

SPATIOTEMPORAL VARIATION IN SURVIVAL OF MALE YELLOW-BELLIED MARMOTS

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Variation in vital demographic (e.g., survival) rates of males can influence population dynamics, but the male segment of the population is frequently ignored in ecological studies of mammals. Using a multistate capture–mark–recapture model and 44 years (1962–2006) of data from 17 habitat patches, we investigated spatial and temporal variation in age-specific survival rates of male yellow-bellied marmots (*Marmota flaviventris*) in Colorado. We hypothesized that apparent survival rate of juvenile males would show the greatest spatial and temporal variation as younger animals are more susceptible to extrinsic environmental factors, survival of yearling males would vary over space because of documented spatial variation in dispersal patterns, and survival of adults would be less variable than that of juveniles or yearlings and would vary over space because of demonstrated spatial variation in site quality. Our results revealed that, as predicted, the survival of juveniles varied over time and among sites, whereas that of yearlings varied among sites but not over time. The survival of adults did not vary significantly over time or among sites. We also examined the effects of several intrinsic and extrinsic environmental factors on spatial and temporal variation in survival rates. Our results suggest that male marmots of different ages respond differentially to temporal and spatial variation in environmental factors.

Key words: capture–mark–recapture, demography, male marmots, *Marmota flaviventris*, multistate capture–mark–recapture model, population dynamics, spatial variation, temporal variation, yellow-bellied marmot

Demographic studies of wildlife populations often focus on females, primarily because females play a more substantial role in the production and care of offspring in most mammal species. Consequently, the segment of the population composed of males is often ignored. However, sex-specific differences in demographic traits are common in species with polygynous mating systems and ignoring the demography of males may be problematic (Lindstrom and Kokko 1998). The male segment of a population may influence local and regional population dynamics, especially when there is significant spatial or temporal variation in demographic traits of males (Mysterud et al. 2002; Rankin and Kokko 2006, 2007; Reid et al. 2002). Ignoring males in ecological studies can, therefore, lead to incomplete understanding of, and misleading conclusions regarding, ecological processes.

Although yellow-bellied marmots (*Marmota flaviventris*) have been the subject of long-term ecological research, existing

demographic studies of this species have focused primarily on females in this polygynous species (Armitage 1991; Ozgul et al. 2006). As a result, little is known about vital demographic rates for males or how such rates vary over time or space. Sex-specific differences in dispersal, aggression, and reproductive strategy have been documented for this species (Armitage 1991), and these differences may give rise to intersexual differences in survival (Schwartz et al. 1998). Male and female marmots may respond differently to spatial and temporal variation in extrinsic (ecological) and intrinsic (social) environmental factors and these differences in response may vary among age classes, thereby influencing overall population dynamics. For example, intersexual differences in turnover rates may affect patterns of kin structure and relatedness within social groups. Such local effects can translate into regional effects in terms of genetic structure and population dynamics. Therefore, ignoring the male segment of the population can potentially hinder our understanding of population dynamics at multiple scales.

We investigated spatial and temporal variation in survival of male yellow-bellied marmots in Gothic, Colorado. We hypothesized that apparent survival rate of juveniles would show the greatest spatial and temporal variation because younger animals are most susceptible to extrinsic environmen-

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tal factors (Ozgul et al. 2006). In contrast, survival rates for older age classes should be less temporally variable, because older animals are relatively more robust to variation in extrinsic environmental factors (Ozgul et al. 2006). We expected the survival rate of yearlings to show substantial spatial variation, because yearling marmots disperse and dispersal is often induced by social conditions that vary among sites (Van Vuren 1990; Van Vuren and Armitage 1994). We also expected the apparent survival rate of adults to show site-specific variation, because competition among males is induced by social conditions that vary among sites (Armitage 1974). These hypotheses were tested using data collected over 44 years (1962–2006) from 17 sites within our study area. The results of these analyses were then used to explore the effects of intrinsic and extrinsic environmental factors on spatial and temporal variation in age-specific survival rates. Our findings provide important new insights into the determinants of spatial and temporal variation in survival rates for male yellow-bellied marmots and add significantly to our understanding of the population dynamics of yellow-bellied marmots.

MATERIALS AND METHODS

Study area and species.—The yellow-bellied marmot is a large, diurnal, burrow-dwelling rodent that is widely distributed throughout the mountainous western United States. Yellow-bellied marmots occur in a variety of habitat types ranging from low-elevation meadows to alpine talus slopes (Svendsen 1974). A long-term study of yellow-bellied marmots in the Upper East River Valley of Gunnison County, Colorado, provided capture–mark–recapture data from 17 sites over 44 years (details in Armitage [1991]).

