Ethology Ecology & Evolution 21: 381-392, 2009

Elevation variation in life-history characteristics of populations of yellow-bellied marmots (*Marmota flaviventris*)

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Received 6 September 2008, accepted 19 May 2009

We examined life history characteristics of populations of yellow-bellied marmots (*Marmota flaviventris*) at 2900 m elevation and 3400 m elevation to test hypotheses about effects of elevation on life history traits. The accumulation of fat is strongly influenced by short growing seasons and marmots living at high elevations often have shorter active seasons than populations at lower elevations due to prolonged snow cover. We compared growth rates and reproductive effort of marmots amongst age and sex classes from the two elevation sites. Growth rates of yellow-bellied marmots vary significantly with sex, age, and location. Juvenile growth rates were significantly higher at lower elevation sites. Yearlings at the high elevation site had significantly higher growth rates compared to low elevation yearlings. Low elevation yearling males were twice the size of high elevation yearling males at the beginning of the summer; the higher growth rates in high elevation populations reduced the mass differences between the two groups prior to hibernation. Adult growth rates and masses were not significantly different between elevation sites. At higher elevation, females did not reproduce in consecutive years. Differences in growth rates between elevation sites may be explained by reproductive status and time allocated to foraging.

KEY WORDS: *Marmota flaviventris*, marmot, growth rates, life history, frequency of reproduction.

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INTRODUCTION

Life history models assume that resources are finite and must be allocated among reproduction, maintenance, and growth (Boyce 1988). Life-history evolution will be impacted by changes in environmental conditions such as those associated with variation in climate, predators, food availability, latitude, and length of active season (Reznick & Endler 1982, Dobson & Murie 1987, Oli et al. 2001, Arendt & Reznick 2005). The availability of energy is an example of a stochastic environmental variable that has received a great deal of attention as an influence on population dynamics (Boutin 1990, O'Donoghue & Krebs 1992). However, ecological factors, such as climate, local density, and active season length may reduce the importance of available food resources on population dynamics, community structure, and life history traits that are observed in nature (Ward & Armitage 1981, Abdellatif et al. 1982, Arcese & Smith 1988, White 1993, Castle & Wunder 1995, Hubbs & Boonstra 1997).

The availability of food is especially important for hibernators. Ground squirrels must gain sufficient mass during the active season to survive hibernation (Armitage et al. 1976, Murie & Boag 1984). However when a group of marmots were supplemented with food, growth rates increased and immergence mass of supplemented animals was significantly higher than control groups, but food addition had no effect on over-winter survival rates (Woods & Armitage 2003a). Furthermore, the addition of food did not affect other life history characteristics, such as female recruitment, age of first reproduction, or reproductive effort, such as increased litter size or weaning masses of young (Woods & Armitage 2003b). Food addition may only have an impact on populations that are naturally limited by food availability, such as may exist at higher elevations. Female yellow-bellied marmots do not wean litters in consecutive years at higher elevations (Andersen et al. 1976, Johns 1978). Changes in life history characteristics may be in response to shorter growing seasons and limited food availability at higher elevations.

Yellow-bellied marmots (*Marmota flaviventris*) are large, diurnal, ground-dwelling squirrels that occur throughout alpine and subalpine meadows or semidesert grasslands of western North America (Frase & Hoffmann 1980). The annual cycle of yellow-bellied marmots is marked by hibernation during long winters. Marmots must carry out maintenance, growth, and reproduction in a relatively short active season (Davis 1976). The variation of habitat, length of active season and food resource availability in the distribution of this species makes it an ideal subject for examining the role of variation of environmental conditions on life-history traits. Yellow-bellied marmots have been studied extensively since 1962 in the East River Valley of Gunni-

son County and the life history characteristics and demography of these animals under natural conditions have been well documented (e.g., ARMITAGE & DOWNHOWER 1974, ARMITAGE 1991, SCHWARTZ et al. 1998). Marmot habitat in the East River Valley is characterized by subalpine meadows, which may be bordered by aspen-fir forests, steep cliffs and interspersed with large shrubs and major clumps of rocky outcrops where active burrows are located (ARMITAGE 1974). Duration of snow cover in the East River Valley varies by as much as 3 weeks and is negatively correlated with frequency of reproduction, mean litter size, and juvenile mass (VAN VUREN & ARMITAGE 1991).

