

The effects of altitude on the life history characteristics of yellow-bellied marmots
(*Marmota flaviventris*)

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August 11, 2007

Abstract. We collected the masses of 51 marmots from two different altitudes (Avery, Cliff, and North Picnic, 9500ft; Not So Stealth Ground Site, Land of the Lost, and The Site That Shall Not Be Named, 11,000ft) in the summer of 2007 to examine the effects of length of growing season on the life history characteristics of yellow-bellied marmots (*Marmota flaviventris*). We compared life history characteristics of marmots amongst age and sex classes from the two altitudes. Juvenile masses and growth rates did not differ between populations, nor did yearling growth rates. However, high altitude yearling masses were significantly less than low altitude yearlings. Growth rate was also significantly greater in high altitude adult males. There was no difference in altitude for litter size. Low altitude yearlings were most likely larger on account of a longer growing season, while extended foraging times in high altitude populations were probably a result of more foraging opportunities per day allowed by cooler temperatures.

Key words: marmots, altitude, growth rate, litter size, mass

Introduction

The life histories of organisms refer to the details of growth, reproduction, and maintenance. The theory of allocation, a general life history model, states that there are finite resources that must be distributed amongst these traits (Gadgil and Bossert, 1970). Variations in life history traits are the result of natural selection (Lack, 54). Resource availability can influence a variety of life history characteristics. If a life history trait consumes an increased amount of the finite resource, it leaves fewer resources for the other functions. When resources are extremely limited, reproduction and growth may be constrained or nonexistent. In yellow-bellied marmots, increased food resources do not alter life history traits (Woods and Armitage, 2003); however, limited food resources can increase mortality (Armitage, 1994; Johns, 1978). By studying the life functions in a

population of limited resources, we can attempt to see the role the environment plays on the natural selection of a species.

Yellow-bellied marmots (*Marmota flaviventris*) are large ground-dwelling squirrels found in alpine areas of western North America. The annual cycle of yellow-bellied marmots is marked by hibernation during long winters. Hibernation is a process which enables mammals to conserve energy during a season of food scarcity. Stored fat is the primary source of energy during hibernation. During the active season, marmots must gain as much weight as possible in order to have enough energy to survive hibernation and undertake costly breeding and rearing processes the following year. Additionally, marmots must breed when they first emerge from hibernation so that the young have enough time to gain sufficient weight for the next winter season (Armitage et al., 2002). Consequently, enough fat must be gained to provide energy for the winter season, reproduction, and emergence until the snow melts and food becomes available (Armitage and Woods, 2003). Furthermore, reproductive females do not gain weight until after their pups are weaned (Barash, 1968). In sub-alpine areas, young must be weaned by the middle of July, which is the height of most plant growth, so that pups may accumulate adequate fat to survive hibernation. If young are weaned after this time of the season, the chances of survival are lowered (Armitage, 1976). While adults are not in danger of mortality as a result of hibernation, females increase their fitness by accumulating weight to have energy for reproduction.

In alpine areas, however, the active season is much shorter due to longer winters. Long winters decrease the chance of survival of young because the shorter growing season limits the opportunities for achieving a proper weight for surviving hibernation.

Females in alpine areas have difficulty reproducing in consecutive years because of their inability to consistently acquire the energy (Johns, 1978). The extended period of summer that still has snow cover affects the fitness of marmots because it constricts the amount of food available throughout the summer.

It is known that for alpine marmots, the shorter the growing season, the lower the weight of individuals at the beginning of winter (Barash, 1968). To compensate for growing season constraints, alpine yellow-bellied marmots have adjusted life history characteristics (Johns, 1978). In Johns' study of alpine marmots in North Pole Basin in western Colorado, only 25% of adult females reproduced. The low fecundity within this population suggests an adjustment to limited resources. The females do not reproduce in consecutive years, but dedicate summers to fat accumulation without spending the energy on reproduction. Johns also found that some reproductive females did not wean their young. This is likely since lactation can be more energetically expensive than all other prenatal expenses (Moen, 1973). Abandoning pups also reflects demographic models of resource availability because since there is high mortality for young, adults should favor maintenance over reproduction (Michod, 1979).

In golden-mantled ground squirrels (*Spermophilus lateralis*), shorter growing seasons resulted in reduced fecundity and increased age of first reproduction (Bronson, 1979). All life functions can be supplied with enough energy, however, fewer resources lowers lifetime reproduction with smaller litter sizes and fewer years spent reproducing. This also reflects the trade-offs that occur with limited resources.