In our study area, sites occupied by marmots varied in size and quality, ranging from 0.01 to 7.2 ha (see Ozgul et al. [2006] for details). The elevations of these sites ranged from 2,700 to 3,100 m above sea level. Habitat characteristics varied within and between sites from rolling grassy meadows to steeper talus slopes. Smaller “satellite” sites typically contained a single adult female, her litter, and sometimes an adult male (Armitage 1991, 1998). In contrast, larger “colony” sites were usually occupied by 1 or more matriline, which typically consisted of 2 or more closely-related adult females, yearlings, and young and with 1 or more territorial males (Armitage 1991, 1998). Colony sites generally contained higher quality habitat that offered more burrow sites and better visibility and food availability (Blumstein et al. 2006). The 4 colony sites included in this study were River (2 adjacent sites that were pooled for analysis), Picnic, Marmot Meadow, and Gothic. Data from 12 satellite sites were pooled because small sample sizes precluded separate analyses of each of these sites.

Field methods and demographic data.—We analyzed capture–mark–recapture data gathered from 1,541 male marmots during 1962–2006. The marmots in our study area were livetrapped during the summer months and individually marked using numbered ear tags (Armitage 1991). Each time a male marmot was captured, its identification number, age, and capture locality were recorded. For data analysis, males

were divided into 3 age classes: juveniles (young of the year), yearlings (1 year old), and adults (≥ 2 years old). Ages for males that were captured as juveniles were known exactly, whereas ages for other males were estimated based on body mass (≤ 2 kg = yearling, > 2 kg = older—Armitage et al. 1976). Our field protocol followed the guidelines of the American Society of Mammalogists (Gannon et al. 2007), and was approved, over the years, by multiple institutional animal care and use committees.

Analyses of survival rates for males.—We used a multistate capture–mark–recapture model (Brownie et al. 1993; Fujiwara and Caswell 2002; Hestbeck et al. 1991; Williams et al. 2001) implemented in the program MARK (White and Burnham 1999) to estimate age-specific annual apparent survival (S) and recapture (ρ) rates. The survival rate, S_x , is the probability of an individual of age-class x surviving the year (until emergence from hibernation). The recapture rate, ρ_x , is the probability that a marmot marked during a previous year is recaptured in age-class x . The transition rate, ψ_{xy} , is the probability of moving from age-class x in 1 year to age-class y in the following year, which is conditional on surviving the period in age-class x . Because all juveniles and yearlings that survive the year move to next age class with probability of 1, juvenile-to-yearling (ψ_{jy}) and yearling-to-adult (ψ_{ya}) transition rates were fixed to 1. Similarly, because all surviving adults stayed as an adult with certainty, the adult-to-adult (ψ_{aa}) transition rate was fixed to 1. Recapture rate of juveniles (ρ_j) was fixed to 0, because juveniles that survive the year will be yearlings the following year; consequently, no individual could be recaptured as a juvenile.

We used the program U-CARE version 2.02 (Choquet et al. 2003) to assess the goodness-of-fit of the general multistate model. The overdispersion parameter (\hat{c}) was calculated as the model deviance divided by the degrees of freedom (Burnham and Anderson 2002). If \hat{c} was greater than 1, we corrected for overdispersion using the calculated \hat{c} . 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. Model comparison was based on differences in AIC_c values (ΔAIC_c); $\Delta AIC_c \leq 2$ indicated no difference between 2 models. We used AIC_c weights to determine the strength of evidence for a given model relative to other models in the model set (Burnham and Anderson 2002). Using this approach, we tested for effects of site and year on age-specific survival rates (S_j , S_y , and S_a) and for the effect of site on recapture rates (ρ_j and ρ_a). We tested for an additive effect of site and year on survival rates, but could not test for the interaction effect between these 2 variables because of the limited size of our data set.

Analyses of environmental correlates.—Using the most-parsimonious models identified by the preceding analyses, we examined the effects of multiple extrinsic (ecological) and intrinsic (social) environmental factors that can potentially influence survival rates (Ozgul et al. 2007). The extrinsic factors examined were elevation of each site and annual measures of average temperature ($^{\circ}C$), spring (April–May) precipitation (cm), average winter (October–March) snow pack

TABLE 1.—Analysis of spatial variation in age-specific apparent survival and recapture rates for male yellow-bellied marmots based on multistate mark–recapture models. The differences in Akaike’s information criterion corrected for small sample size (ΔAIC_c), AIC_c weights, number of parameters (#p), and deviances are given for each model. Each age class is indicated as a subscript: juvenile (*j*), yearling (*y*), and adult (*a*). Symbols are: *S* = apparent annual survival rate, ρ = annual recapture rate, and *site* = site effect. A period (.) indicates a constant value of the parameter (model with intercept only). The transition rate from each age class to the next was fixed to 1. The recapture rate for juveniles was fixed to 0. Only models with AIC_c weight ≥ 0.001 are shown (see Appendix I for the complete table).