Marmot populations in regions with longer snow cover, such as North Pole Basin, are expected to have life history characteristics consistent with the impact of a shorter growing season on various aspects of reproduction. North Pole Basin is characterized by open alpine meadows with vegetation patchily distributed over half the study area. A creek flows through the center of the basin where clumps of willow are distributed. It is at an elevation of 3400 m, compared to East River Valley sites at 2900 m.

The purpose of this study was to compare the life history characteristics of low and high elevation yellow-bellied marmots. We examined growth rates of individuals across age and reproductive class, weaning mass, and differences in time allocated to various behaviors that may account for differences in growth rates.

METHODS

We studied marmot populations at two colony sites in the Elk Mountains of Gunnison County, Colorado; two sites in the upper East River Valley near the Rocky Mountain Biological Laboratory at an elevation of 2900 m and three high elevation sites in North Pole Basin at an elevation of 3400 m.

The lower elevation sites, Cliff and North Picnic, are steep slopes located along the East River. The first site, Cliff, is located on a cliff face adjacent to sloping meadows. Burrows are located within the rocky outcrops. The second site, North Picnic, is a large meadow with major grouping of rocks. Burrows are located throughout the meadow near boulders, shrubs, and fallen trees.

Three high elevation sites are along the valley in North Pole Basin. The basin has several meadows divided by willow thickets and clumps of woody vegetation. Stealth site is a slope divided by two historically-used mining roads. Large rocks mark the localities of most burrows, which extend up into stunted pine forests. The Lost site is a gentle slope beneath the lower mining road. Burrows are located at the base of the slope near the stream. Voldemarmot site is a small, steep slope with rock exposures along most of the site.

Marmots were live-trapped using 81.3 × 24.5 × 30.5 cm Tomahawk (Tomahawk Live Trap, Tomahawk, WI) wire traps baited with whole oats (Land O' Lakes Purina Feed, Grey Summit, MO) soaked in salt water. We tagged each marmot with self-piercing ear tags, weighed, marked, sexed, and determined reproductive status and approximate age as described by ARMITAGE (1974). Analysis of Covariance (ANCOVA) was used to compare growth rates of different sexes, locations, and years. We fitted linear regression lines to marmot masses to estimate growth rates (slope of the regression) for each age and sex class of marmots at the two elevation sites.

Six behaviors were recorded for time budget analysis: vigilance, foraging, sitting/lying, agonistic behaviors, grooming and locomotion. Sites were observed for two periods per day. Morning observations occurred from marmot emergence until 11:00 hr. Afternoon observations were from 16:00 hr until the last observed activity. Observations took place in June and July of 2007. North Pole Basin was inaccessible until July 2008, and observations could not be conducted. We used both scan and focal sampling (ALTMANN 1974). At the beginning of each observational period we censused all active animals. We observed individual marmots for 2 min periods, and repeated the census of the population every 30 min. For each 2 min observational period the behaviors of each marmot were recorded in seconds. Stop watches were used to keep track of time. Percentage time allocated to each behavior was calculated for each individual. Percentages were arcsine transformed and compared using ANOVA.

High elevation marmots had not been trapped in 30 years (JOHNS & ARMITAGE 1979). Marmots were categorized as juvenile, yearlings, or adult by body mass. Low elevation marmots have been studied extensively since 1962 and ages were well documented.

RESULTS

Weaning mass

We compared the body mass (g) at weaning of seven juveniles at NPB (4 Stealth, 3 Lost) and seven juveniles at lower elevation (4 North Picnic, 3 Cliff). Mean body mass for NPB was 495 g $\pm$ 12.0 (12.0) and lower elevation mean weaning mass was 395 g $\pm$ 16.97 (SE). Although juveniles at the higher elevation sites were weaned at larger mean body mass, the difference was not significant ($P = 0.13$).

Growth rates

Juvenile growth rates were significantly higher at lower elevation sites ($F_{1,25} = 5.42$, $P = 0.028$) (Fig. 1). Juveniles at lower elevation had average growth rates of 24 g per day based on regression analysis ($R^2 = 0.66$), compared to 13 g per day ($R^2 = 0.39$) for juveniles at higher elevation. Juveniles were not observed in North Pole Basin in 2008, a year in which snow cover persisted until mid July.

Yearlings at NPB had higher growth rates compared to lower elevation yearlings (Fig. 2; $F_{1,44} = 130.06$, $P < 0.0001$). High elevation yearlings had mean growth rates of 28 g per day ($R^2 = 0.89$), compared to 15 g per day ($R^2 = 0.26$) for low elevation yearlings. Mean mass of yearlings at the lower elevation sites was 1778 g and significantly higher than higher elevation yearlings (1233 g: $F_{1,28} = 44.86$, $P < 0.0001$). Because of higher growth rates at higher elevation sites, differences between average mass of lower elevation animals (2160 g) and higher elevation animals (1993 g) was not significant toward the end of the summer ($F_{1,6} = 4.36$, $P = 0.0819$). Yearlings were not observed at high elevation in 2008.

