substantially to the spatial and temporal variations in the realized population growth rate. Our results, combined with those of Ozgul et al. (2006), indicate that components of recruitment (juvenile survival, litter size and breeding probability) are likely to be the main demographic factors driving the temporal fluctuations in the size of the yellow-bellied marmot population.

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