No.	Survival model	Recapture model	ΔAIC_c	AIC_c weights	#p	Deviance
1	$S_j(site) S_y(site) S_a(.)$	$\rho_y(site) \rho_a(site)$	0.0	0.188	18	1,382.1
2	$S_j(site) S_y(.) S_a(.)$	$\rho_y(.) \rho_a(site)$	0.6	0.141	16	1,386.7
3	$S_j(site) S_y(site) S_a(site)$	$\rho_y(site) \rho_a(site)$	0.9	0.118	22	1,374.9
4	$S_j(.) S_y(.) S_a(site)$	$\rho_y(.) \rho_a(site)$	1.5	0.089	20	1,379.5
5	$S_j(.) S_y(site) S_a(.)$	$\rho_y(site) \rho_a(site)$	1.7	0.080	14	1,391.9
6	$S_j(site) S_y(.) S_a(.)$	$\rho_y(site) \rho_a(site)$	1.7	0.079	14	1,391.9
7	$S_j(site) S_y(.) S_a(.)$	$\rho_y(.) \rho_a(site)$	2.0	0.069	12	1,396.3
8	$S_j(.) S_y(.) S_a(.)$	$\rho_y(.) \rho_a(site)$	2.4	0.056	10	1,400.7
9	$S_j(.) S_y(site) S_a(site)$	$\rho_y(site) \rho_a(site)$	2.6	0.050	18	1,384.7
10	$S_j(site) S_y(.) S_a(site)$	$\rho_y(site) \rho_a(site)$	2.7	0.050	18	1,384.7
11	$S_j(site) S_y(.) S_a(site)$	$\rho_y(.) \rho_a(site)$	2.9	0.044	16	1,389.0
12	$S_j(.) S_y(.) S_a(site)$	$\rho_y(site) \rho_a(site)$	3.4	0.035	14	1,393.6

(cm), average winter (October–March) temperature ($^{\circ}C$), length of the growing season (days), and the Julian calendar date of snow melt. The intrinsic factors examined were the average number of juveniles, yearling males, adult males, and adult females at each site. Details regarding the methods used to quantify these variables are provided in Ozgul et al. (2007). The effect of each of these parameters on survival rates was examined by modeling the logit of each rate as a linear function of the extrinsic and intrinsic variables using the program MARK. We investigated the influence of each of these variables separately. The influence of each variable on a model parameter was evaluated by examining the ΔAIC_c between models with and without the variable; $\Delta AIC_c > 2$ was interpreted as evidence of a significant relationship between the variable and the model parameter. The 95% confidence interval (95% CI) for the slope parameter (β) was used to indicate the direction and magnitude of this relationship (e.g., Blums et al. 2003; Ozgul et al. 2006). Results are reported as mean $\pm SE$.

RESULTS

Spatial variation in survival of males.—The goodness-of-fit test provided no evidence for lack of fit ($\chi^2 = 89.1, df = 141, P > 0.99$) and thus we did not correct for overdispersion in the data. The candidate model set examined is shown in Table 1; all specific models referred to in the “Results” are included in this table. The most-parsimonious model (model 1) provided evidence for an effect of site on recapture rates of both yearlings and adults. Recapture rates of yearlings (the probability of recapturing juveniles in the yearling stage, given that juveniles survive the year) were ≥ 0.90 for all sites (Fig. 1) and were generally higher than recapture rates of adults, which ranged from 0.56 ± 0.10 in Gothic to 1.00 ± 0.00 in Marmot Meadow. In general, recapture rates were the lowest in Gothic. Model 2, which had a level of support similar to that for model 1 (AIC_c weight = 0.141 versus 0.188; Table 1), indicated that the effect of site on recapture rate of yearlings was not substantial. Based on model 2, the overall recapture rate of year-

lings was estimated at 0.96 ± 0.02 . As indicated previously, recapture rates of juveniles were fixed to 0.

We next tested for spatial variation in age-specific survival rates. Survival rates of juveniles and adults were, in general, higher than survival rates of yearlings (Fig. 2). It is important to note that these were estimates of apparent, rather than true, survival and thus likely included examples of permanent emigration that could not be distinguished from mortality. The most-parsimonious model (model 1) indicated an effect of site on survival rates for juveniles and yearlings, but not for adults (Table 1). However, 2 other models with $\Delta AIC_c < 1$ indicated no evidence of an effect of site on survival rates of juveniles (model 5) or yearlings (model 6). Conversely, a competing model with $\Delta AIC_c < 1$ indicated a possible effect of site on survival rates of adults (model 3). Given these apparently conflicting outcomes, we examined the sum of AIC_c weights (the strength of evidence) for the models that included a significant site effect. These values were 0.778 for juveniles, 0.668 for yearlings, and 0.386 for adults (Table 1), providing relatively strong evidence for an effect of site on survival rates

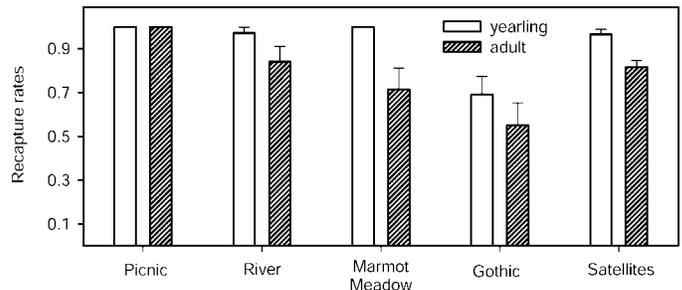


FIG. 1.—Site-specific recapture rates (mean $\pm SE$) for yearling and adult male yellow-bellied marmots. Data are from 4 colony and 12 satellite sites; data from the latter were pooled for analysis. Recapture rates were estimated using model 1 in Table 1. Recapture rates for yearlings in Picnic and Marmot Meadow sites were 1.00 and thus standard errors are not presented for these sites.