In 2007, there was no statistical difference between growth rates of non-reproductive females at high and low elevation (Fig. 3; $F_{1,12} = 0.73$, $P = 0.56$).

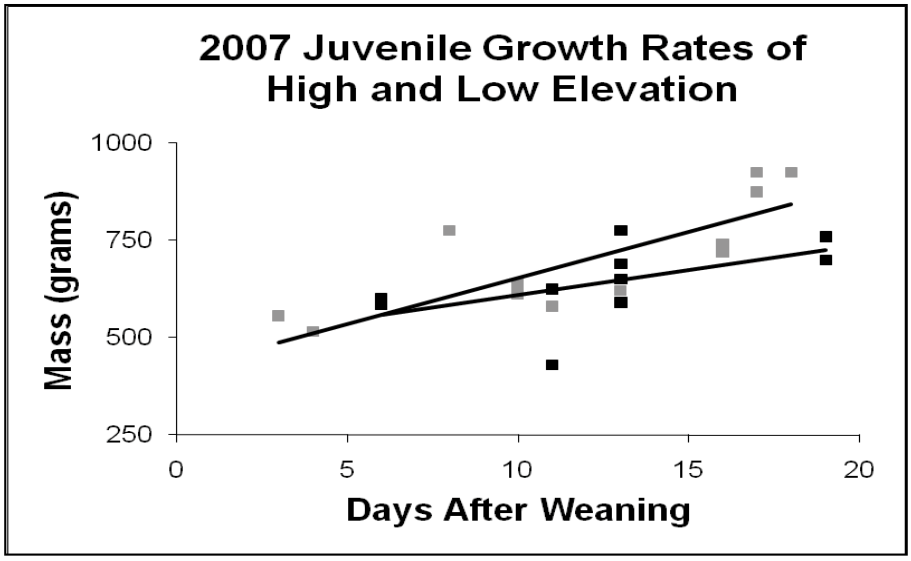

Fig. 1. — Growth rates of high and low elevation juveniles differed statistically. High elevation is denoted with the black squares; low elevation with grey squares.

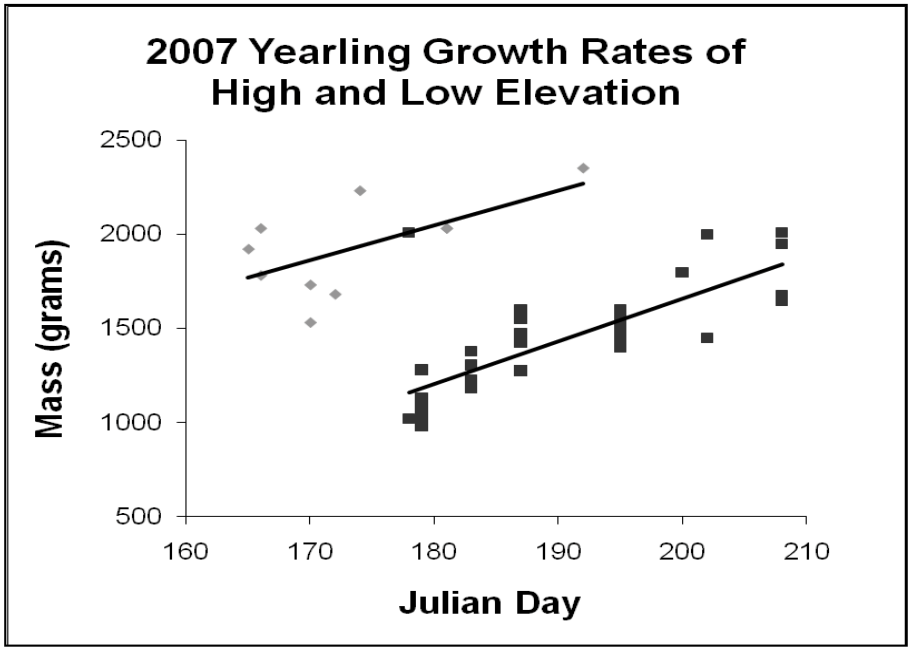

Fig. 2. — Growth rates of high and low elevation yearlings differed statistically. High elevation is denoted with the black squares; low elevation with grey squares.