Armitage's previous study (2002) stated that a survival requirement for marmots living in sub-alpine areas was to be weaned in the middle of July and, thus, be in sync

with vegetation growth. However, this study did not include higher elevation populations where the growing season is considerably shorter and animals have limited time to obtain sufficient mass. An organism's environment plays an important role in its life history decisions. The environment drastically alters with altitudinal changes. Thus, the purpose of our study was to compare the life history characteristics of low and high elevation yellow-bellied marmots to find how populations are compensating for the limitations of a shorter summer.

To determine the effects of altitude on life history, we compared growth rates, body mass, and litter sizes of two colonies at an altitude of 2900m to 3 colonies at an altitude of 3400m. We tested the following hypotheses within age and sex:

1. Low altitude marmots will have greater body masses than high altitude marmots.
2. High altitude marmots will have faster growth rates than low altitude marmots.
3. Low altitude marmots will have larger litter sizes than high altitude marmots.
4. High altitude marmots will spend more time foraging than low altitude marmots.

Methods

We studied marmot populations in four localities in the Elk Mountains of Gunnison County in western Colorado; three low altitudes localities at altitudes in the East River Valley of 2900m and three high altitude localities in North Pole Basin at an altitude of 3400m.

The three low altitude localities are slopes located along the East River. The first site, Avery, is a clear meadow with a few main large rocks exposed on a gentle slope. The area directly above the meadow is forested by spruce trees and below is a small stream. The second site, Cliff, is a steep slope with rock exposures adjacent to a cliff face. Burrows are located within the rock on top of the cliff which is followed by a meadow that leads to another steep slope. The third site, North Picnic, is a steep slope with a major grouping of rocks in a large meadow. Burrows are located throughout the meadow near boulders, shrubs, and fallen trees.

The three high altitude localities are along the valley in North Pole Basin. The basin has several meadows divided by willow thickets and clumps of woody vegetation. Not So Stealth Ground 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 Land of the Lost site is a gentle slope beneath the lower mining road. Burrows are located at the base of the slope that levels out into towards a stream. The Site That Shall Not Be Named is a small, steep slope with rock exposures along most of the site. Above the steep grade of the slope are stunted pine trees, which are frequently traveled through by the colony.

Marmots were live-trapped using 32 x 10 x 12 Tomahawk wire traps baited with whole oats (Purina Mills Oats Feed) soaked in salt water. We tagged each marmot with self-piercing ear tags, weighed, marked, sexed, and determined reproductive status and approximate age. Methods of trapping, handling, and marking are described elsewhere (Armitage, 1974). Body mass was analyzed by constructing linear regressions of marmot masses in the two altitudes amongst sex and age. These regressions of body mass over

time were then compared by altitude with an ANCOVA. Growth rates (grams/day) were compared by using a Student's t-test.

Observations took place during all times of marmot activity, ranging from sunrise to early evening. We did not observe each locality the same number of hours. Using 20-60x sighting scopes, we observed foraging and colony demographics. We created time budgets by recording the activity type (i.e. foraging, sitting, grooming, vigilant, and fighting) and duration (seconds) of said activity of one randomly chosen animal for a two minute interval (Altmann, 1973, Armitage et al. 1996). The times were converted into percentages for an activity log for each animal observed. Due to possible biases in observation sites, we did not use observations taken in the Avery and Cliff sites; only North Picnic was used in the statistical analysis as the low altitude site. These data were analyzed by using a Mann-Whitney nonparametric test to use data transformations to correct for the percentages.

The high altitude marmots had not been trapped in 30 years (Johns, 1978), so we were only able to approximate their ages into the categories of juvenile, yearlings, and adults. This contributed to the variation adult mass in males and females because of our inability to distinguish two-year-olds from adults three years and older. This is a necessary distinction because juveniles, yearlings, two-year-olds, and adults three years or older have significantly different mean body masses (Armitage et al., 1976). Low altitude marmots have been studied extensively since 1962 and marmot ages have been documented. However, the colonies did not have the demographic variation to perform some of the comparisons.