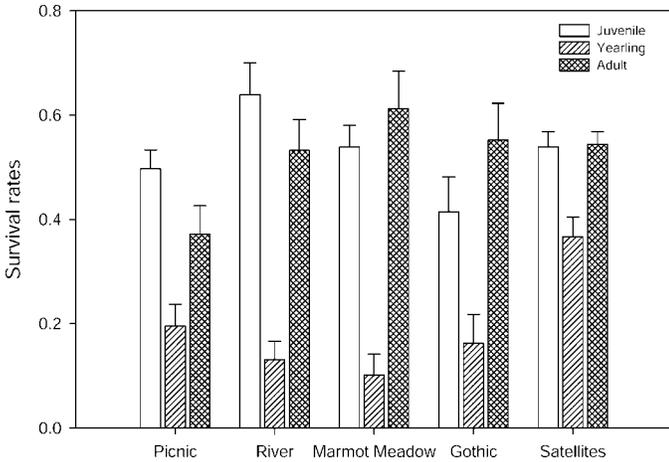


FIG. 2.—Site-specific estimates (mean \pm SE) of apparent survival rates of juvenile, yearling, and adult male yellow-bellied marmots. Data are from 4 colony and 12 satellite sites; data from the latter were pooled for analysis. Mean values and standard errors were estimated using the most-parsimonious model that included an effect of site on survival (juveniles: model 2; yearlings and adults: model 1); all models are shown in Table 1.

of juveniles and yearlings, but not on survival rates of adults. Site-specific estimates for apparent survival rates ranged from 0.41 ± 0.06 (Gothic) to 0.60 ± 0.06 (River) for juveniles, from 0.12 ± 0.03 (Marmot Meadow and River) to 0.26 ± 0.04 (Picnic) for yearlings, and from 0.37 ± 0.07 (Marmot Meadow) to 0.55 ± 0.05 (River) for adults.

Temporal variation in survival of males.—Using the most-parsimonious model identified above, we investigated annual variation in age-specific survival rates (Table 2). Only the survival rates of juveniles showed substantial variation among years. Annual estimates ranged from 0.18 ± 0.07 (1981) to 0.93 ± 0.21 (1995) for juveniles, from 0.04 ± 0.04 (2003) to 0.43 ± 0.36 (1983) for yearlings, and from 0.17 ± 0.16 (1963) to 0.73 ± 0.15 (2002) for adults (Fig. 3). We did not test for temporal variation in recapture rates, because similar studies on female marmots indicated no evidence for temporal variation in recapture rates of yearling or older age classes and because we did not have enough data to test for additive effects of year and site on recapture rates.

TABLE 2.—Analysis of temporal variation in age-specific apparent survival rates for male yellow-bellied marmots. All the models include the recapture rate model $\{\rho_y(\text{site}) \rho_a(\text{site})\}$. Year = year effect and site + year = additive effects of site and year. Other symbols are defined as in Table 1.

No.	Survival model	ΔAIC_c	AIC _c weights	#p	Deviance
1	$S_j(\text{year}) S_y(\text{site}) S_a(\cdot)$	0.0	0.670	55	1,259.6
2	$S_j(\text{site} + \text{year}) S_y(\text{site}) S_a(\cdot)$	1.4	0.330	59	1,252.6
3	$S_j(\text{site}) S_y(\text{site}) S_a(\cdot)$	45.9	0.000	18	1,382.1
4	$S_j(\text{site}) S_y(\text{site} + \text{year}) S_a(\cdot)$	48.6	0.000	52	1,314.5
5	$S_j(\text{site}) S_y(\text{year}) S_a(\cdot)$	49.9	0.000	48	1,324.2
6	$S_j(\text{site}) S_y(\text{site}) S_a(\text{year})$	92.0	0.000	60	1,341.1