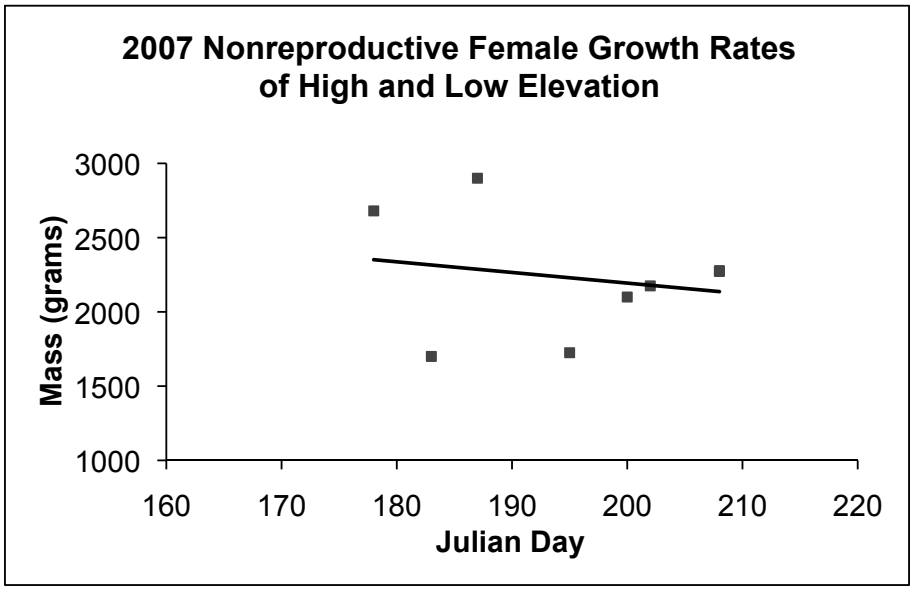

Fig. 3. — Growth rates of high and low elevation non-reproductive adult females did not differ significantly in 2007. High elevation is denoted with the black squares; low elevation with grey squares.

Non-reproductive females at lower elevation had positive growth rates, 11.2 g/day (R^2 = 0.42), but the slope of the regression did not differ significantly from zero ($F_{1,4}$ = 2.21, P = 0.23). Non-reproductive females at high elevation lost on average 7.2 g/day (R^2 = 0.04) but growth rates were also not statistically significant ($F_{1,7}$ = 0.24, P = 0.64). There was also no statistical difference between growth rates of high and low elevation reproductive females (Fig. 4; $F_{1,14}$ = 1.09, P = 0.46). Neither group of reproductive females showed significant growth rates. Both groups loss mass during the trapping period with losses of 13.6 and 2.1 g/day for high and low elevation groups respectively.

In 2008, there was no evidence of reproductive females at North Pole Basin. Although snow cover prevented trapping of animals at the high elevation until July 12, adult females showed a significant difference in growth rate (Fig. 5; $F_{1,85}$ = 19.08, P < 0.0001) between the two elevation sites. North Pole Basin females had significantly faster growth rates, 31 g per day (R^2 = 0.44) compared to 18 g per day for low elevation non-reproductive females (R^2 = 0.38).

Time budgets

The mean percentage of time allocated to foraging was significantly higher for marmots at higher elevation sites (18.9%) compared to lower site animals (2%: P = 0.008). Foraging time of lower elevation site animals

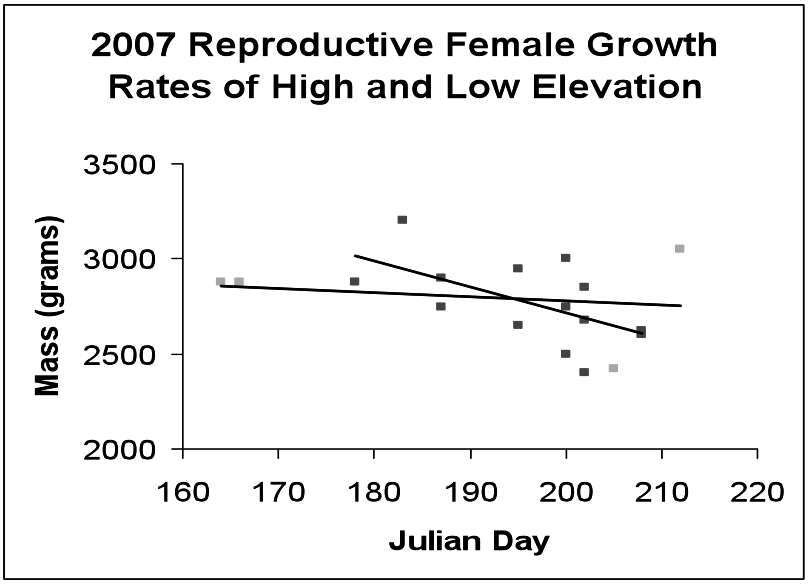

Fig. 4. — Growth rates of high and low elevation reproductive adult females did not differ significantly in 2007. High elevation is denoted with the black squares; low elevation with grey squares.