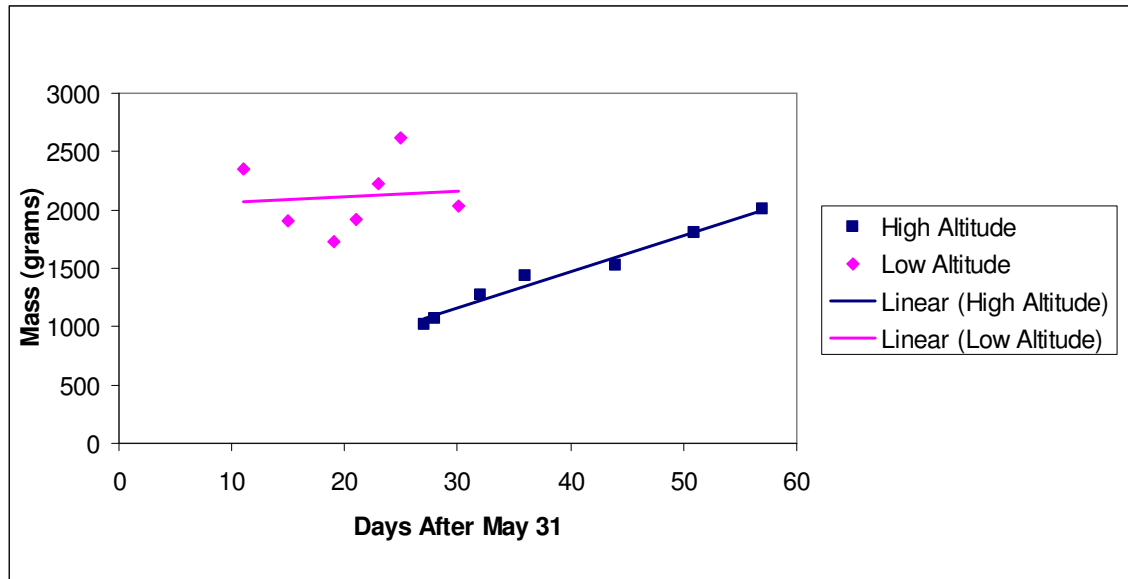


Figure 1. Mean body mass of high and low altitude yearling male yellow-bellied marmots. High altitude yearling males had linear growth while low altitude yearling males had variance in growth over time.

Results

Body Mass — We compared juvenile body mass at high and low altitudes. Juvenile male body mass did not vary between altitudes ($F = 0.5194$, $df = 2$, $p = 0.6660$). Similarly, body mass did not differ for juvenile females ($F = 1.9718$, $df = 2$, $p = 0.9186$) between altitudes. High and low altitude juveniles emerged during the same week (week of July 8th).

In our comparison of yearling body mass at high and low altitudes, the body mass of high altitude yearling males was significantly less than low altitude yearling males ($F = 17.4449$, $df = 2$, $p = 0.0001$), see Figure 1. We found similar results in yearling females ($F = 59.8675$, $df = 2$, $p < 0.0001$). However, our sample size for females was small because we were only able to trap two low altitude females one time each for the comparison.

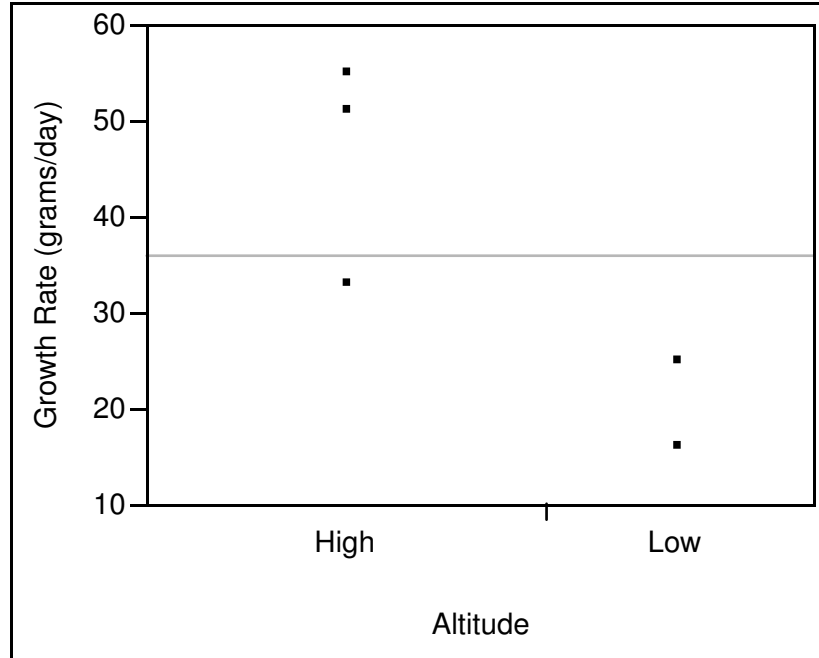


Figure 2. Growth rate in high and low altitude yearling male yellow-bellied marmots. High altitude yearling males had a faster growth rate and also a larger range of rates than low altitude yearling males.