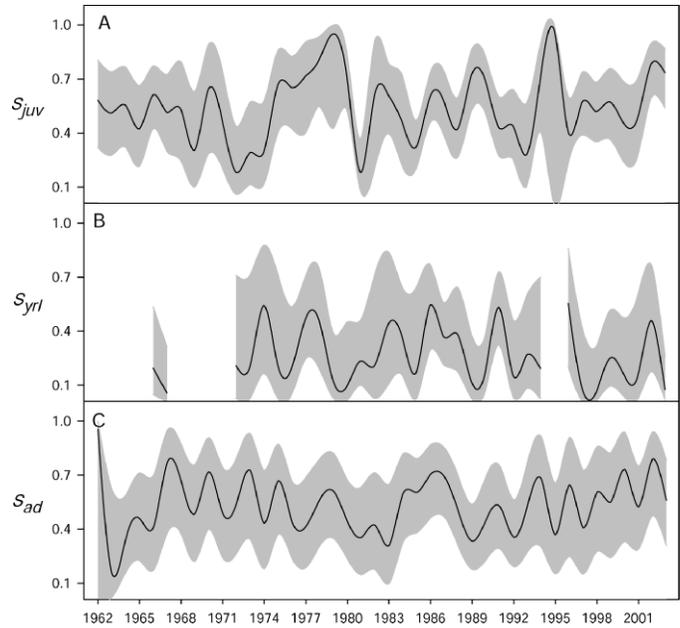


FIG. 3.—Annual estimates of apparent survival rates for A) juvenile, B) yearling, and C) adult male yellow-bellied marmots. Mean values (solid lines) and 95% confidence intervals (shaded areas) were estimated using the most-parsimonious model that included an effect of year on survival (juveniles: model 1; yearlings: model 2; adults: model 5); all models are shown in Table 2. Gaps in survival rate of yearlings reflect low sample sizes, which made model parameters inestimable because of small sample sizes for those years.

Effects of environmental factors.—We examined the influence of environmental factors on age-specific survival rates (see Appendices II and III for model comparisons). Among the extrinsic factors considered, only the elevation of sites had a significant positive influence on survival of yearlings ($\beta = 0.006$, 95% CI: 0.002, 0.011). All intrinsic factors had a significant positive influence on survival of yearlings; survival of yearlings increased with the average number of adult males ($\beta = 0.50$, 95% CI: 0.23, 0.77), adult females ($\beta = 0.17$, 95% CI: 0.05, 0.29), and yearling males ($\beta = 0.41$, 95% CI: 0.01, 0.82) at a given site. There was no evidence for the influence of environmental factors on survival rates of juveniles or adults.

DISCUSSION

Variation in age-specific demographic rates for female yellow-bellied marmots has been thoroughly examined (Ozgul et al. 2006, 2007). However, little is known about demographic rates for male marmots. Our goal was to investigate variation over time and space in the age-specific survival of male yellow-bellied marmots using data from a long-term study. As predicted, we found that survival rates for adult males did not vary substantially over time or among sites and were less variable than those for juvenile or yearling males; survival rates for yearling males varied among sites, but not over time; and survival rates for juvenile males varied substantially over both time and space and were more variable than survival rates for marmots of other ages. These findings indicate that the demo-

graphic rates for male yellow-bellied marmots are variable among age classes and may be influenced by environmental conditions.

Among female yellow-bellied marmots, survival of adults is higher than that of other age classes (Ozgul et al. 2006), a pattern also evident in other species of ground-dwelling sciurids (e.g., Bronson 1979; Farand et al. 2002). In male yellow-bellied marmots, however, overall apparent survival of adults was not greater than that of juveniles. This sex-specific difference in survival of adults may be related to intersexual differences in reproductive strategies; the greater degree of aggression among adult males (potentially leading to death or permanent emigration) may cause higher turnover rates among these animals than among adult females (Armitage 1998; Schwartz et al. 1998). An important determinant of lifetime reproductive success for males is the length of time that an individual holds a territory (Armitage 2004b). Complete reproductive failure may occur at a site when no new male replaces a male that failed to return or when the new male immigrates too late for reproduction to occur (Armitage 2003a). Thus, survival of adult males has critical consequences for reproductive success of females, and therefore, the overall dynamics of the population.

Survival rates for yearling males were, in general, lower than those for adults and juveniles and varied among sites; this pattern was consistent with differences in the age-specific survival rates for female yellow-bellied marmots (Ozgul et al. 2006). However, we note that our estimated survival rates were apparent, rather than true, survival rates, meaning that these rates likely included data for individuals that emigrated. Yearling males are much more likely to disperse than are juveniles or adults (Van Vuren 1990; Van Vuren and Armitage 1994). This dispersal pattern can be attributed to the agonistic behavior of adult males toward yearlings (Armitage 1974). Adult males do not tolerate potential reproductive competition from yearling males, thus making the dispersal of yearling males inevitable (Armitage 1991). Frequent dispersal by yearling males may have contributed to lower apparent survival rates for these animals compared to adults or juveniles. Surprisingly, our analysis of environmental factors indicated that yearling males survived better at sites with larger numbers of yearlings and adults, a result that seems to contradict the influence of adult males on dispersal of yearlings and, potentially, survival. One possible explanation is that, as the colony size increases, the territory that an adult male has to defend gets larger and so does the number of adult males competing with each other (Armitage 1974). Under such circumstances, yearling marmots may be better able to avoid the adult males and stay in the colony. At the same time, it is possible that sites with more animals may be of better quality, which also could affect survival of yearlings.