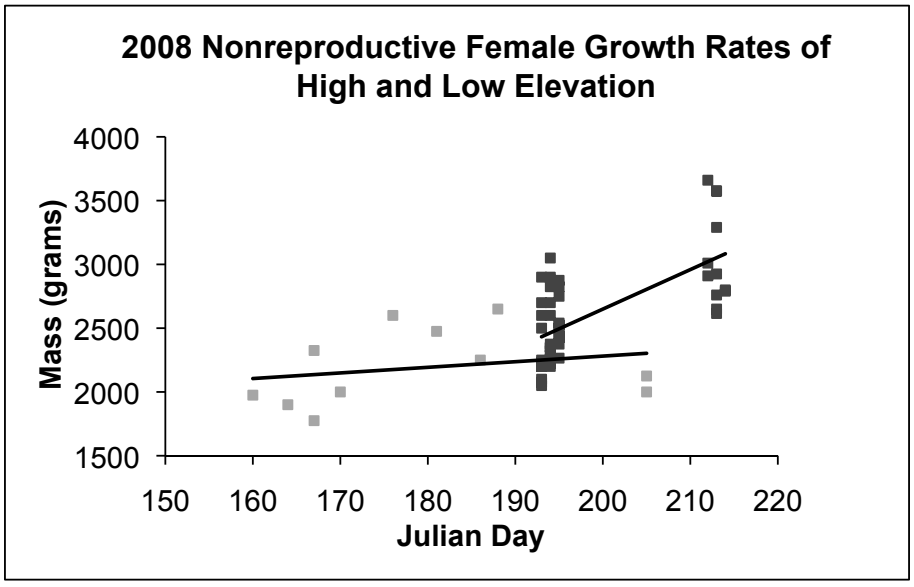

Fig. 5. — Growth rates of high and low elevation non-reproductive adult females differed significantly in 2008. High elevation is denoted with he black squares; low elevation with grey squares.

was atypical (see ARMITAGE et al. 1996) and likely to be a product of under sampling. The mean percentage time allocated to sitting/lying did not differ between sites (60.5% lower versus 62% higher elevation sites). Marmots at lower elevation sites allocated significantly more time to vigilance behaviors (32.9%) than higher elevation animals (4.9%). The number of males at the lower elevation sites were too few for analysis; however, at the higher elevation sites, yearling females spent a greater percentage of their time (41.5%) in foraging compared to yearling males (16%), but the difference was not significant ($P = 0.25$). We did not find significant differences in other behaviors, nor were we able to make further group distinctions, such as age, sex, or reproductive status comparisons in time budgets due to sample size.

DISCUSSION

Populations of yellow-bellied marmots are distributed across a wide variety of habitats throughout western North America from semi-desert grasslands to alpine meadows (FRASE & HOFFMANN 1980). Variation in distribution of meadow habitat, or of food availability may predict differences in life history traits and/or behaviors (BARASH 1974, JOHNS & ARMITAGE 1979, HOLMES 1984). This study provides evidence of variation in life history traits as they may be related to variation in environmental conditions.

BARASH (1973) predicted that young marmots should have slower growth rates when growing season is short and delay dispersal. Subsequent studies have not supported the hypothesis of slower growth rates for marmots experiencing shorter growing seasons. SALSBURY & ARMITAGE (2003) observed that marmot growth rates varied significantly by sex, age, year, and location and found no evidence that marmot growth rates were correlated, positively or negatively with elevation. Although higher elevation juveniles in this study had significantly slower growth rates, late summer masses were very similar between the two elevation groups. If dispersal is delayed at higher elevation, it should lead to social groups of high relatedness and provide evidence for the evolution of sociality in marmots (ARMITAGE 1999). This study does not provide evidence that dispersal is delayed beyond that of other populations. In contrast to juveniles, yearlings at North Pole Basin had higher growth rates. Low elevation yearlings were twice the size of high elevation yearling males at the beginning of the summer; the higher growth rates in high elevation populations reduced the mass differences between the two groups prior to hibernation. Yearlings at higher elevation may receive less agonistic behaviors from adults which could lead to their increased growth rates and delayed dispersal. The mechanisms that have led to increased growth rates of yearlings at higher elevation remain unclear.