Growth Rate (Juveniles) — We compared juvenile growth rates at high and low altitudes. Growth rate was not significantly different for high and low altitude juvenile males ($p = 0.0638$). Likewise, the rates did not differ for juvenile females ($p = 1.0000$).

Growth Rate (Yearlings) — We compared growth rates of only yearling males of high and low altitudes. We did not trap low altitude yearling female multiple times so calculating a growth rate was impossible. Growth rate was significantly faster in high altitude yearling males ($p = 0.0503$), see Figure 2.

Growth Rate (Adult Males) — We compared growth rates of only adult males of high and low altitude because we did not trap low altitude adult females with enough repetition to

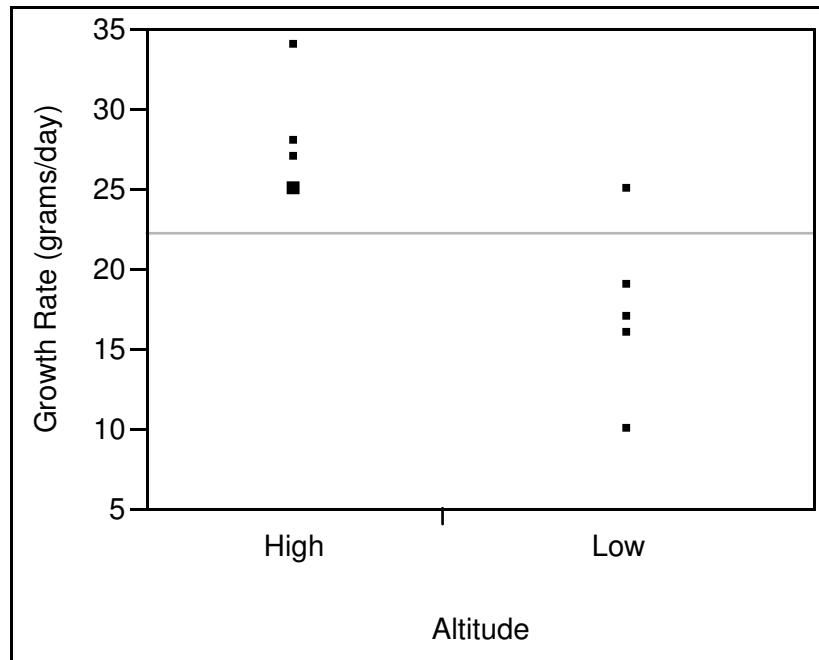


Figure 3. Growth rate of high and low altitude adult male yellow-bellied marmots. High altitude adult males have greater growth rates, while low altitude adult males show a greater range of rates.

calculate growth rate. Growth rate was significantly faster in high altitude adult males ($p = 0.0091$), see Figure 3.

Litter Size — We compared the sizes of litters from our high and low altitude sites. There were only two litters for each altitude, and they did not differ in size ($p = 1.0000$).

Foraging Time — We observed the time spent foraging in one of our low altitude sites (North Picnic), and all three of our high altitude sites. We found that high altitude marmots spent more of their time spent foraging ($p = 0.0196$), see Figure 4.

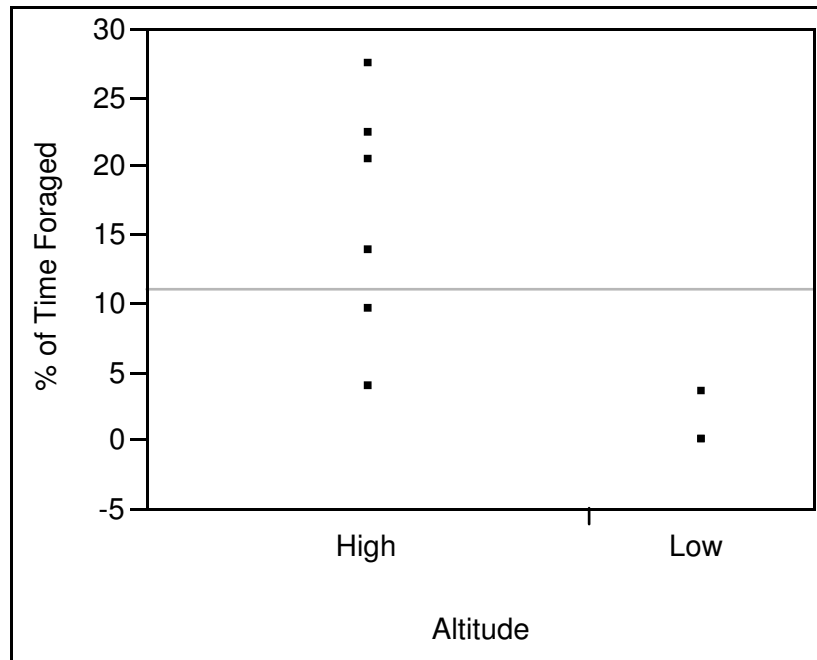


Figure 4. Percentage of time observed foraging in yellow-bellied marmots. High altitude marmots were observed foraging a greater percentage of their time than low altitude marmots. High altitude marmots also had a greater range of percentages.