Among the 3 age classes examined, only the survival of juvenile males showed substantial temporal variation. This variation was most likely due to temporal differences in extrinsic climatic conditions, because younger animals are more susceptible to climatic influences than are yearlings or adults. Mortality of juveniles tends to be high if a short growing

season is followed by a long, severe winter (Armitage 1994, 2003b; Armitage and Downhower 1974). Ozgul et al. (2006) reported that the survival of juvenile female marmots in our study population varied significantly over time, and that this variation was influenced by the length of permanent snow cover (see also Schwartz et al. 1998). However, we found no evidence that extrinsic environmental factors influenced survival of juvenile males. Multiple extrinsic and intrinsic environmental factors may act synergistically to influence survival rates of juveniles, and hence the effects of individual factors may be insufficient to explain the observed variation in juvenile survival.

One factor not considered in this study was predation, which is also an important mortality factor for marmots that can vary across sites and over time. Previous studies reported pulses of predator activity in colonies of yellow-bellied marmots (Armitage 2004a), and habitat features that offer detection of predators have been found to be important determinants of the persistence of colonies of marmots (Blumstein et al. 2006). Younger animals are often more susceptible to predation (Armitage 2004a; Van Vuren 2001). If predation pressure varied over time and among sites then this variation may have contributed to the spatial and temporal variation in survival of male marmots at our study sites (Van Vuren 2001). Future analyses of sex- and age-specific differences in demography should consider the role of predation pressure in determining rates of survival.

In conclusion, our analyses revealed that survival rates of male yellow-bellied marmots exhibited significant spatial and temporal variation and that the nature of this variation differed among age classes, with survival of adults being the least variable. Our findings also revealed that extrinsic and intrinsic environmental factors affected the survival of yearling males. Collectively, these results suggest that male yellow-bellied marmots of different ages respond differentially to spatiotemporal variation in the environment. While the survival rates of juvenile marmots were similar between sexes, the apparent survival of adult males was substantially lower than that of adult females, mostly due to sex-specific differences in reproductive strategies (Armitage 1998). Sex-specific differences in vital demographic rates may have important consequences for population dynamics (Lindstrom and Kokko 1998; Myrsetrud et al. 2002; Rankin and Kokko 2007, 2006; Reid et al. 2002) and should be considered as part of studies of mammalian behavior and ecology.

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APPENDIX I

Analysis of spatial variation in age-specific apparent survival and recapture rates for male yellow-bellied marmots based on multistate mark-recapture models. The differences in Akaike’s information criterion corrected for small sample size (ΔAIC_c), AIC_c weights, number of parameters (#p), and deviances are given for each model. Each age class is indicated as a subscript: juvenile (*j*), yearling (*y*), and adult (*a*). Symbols are: *S* = apparent annual survival rate, ρ = annual recapture rate, and *site* = site effect. A period (.) indicates a constant value of the parameter (model with intercept only). The transition rate from each age class to the next was fixed to 1. The recapture rate for juveniles was fixed to 0. All models (AIC_c weight ≥ 0) are shown.