Maximum growth rates will vary with food availability and some females may not reach maximum growth rates until after weaning even in the presence of added food (WOODS & ARMITAGE 2003b). Therefore, length of season in which marmots can deposit fat for hibernation should be a major factor for determining over winter survival. For example, weaning date is

negatively correlated with predicted mass at hibernation for females at higher elevation sites where the length of active season is shorter (SALSBURY & ARMITAGE 2003). Females that breed early should have an advantage as significant growth may not occur until post weaning (ARMITAGE 1996). However, females that breed early must rely on emergence fat stores and may not successfully wean litters if snow melt is late and food availability is low (ANDERSEN et al. 1976). A facultative reproductive strategy would be advantageous at higher elevations where growing seasons are short. If females can increase growth rates when reproduction fails, they may increase their reproductive success in the subsequent year.

In 2008, adult females at North Pole Basin were not reproductive and had significant positive growth rates (31 g/day). However, when females were reproductive in 2007, they loss on average 13 g/day. Reproduction is energetically demanding for adult females (ARMITAGE 1998) and may be exacerbated by the extreme conditions of higher elevation. Adult females are expected to have higher emergence masses after a non-reproductive year, which should increase weaning success in the subsequent season. In this study, consecutive weaning of litters was not observed, but more years of study are necessary to confirm this phenomenon. Furthermore, if consecutive reproduction is dependent on food availability, then food addition should increase reproductive success at North Pole Basin. Further study is necessary.

It is difficult to determine if variation in time allocated to different behaviors at the different elevation sites are the result of variation in environmental conditions. Time budgets can be affected by weather conditions (MELCHER et al. 1989). Marmots have reduced activity during midday which is primarily a consequence of thermal stress (MELCHER et al. 1989, ARMITAGE et al. 1996). Although ambient temperature was not recorded at any of the sites, based on experience, North Pole Basin is cooler than lower elevation sites and is consistent with climatic changes associated with elevation gradients. If thermal stress is reduced at higher elevation, marmots will have more available time during the day to spend foraging. Future studies of time budgets of marmot populations at higher elevation could provide evidence of behavioral mechanisms to compensate for a shorter growing season.

The two summers that we collected data vastly differed. The summer of 2007 followed a winter of low snowfall and record high temperatures (B. BARR pers. comm.) compared to the summer of 2008 that followed a winter with heavy snow fall and snow cover lasting until mid-July at North Pole Basin. Food availability in 2008 would have been reduced compared to 2007. Juveniles did not emerge in 2008 and yearlings were neither captured nor observed in August of the same year. The absence of yearlings and juveniles during the second year of this study, suggests the importance of adult reproductive effort as a major determinant of population persistence at the higher elevation site. If juveniles were weaned after August, they would not have accumulated enough mass to survive hibernation (ARMITAGE & DOWNHOWER 1974). Juveniles from 2007 may not have accumulated enough fat reserves to survive the long winter season. Lastly, the length of the winter season may have depleted spring fat reserves preventing reproduction in 2008. We did not observe any social dynamics, such as agonistic behaviors between dominant

and subordinate females, that may have accounted for reproductive suppression (Armitage 1965, Johns & Armitage 1979, Oli & Armitage 2008).

Our study shows the importance of reproductive plasticity in life history traits in yellow-bellied marmots. Adult females provided us with the strongest evidence to support the effect of elevation on the life history traits of yellow-bellied marmots. Further studies of extreme habitats of this species are necessary. Studying marmot populations in more extreme environments such as those experienced at higher elevation sites may provide important information on the evolution of life history traits and how variation in energy allocation may lead to different selection pressures on a species.

ACKNOWLEDGEMENTS

This study was funded in part by Beloit College, the 2007 RMBL REU Program, Wisconsin Alliance for Minority Participation (WiscAMP) Scholars Program, and the McNair Scholars program. We thank Dr Yaffa Grossman and Dr Ken Yasukawa for their help in the statistical analyses. Dr Kenneth Armitage provided many insightful comments and helpful suggestions. We would also like to thank Anacelia Saenz, Caroline Leitschuh, Dr Dan Blumstein, and several graduate students for their assistance in collecting data.

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