Discussion

Resource availability can alter the life history characteristics of a species. Resource limitation can drastically constrict the growth, reproduction, and maintenance of yellow-bellied marmots (Johns, 1978). For ground squirrels, there is a positive correlation between growing season and mass (Bronson, 1979; Johns, 1978). Corresponding to these studies, yellow-bellied marmots living in high elevations with shorter growing seasons weigh less than those in lower elevations. High elevation marmots compensate for their limited resources by increasing the percentage of time they spent foraging, hence increasing their growth rate.

Body Mass — Organisms make trade-off decisions with life history traits, and can reduce one trait to compensate for limited resources. A common trade-off is between juvenile body mass and litter size. Juvenile body mass at weaning tends to be smaller in areas that

are more resource limited. Reproductive females try to better their fitness by finding balance (or imbalance) between size of young and litter size. Resource limited reproductive females may have smaller or fewer pups. This was not the case in our study; body masses in high and low altitudes stayed consistent in both males and females juveniles. In yearlings, however, body masses of low altitude yearlings were significantly greater in both males and females. This discrepancy of mass is due to the differences in the length of growing season of high and low altitude populations. North Pole Basin annually receives approximately 50% more snow than the East River Valley (Natural Resources Conservation Service snow pack sensor for Schofield Pass; Gothic weather station), therefore extending the length of winter for the higher elevation. Low altitude marmots are able to begin their growing season at a time when high altitude marmots are still experiencing food shortages due to snow cover.

Growth Rate — Increased growth rates can compensate for shorter growing season (Woods and Armitage, 2003). This was also evident in our study; both high altitude yearling and adult males had increased growth rates compared to those in low altitude. The increased growth rates could be a result of the shorter growing season in high altitudes. Marmots must wait after emergence from hibernation for the snow to melt and expose foliage in order to feed. To make up for this lost time, high altitude marmots enhance their food intake, thus increasing their growth rate.

Litter Size — Litter size can fluctuate as a result of resource availability. An abundance of a limiting resource can increase litter sizes, while alternatively, inadequate resources can decrease litter sizes (Mountford, 1968, Mattingly and McClure, 1985). In our study, we only had two litters at each population; litters of three and four in low altitude and

litters of three and four in high altitude. Despite the small sample size, there is still no evidence of increased or reduced reproductive effort. However, high altitude females could still have a lower fitness due to a possible increase in age of first reproduction. The undersized yearlings in high altitudes suggest that it could take them multiple growing seasons to attain an average low altitude adult body mass. While most low altitude females have their first litter when they are 3 years old, high altitude females may delay their first reproduction until they have accumulated enough mass to go through the costly reproductive process. Additionally, high altitude females could be further lowering their fitness by potentially having more years intermittently between reproductions.

Foraging Time — Organisms' daily activity can be framed by environmental cues. Daily activity depends on if the environmental temperature falls within the organism's thermal neutral zone. Low altitude marmots spend most of their afternoon hours inside their burrows to avoid daily temperature highs. High altitude must compensate for their short growing season by spending more time each day foraging. Cooler temperatures in high altitudes allow marmots more opportunities throughout the day to forage. Additionally, marmots at North Pole Basin utilized trees and willows in their home ranges that provided shaded foraging areas.

Conclusions — Growth in marmots is evidently dependent on their growing season. Juveniles in both high and low populations were weaned during the same week at the same mass, had similar growth rates, and will thus immerse into hibernation in the same mass range. However, yearling mass for both males and females in low altitude sites were nearly twice that of high altitude yearlings. Differences in body mass in the transition of juveniles to yearlings are due to differences in growing season length.

Marmot growth is limited by their food supply (Woods and Armitage, 2003); therefore the limited food supply in high altitudes for the beginning of summer stunts the growth potential for the season. This restriction is nonexistent for low altitude marmots, which are able to begin their growing season much earlier in the summer. To counter-act the restrictions of a shorter growing season, high altitude marmots spend more time foraging per day. We suggest that the environment limits the amount of growth throughout the summer for high altitude marmots, but alternatively allots for more daily growth.

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