No.	Survival model	Recapture model	ΔAIC_c	AIC_c weights	#p	Deviance
1	$S_j (site) S_y (site) S_a (.)$	$\rho_y (site) \rho_a (site)$	0.0	0.188	18	1,382.1
2	$S_j (site) S_y (site) S_a (.)$	$\rho_y (.) \rho_a (site)$	0.6	0.141	16	1,386.7
3	$S_j (site) S_y (site) S_a (site)$	$\rho_y (site) \rho_a (site)$	0.9	0.118	22	1,374.9
4	$S_j (site) S_y (site) S_a (site)$	$\rho_y (.) \rho_a (site)$	1.5	0.089	20	1,379.5
5	$S_j (.) S_y (site) S_a (.)$	$\rho_y (site) \rho_a (site)$	1.7	0.080	14	1,391.9
6	$S_j (site) S_y (.) S_a (.)$	$\rho_y (site) \rho_a (site)$	1.7	0.079	14	1,391.9
7	$S_j (site) S_y (.) S_a (.)$	$\rho_y (.) \rho_a (site)$	2.0	0.069	12	1,396.3
8	$S_j (.) S_y (.) S_a (.)$	$\rho_y (site) \rho_a (site)$	2.4	0.056	10	1,400.7
9	$S_j (.) S_y (site) S_a (site)$	$\rho_y (site) \rho_a (site)$	2.6	0.050	18	1,384.7
10	$S_j (site) S_y (.) S_a (site)$	$\rho_y (site) \rho_a (site)$	2.7	0.050	18	1,384.7
11	$S_j (site) S_y (.) S_a (site)$	$\rho_y (.) \rho_a (site)$	2.9	0.044	16	1,389.0
12	$S_j (.) S_y (.) S_a (site)$	$\rho_y (site) \rho_a (site)$	3.4	0.035	14	1,393.6
13	$S_j (site) S_y (site) S_a (site)$	$\rho_y (site) \rho_a (.)$	14.8	0.000	19	1,394.8
14	$S_j (site) S_y (site) S_a (.)$	$\rho_y (site) \rho_a (.)$	15.2	0.000	15	1,403.3
15	$S_j (site) S_y (site) S_a (site)$	$\rho_y (.) \rho_a (.)$	15.4	0.000	17	1,399.5
16	$S_j (site) S_y (site) S_a (.)$	$\rho_y (.) \rho_a (.)$	15.8	0.000	13	1,408.0
17	$S_j (site) S_y (.) S_a (site)$	$\rho_y (.) \rho_a (.)$	15.8	0.000	13	1,408.0
18	$S_j (site) S_y (.) S_a (site)$	$\rho_y (site) \rho_a (.)$	16.2	0.000	15	1,404.3
19	$S_j (site) S_y (.) S_a (.)$	$\rho_y (.) \rho_a (.)$	16.4	0.000	9	1,416.7
20	$S_j (.) S_y (site) S_a (site)$	$\rho_y (site) \rho_a (.)$	16.5	0.000	15	1,404.7
21	$S_j (site) S_y (.) S_a (.)$	$\rho_y (site) \rho_a (.)$	16.7	0.000	11	1,413.0
22	$S_j (.) S_y (site) S_a (.)$	$\rho_y (site) \rho_a (.)$	16.9	0.000	11	1,413.2
23	$S_j (.) S_y (.) S_a (site)$	$\rho_y (site) \rho_a (.)$	18.6	0.000	11	1,414.9
24	$S_j (.) S_y (.) S_a (.)$	$\rho_y (site) \rho_a (.)$	19.4	0.000	7	1,423.7
25	$S_j (.) S_y (site) S_a (.)$	$\rho_y (.) \rho_a (site)$	21.2	0.000	12	1,415.4
26	$S_j (.) S_y (site) S_a (site)$	$\rho_y (.) \rho_a (site)$	22.1	0.000	16	1,408.2
27	$S_j (.) S_y (.) S_a (.)$	$\rho_y (.) \rho_a (site)$	22.6	0.000	8	1,424.9
28	$S_j (.) S_y (.) S_a (site)$	$\rho_y (.) \rho_a (site)$	23.4	0.000	12	1,417.7
29	$S_j (.) S_y (site) S_a (site)$	$\rho_y (.) \rho_a (.)$	36.0	0.000	13	1,428.2
30	$S_j (.) S_y (site) S_a (.)$	$\rho_y (.) \rho_a (.)$	36.4	0.000	9	1,436.7
31	$S_j (.) S_y (.) S_a (site)$	$\rho_y (.) \rho_a (.)$	36.5	0.000	9	1,436.8
32	$S_j (.) S_y (.) S_a (.)$	$\rho_y (.) \rho_a (.)$	37.2	0.000	5	1,445.5

APPENDIX II

Effects of site-specific environmental covariates (elevation and intrinsic factors) on age-specific survival rates of male yellow-bellied marmots. All the models include the recapture rate model $\{\rho_y(\text{site}) \rho_a(\text{site})\}$. The general and constant models for each age class are indicated in bold. The environmental covariates are *elevation* = site elevation, *adult females* = average number of adult females, *adult males* = average number of adult males, *yearling males* = average number of yearling males, and *juveniles* = average number of juveniles at each site. Other symbols are defined in Tables 1 and 2.

No.	Survival model	ΔAIC_c	AIC _c weight	#p	Deviance
Juveniles					
1	$S_j(\text{site}) S_y(\text{site}) S_a(\text{site})$	7.2	0.014	22	1,374.9
2	$S_j(\text{adult females}) S_y(\text{site}) S_a(\text{site})$	9	0.006	20	2,990.0
3	$S_j(\text{adult males}) S_y(\text{site}) S_a(\text{site})$	10.3	0.003	20	2,991.3
4	$S_j(\text{elevation}) S_y(\text{site}) S_a(\text{site})$	9.5	0.004	19	2,992.5
5	$S_j(\text{juveniles}) S_y(\text{site}) S_a(\text{site})$	9	0.006	19	2,992.0
6	$S_j(\cdot) S_y(\text{site}) S_a(\text{site})$	8.9	0.006	18	1,384.7
Yearlings					
7	$S_j(\text{site}) S_y(\text{site}) S_a(\text{site})$	7.2	0.014	22	1,374.9
8	$S_j(\text{site}) S_y(\text{yearling males}) S_a(\text{site})$	6.8	0.017	19	2,989.8
9	$S_j(\text{site}) S_y(\text{adult females}) S_a(\text{site})$	5.6	0.031	20	2,986.6
10	$S_j(\text{site}) S_y(\text{adult males}) S_a(\text{site})$	0	0.506	20	2,981.0
11	$S_j(\text{site}) S_y(\text{elevation}) S_a(\text{site})$	1.2	0.278	19	2,984.3
12	$S_j(\text{site}) S_y(\cdot) S_a(\text{site})$	8.9	0.006	18	1,384.7
Adults					
13	$S_j(\text{site}) S_y(\text{site}) S_a(\text{site})$	7.2	0.014	22	1,374.9
14	$S_j(\text{site}) S_y(\text{site}) S_a(\text{adult females})$	5.9	0.026	20	2,986.9
15	$S_j(\text{site}) S_y(\text{site}) S_a(\text{adult males})$	5.7	0.029	19	2,988.7
16	$S_j(\text{site}) S_y(\text{site}) S_a(\text{elevation})$	7.3	0.013	19	2,990.4
17	$S_j(\text{site}) S_y(\text{site}) S_a(\text{juveniles})$	9.2	0.005	21	2,988.2
18	$S_j(\text{site}) S_y(\text{site}) S_a(\cdot)$	6.2	0.023	18	1,382.1

APPENDIX III

Effect of time-specific environmental covariates on age-specific survival rates of male yellow-bellied marmots. All the models include the recapture rate model $\{\rho_y (site) \rho_a (site)\}$. The general and constant models for each age class are indicated in bold. Because some of the climatic data were available after 1975, related models include year effect for years 1962–1974 ($year_{62-74}$). The covariates are: *smr.temp* = early summer (April–May) temperature (°C), *smr.prec* = early summer precipitation (cm), *snw.pck* = average winter snow pack (cm), *wtr.temp* = average winter temperature (°C), *grw.ssn* = length of the growing season (days), and *snw.mlt* = the Julian date of snow melt. Other symbols are defined in Tables 1 and 2.

No.	Survival model	ΔAIC_c	AIC _c weight	#p	Deviance
Juveniles					
1	$S_j (site + year) S_y (site) S_a (site)$	0.0	1.000	63	1,245.4
2	$S_j (site + smr.prec) S_y (site) S_a (site)$	45.6	0.000	23	1,374.2
3	$S_j (site + smr.temp) S_y (site) S_a (site)$	44.7	0.000	23	1,373.4
4	$S_j (site) S_y (site) S_a (site)$	44.2	0.000	22	1,374.9
5	$S_j (site + year_{62-74} + snw.pck) S_y (site) S_a (site)$	36.5	0.000	35	1,340.5
6	$S_j (site + year_{62-74} + wtr.temp) S_y (site) S_a (site)$	39.4	0.000	35	1,343.4
7	$S_j (site + year_{62-74} + grw.ssn) S_y (site) S_a (site)$	38.2	0.000	35	1,342.2
8	$S_j (site + year_{62-74} + snw.mlt) S_y (site) S_a (site)$	39.6	0.000	35	1,343.6
9	$S_j (site + year_{62-74}) S_y (site) S_a (site)$	37.7	0.000	34	1,343.8
Yearlings					
10	$S_j (site) S_y (site + year) S_a (site)$	46.9	0.000	56	1,307.1
11	$S_j (site) S_y (site + smr.prec) S_a (site)$	44.0	0.000	23	1,372.6
12	$S_j (site) S_y (site + smr.temp) S_a (site)$	46.0	0.000	23	1,374.6
13	$S_j (site) S_y (site) S_a (site)$	44.2	0.000	22	1,374.9
14	$S_j (site) S_y (site + year_{62-74} + snw.pck) S_a (site)$	34.9	0.000	29	1,351.3
15	$S_j (site) S_y (site + year_{62-74} + wtr.temp) S_a (site)$	36.7	0.000	29	1,353.1
16	$S_j (site) S_y (site + year_{62-74} + grw.ssn) S_a (site)$	36.9	0.000	29	1,353.3
17	$S_j (site) S_y (site + year_{62-74} + snw.mlt) S_a (site)$	35.1	0.000	29	1,351.4
18	$S_j (site) S_y (site + year_{62-74}) S_a (site)$	35.0	0.000	28	1,353.4
Adults					
19	$S_j (site) S_y (site) S_a (site + year)$	91.2	0.000	64	1,334.5
20	$S_j (site) S_y (site) S_a (site + smr.prec)$	45.5	0.000	23	1,374.1
21	$S_j (site) S_y (site) S_a (site + smr.temp)$	45.9	0.000	23	1,374.5
22	$S_j (site) S_y (site) S_a (site)$	44.2	0.000	22	1,374.9
23	$S_j (site) S_y (site) S_a (site + year_{62-74} + snw.pck)$	57.4	0.000	35	1,361.4
24	$S_j (site) S_y (site) S_a (site + year_{62-74} + wtr.temp)$	57.1	0.000	35	1,361.1
25	$S_j (site) S_y (site) S_a (site + year_{62-74} + grw.ssn)$	57.2	0.000	35	1,361.2
26	$S_j (site) S_y (site) S_a (site + year_{62-74} + snw.mlt)$	57.1	0.000	35	1,361.0
27	$S_j (site) S_y (site) S_a (site + year_{62-74})$	55.4	0.000	34	1,361.4